Guido H.E. Gendolla · Mattie Tops
Sander L. Koole *Editors*

Handbook of Biobehavioral Approaches to Self-Regulation

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Foreword

In contrast to other books on self-regulation and control, which are focused largely on classical measures such as self-reports and behavior—all in the social psychological tradition—this edited volume opens an entirely innovative perspective. A healthy plethora of physiological processes underlying and accompanying self-regulation form the center of this work. These processes are tied cogently to such psychological states and themes as motivation, energy expenditure, planning, decisions, and memory. This colorful assembly of contributions has probed the neurobiological, hormonal, and cardiovascular parallels of self-regulation. The latter term often stands for the individual's drawing on well-internalized norms bearing on performance and morality, or to stretch the language a bit, norms bound up with the person's potential strength of character.

Most of the chapters depict the human as an autonomously acting entity. The idea is to isolate the variables that draw out the person's implementing higher or more noble standards and in so doing, the person does not succumb to instant gratifications. This is the human that plans rationally, at least with the rationality of surrounding cultural standards, and that expends energy to move toward culturally esteemed goals. The theoretical language implicit in the chapters is reminiscent of that of David McClelland and Max Weber.

There is a similarity between the overriding theme of this edited volume and a theory of self-awareness, which I wrote with Shelley Duval in 1972. The core moment here was the discrepancy between current performance/achievement and the person's own standards for performance and for civilized behavior. An increment in self-focused attention was said to render the person attuned to such discrepancies, and one predicted result was the increment in striving toward reducing discrepancies. The chapters in this volume also revolve around discrepancy reduction, whereby the term self-regulation refers to the seemingly autonomous self-regulator, one whose efforts are mirrored in physiological change.

Again parallel to self-awareness thinking, many of the current contributions deal with the individual's deviating from the path toward the salient end point for behavior. The physiological accompaniments of such anxieties, repetitions, or leaving the field are impressive in rounding out the broad field of motivated behavior.

Finally, the reader is teased into psychological-sociological thoughts as to the “self” in self-regulation. The motivationally laden projects that are self-regulated have an underpinning in imitation and internalization, in that somewhere along the line, each person has come to incorporate the standards of the immediate culture. In this sense, the regulations that one undertakes stem from directions for movement given by the culture.

Thus, the reader will find a well-pieced together, integrative set of theoretical notions that join the worlds of social influence, deprivation and motivation, and the physiological correlates of the thinking, behavioral, and affective effects entailed. It makes for rich reading, and is timely in the broad field of "What is the motor behind human action?"

Robert A. Wicklund

Contents

Part III The Central Nervous System and Self-Regulation

Part IV Self-Regulation of Effort

Part V Self-Regulatory Problems and Their Development

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Introduction: Grounding Self-Regulation in the Brain and Body

1

Guido H.E. Gendolla, Mattie Tops and Sander L. Koole

1.1 Introduction: Grounding Self-Regulation in the Brain and Body

Self-regulation is a process that allows organisms to guide their behavior in the pursuit of their goals—desired end states they are committed to. Self-regulation is also a vital capacity that allows people to master their thoughts, feelings, and actions and concerns a high number of psychological processes, ranging from executive cognitive functions like attention control to higher-order processes like affect regulation or conflict resolution. But what goes on within people's brains and bodies when they are engaged in self-regulation? Does the biological machinery contribute efficiently to self-regulation or does it rather set natural limits to it? Can it contribute to understanding why people sometimes fail in the pursuit of their action goals? And, perhaps most importantly, can we use our understanding of the biobehavioral foundations of self-regulation to increase people's chances of succeeding at self-regulation? These are the central questions that led us, together with our colleagues, to create this volume.

1.1.1 The Origins of Self-Regulation Research

It might be said that self-regulation research began around the beginning of the twentieth century with German will psychologists who investigated how people form intentions and how they try to realize their goals (see Ach 1935). This promising beginning, however, was followed by decades of silence in which mechanistic models of human behavior, mostly rooted in behaviorism, dominated behavior research (see Cofer and Appley 1964). The first formal models of self-regulation, rooted in cognitive psychology, still followed the mechanistic tradition by proposing that the basic working principles of so-called intelligent machines might be applied to human behavior (Miller et al. 1960; Powers 1973). These models applied feedback loops according to the principles of cybernetics to explain how organisms pursue goals by comparing their current states with their desired end states and execute behavior in order to minimize the eventual discrepancies between both. Such cybernetic principles are still part of modern self-regulation theories (Baumeister et al. 1994; Carver and Scheier 1998).

Yet modern theories have gone beyond their mechanistic beginnings. In modern theories of

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self-regulation, the self is an active agent (rather than a machine) who strives for attaining self-set goals or to comply with behavioral standards the individual is committed to (see Bandura 2001). This agentic perspective on self-regulation was kick-started in social and personality psychology in the early 1970s. Rediscovering early ideas about symbolic interactionism, a pioneering work on self-awareness theory (Duval and Wicklund 1972), explained how and why people can regulate their behavior to comply with their personal standards. About the same time, work on self-control, focusing on how people apply self-regulatory strategies to cope with conflicts between their short-term impulses and long-term goals emerged in developmental psychology (Mischel and Ebbesen 1970). Simultaneously, the role of self-beliefs in coping with challenges became a hot topic in behavior research (Bandura 1977). This was followed by modern approaches to action control that considered both cognitive and affective processes (Carver and Scheier 1981, 1998), a revival of will psychology (Heckhausen and Gollwitzer 1987; Kuhl 1986), and a groundswell of research on self-control failure (Baumeister and Heatherton 1996; Hagger et al. 2010).

Over the decades, self-regulation has attracted a great deal of attention from behavioral researchers (see Vohs and Baumeister 2011, for a recent overview). The biological aspects of self-regulation have received so far much less empirical attention. This seems surprising given the tremendous impact that biological approaches have had on adjoining areas of psychology, such as psychophysiology (Cacioppo et al. 2007), the cognitive and affective neurosciences (Gazzaniga 2004; Panksepp 1998), and also evolutionary psychology (Schaller et al. 2013). Conceivably, self-regulation researchers have neglected biological processes because their focus on an active, agentic self seemed hard to reconcile with the reductionism that has been historically associated with biological approaches to psychology (Geen 1995)—though the application of cybernetic principles of machines to human behavior has been regarded as less problematic, as evident in action control research. However, more modern work has made it clear that a focus on biological mechanisms is perfectly compatible with the existence of higher-order regulatory processes (Kuhl and Koole 2004; Ryan et al. 1997). Consequently, the time is ripe for researchers to address the biobehavioral foundations of self-regulation. With the present volume, we seek to catalyze this development and to close a gap in the psychological and physiological literature by making an integrative link between self-regulation and biological processes.

1.1.2 Self-Regulation and Biological Systems

This volume gives the first overview of contemporary research on biobehavioral processes involved in self-regulation. This is important for at least three reasons. The first reason is that a biological focus greatly enriches self-regulation theory, by grounding self-regulation in the workings of the body and brain. Popular notions of self-regulation have traditionally been dualistic, portraying self-regulation as the product of a detached mind that in some mysterious way makes contact with the body and its needs, drives, and habits. Although most self-regulation theorists reject such dualism, neglecting the fundamental biological nature of self-regulation creates the risk of enshrining a mind–body dualism in theories of self-regulation. Self-regulation unfolds within the living tissue of our biological organism. It is therefore vital for behavioral theorists to heed the fundamental embodied, biological nature of self-regulation.

Studying the biobehavioral foundations of self-regulation is not just a one-way street. Indeed, a second reason for studying this topic is that a focus on self-regulation greatly enriches the scope of biological theories. Especially during the first half of the twentieth century, biological approaches within psychology were characterized by strong deterministic tendencies, by seeking to reduce the complexity of human behavior to simple drives or stimulus–response learning (see Cofer and Appley 1964). Fortunately, biological psychology has come a long way since then. Theories in social, cognitive, and affective neuroscience have become increasingly attuned to the complex, multilayered systems that are involved in behavioral regulation (e.g., Gazzaniga 2004; Panksepp 1998). Importantly, modern theories allow for higher-level behavioral systems and interplay between different levels of control (e.g., Kuhl and Koole 2004). Behavioral research on self-regulation can inform and constrain these theories, creating a mutually beneficial dialogue between biological and behavioral researchers—as evident in several chapters of this book and especially in this book section that presents integrative perspectives.

Beyond addressing the basic question on how organisms can attain self-set goals, understanding the biobehavioral foundations of self-regulation has important implications for real-life problems. Self-regulatory success is associated with better health, achievement, and interpersonal relationships. Self-regulatory failure is associated with overeating, impulsive spending, drug abuse, delinquency, and other forms of misbehavior (Baumeister et al. 1994). This leads to the third reason, why considering brain and body processes in self-regulation promises important progress: Improving scientific insight into the biological aspects of self-regulation is likely to point to new ways for enhancing self-regulatory success while reducing self-regulatory failure.

1.1.3 Organization of This Book

As evident in this volume's 25 chapters, researchers have developed sophisticated models of biological processes in self-regulation in recent years. These approaches have developed from many different perspectives and subdisciplines. As a result, they are quite heterogeneous and involve many different physiological systems. Some approaches focus on the central nervous system, others focus on the peripheral/autonomic nervous system, and still others focus on the interaction of both. For instance, some models have addressed neurobiological processes, others hormonal influences, yet others cardiovascular processes, and so on. This heterogeneity is expectable and probably the result of the complex, multifaceted nature of self-regulation. At the same time, the staggering complexity of the biology of self-regulation has made it important to allow different approaches to interface with each other and to facilitate mutual exchange of insights and ideas.

This volume starts with a foreword by Robert Wicklund who puts the original ideas about the self as the active agent and the importance of self-awareness in self-regulation in the broader context of the contemporary research focusing on biobehavioral processes presented in this book. The remainder of the volume is organized into five parts. The stage is set in Part I with five chapters on basic and integrative perspectives on biobehavioral aspects of self-regulation. The opening chapter provides an overview of the development of self-regulation research, covering the way forward from early cybernetic models to modern neuroscientific perspectives (Carver, Johnson, Joorman, and Scheier: "An evolving view of the structure of self-regulation"). The subsequent chapters focus on phylogenetic aspects and the evolutionary advantage of the development of self-regulation systems (Del Giudice: "Self-regulation in an evolutionary perspective") and the neural mechanisms involved in efficient self-control and self-control failure (Lopez, Vohs, Wagner, Heatherton: "Self-regulatory strength: neural mechanisms and implications for training"). This is followed by a chapter on muscle physiology and energetic processes that discusses the question if a muscle is a suitable metaphor for explaining self-control strength and self-control failure (Richter and Stanek: "The muscle metaphor in self-regulation in the light of current theorizing on muscle physiology"). The first section of this volume ends with a new perspective on protective inhibition in self-regulation and related adjustments in the neuroendocrine system (Tops, Schlinkert, Tjew A Sin, Samur, and Koole: "Protective inhibition of self-regulation and motivation—extending a classic Pavlovian principle to social and personality functioning"). Together, these contributions give an overview of the basic biobehavioral perspectives on self-regulation.

Part II of this volume includes four chapters focusing on the interaction of the affective and cognitive systems in self-regulation and related physiological processes. The first two of these chapters present new perspectives on affective influences on cognitive control (van Steenbergen: “Affective modulation of cognitive control—a biobehavioral perspective”) and error monitoring (Aarts and Pourtois: “Error monitoring under negative affect—a window into maladaptive self-regulation processes”). These are followed by a chapter on pupillometry, memory, and cognitive control (Papesh and Goldinger: “External signals of metacognitive control”) and another one that treats neural aspects of attention strategies in self-regulation (van Dillen and Papies: “From distraction to mindfulness—psychological and neural mechanisms of attention strategies in self-regulation”). Together, the chapters in this section provide an up-to-date overview of the affective influences on cognitive processes that are fundamental aspects of self-regulation.

Part III focuses on processes in the central nervous system in self-regulation. This section starts with two chapters that highlight central motivational processes that are important for self-regulation: The neuroscience of the reward system (Pessiglione and Lebreton: “From the reward circuit to the valuation system—how the brain motivates behavior”) and motivational orientations (Harmon Jones and Harmon Jones: “Neural foundations of motivational orientations”). This is followed by a neuroscientific model for the self-regulation of emotion and motivation (Livingston, Kahn, and Berkman: “Motus moderari—a neuroscience-informed model for self-regulation of emotion and motivation”) and a chapter dealing with the neural processes involved in self-insight (Beer and Flagan: “More than the medial prefrontal cortex (MPFC)—new advances in understanding the neural foundations of self-insight”). This part ends with a chapter presenting a neuroscientific perspective on social decision making (Knoch and Nash: “Self-regulation in social decision making—a neurobiological perspective”). Taken together, this section provides an overview of recent insights in the implication of the central nervous system in important subprocesses that are involved in the self-regulation process and that are necessary for effective self-regulation.

Part IV presents six chapters dealing with the self-regulation of effort, i.e., resource mobilization for setting self-regulation processes into action. The section starts with the presentation of new insights in how the central and autonomic nervous systems interact in the mobilization of mental effort with links to health and disease (Radulescu, Nagai, and Critchley: “Mental effort—brain and autonomic correlates in health and disease”) and on the neural mechanisms involved in effort perception during physical tasks (de Morree and Marcora: “Psychobiology of perceived effort during physical tasks”). Next, there is a set of four chapters focusing on the autonomic nervous system and highlighting the role of the cardiovascular responses in self-regulation. The first chapter of these presents a new perspective on bounded automaticity in effort mobilization (Gendolla and Silvestrini: “Bounded effort automaticity—a drama in four parts”). This is followed by chapters dealing with cardiovascular responses in behavior restraint and self-control (Wright and Agtarap: “The intensity of behavioral restraint—determinants and cardiovascular correlates”), the role of self-focused attention in effort mobilization (Silvia: “How self-focused attention affects effort-related cardiovascular activity”), and future projections of the self and energization (Sevincer and Oettingen: “Future thought and the self-regulation of energization”). In summary, this section provides an overview of new insights in how the central and autonomic nervous systems contribute to the self-regulation of resource mobilization.

Finally, Part V presents five chapters dealing with problems in self-regulation and how these develop. This section starts with a chapter focusing on depression’s impact on resource mobilization (Brinkmann and Franzen: “Depression and self-regulation—a motivational analysis and insights from effort-related cardiovascular reactivity”). This is followed by an ontogenetic perspective discussing perinatal developmental aspects of self-regulation (Henrichs and Van den Bergh: “Perinatal developmental origins of self-regulation"). Two further contributions deal with the biobehavioral mechanisms in self-regulation by rumination (Koster, Fang, and Marchetti: "Self-regulation through rumination—consequences and mechanisms") and the impact of self-esteem on selective attention (Pruessner and Baldwin: "Biological aspects of self-esteem and attentional bias"). This section ends with a chapter discussing the interaction of the body–mind system considering central and autonomic nervous system processes and implications for psychopathology (Bernstein: "A basic and applied model of the body–mind system").

1.1.4 Concluding Thoughts

As we stated at the outset, we have edited this volume to fill a gap in the literature dealing with understanding the processes underlying human behavior—a state-of-the-art overview of approaches to the role of the body and biobehavioral processes in self-regulation. We have done so by taking a diversity approach. One aspect of this diversity concerns the consideration of different physiological systems involved in self-regulation. Rather than limiting the overview to one system, we have included approaches focusing on the central nervous system, on the autonomic/peripheral nervous system, and on the interaction between both. We did so to capture multiple perspectives in current biobehavioral research. Another diversity aspect concerns the variety of self-regulation aspects and subprocesses this volume treats, reaching from physiological processes involved in fundamental aspects like attention and memory mechanisms to higher-order processes like the volitional control of desires and temptations in the pursuit of self-set goals. Finally, we have not limited this overview to fundamental theories and research findings, but have also considered applied problems like conditions of self-control failure and the link between self-regulation processes and pathologies.

Despite the large scope of this volume, we are aware that it does not provide an exhaustive summary of what researchers have learned about how self-regulation unfolds in the body. Many more processes can and will be explored. We hope that this edited volume may serve as a starting point for readers to integrate what is known and to develop new ideas on how the body is involved in self-regulation to make the next important steps in better understanding human behavior.

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Part I

Integrative Perspectives

An Evolving View of the Structure of Self-Regulation

2

Charles S. Carver, Sheri L. Johnson, Jutta Joormann
and Michael F. Scheier

2.1 Introduction

This chapter begins by describing a viewpoint on behavior that has been identified with the term *self-regulation* for nearly four decades (Carver and Scheier 1981, 1998). The term was chosen because this viewpoint depends heavily on the principles of feedback control (Powers 1973). The broad outlines of this view remain much the same today as they were then. However, the state of knowledge in genetics and neuroscience, as well as in behavioral science itself, has changed dramatically since that time. Accordingly, this picture of self-regulatory phenomena has also evolved, and a subsequent part of the chapter describes some of that evolution. The picture remains a work in progress, a set of conceptual guidelines rather than a finished statement, but we think it provides a useful complement to other theories.

This chapter is mostly about the occurrence of normal behavior, but it also addresses problems in behavior. The idea that normal and problem behaviors represent different locations on a multidimensional matrix of basic functions—self-regulation that is functional versus self-regulation that has gone awry for some reason—is becoming more prominent in today's views of psychopathology. Reflecting that development, this chapter also includes some discussion of behavioral problems and how they might be interpreted within a self-regulatory framework.

2.2 Behavior as Goal Directed and Feedback Controlled

We begin by briefly describing a feedback-based view of action control, starting with the goal concept. This construct is prominent in today's psychology, under a wide variety of labels (Austin and Vancouver 1996; Elliot 2008; Johnson et al. 2006). It is broad enough to cover long-term aspirations (e.g., creating and maintaining a good impression among colleagues) as well as the endpoints of very short-term acts (e.g., reaching to pick up a water glass without knocking it over). Goals generally can be reached in diverse ways, and a given action often can be done in the service of diverse goals (Carver and Scheier 1998;

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Kruglanski et al. 2002). This results in potentially vast complexity in the organization of action.

The goal concept has a strong foothold in psychology. People who treat goals as an organizing construct tend to assume that understanding who a person is means understanding that person's goals—indeed, that the substance of the self consists partly of the person's goals and the organization among them (cf. Mischel and Shoda 1995).

2.2.1 Feedback Loops

The main point of this section, though, is actually less about the content of goals than the process of attaining them. Long ago, two of us (Carver and Scheier 1981) adopted the view that movement toward a goal reflects the occurrence of a discrepancy reducing (thus, negative) feedback loop (MacKay 1966; Miller et al. 1960; Powers 1973; Wiener 1948). Such a loop (Fig. 2.1) entails the sensing of some present condition and comparing it to a desired or intended condition. If a discrepancy between the two is detected, it is countered by action that changes the sensed condition. The overall effect is to bring the sensed condition into conformity with the intended one (Powers 1973). If one thinks of the intended condition as a goal, the overall effect is to bring behavior into conformity to the goal—thus, goal attainment.

There also exist discrepancy-enlarging loops, which increase deviations from the comparison point rather than decrease them. The comparison point in this case is a threat, an "anti-goal." Effects of discrepancy enlargement in living systems are typically constrained by discrepancy reducing processes. Thus, for example, people often are able to avoid something aversive by the very act of approaching something else. Such dual influence defines active avoidance: organism fleeing a threat spots a relatively safe location and approaches it.

People sometimes infer from descriptions such as this that feedback loops act only to create and maintain steady states and are therefore irrelevant to behavior. Some reference values (and goals) *are* static, but others are dynamic (e.g., taking a vacation trip across Europe, raising children to be good citizens). In the latter cases, the goal is the process of traversing the changing trajectory of the activity, not just the arrival at the end point. Thus, the principle of feedback control can be applied easily to moving targets (Beer 1995).

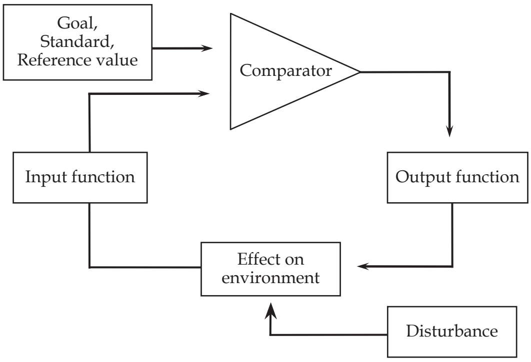

Fig. 2.1 Schematic depiction of a feedback loop, the basic unit of cybernetic control. In such a loop, a sensed value is compared to a reference value or standard, and adjustments are made in an output function (if necessary) to shift the sensed value in the appropriate direction

Why this emphasis on feedback control? Many think of feedback as an engineering concept (yes, engineers do use it), but the concept also has roots in physiology and other fields. Homeostasis, the processes by which the body self-regulates parameters, such as temperature, blood sugar, and heart rate, is a feedback process (Cannon 1932). The concept has been useful enough in many fields that it is sometimes suggested that feedback processes are some of the fundamental building blocks of all complex systems.

Some believe there is merit in recognizing functional similarities between the processes underlying various kinds of complex systems (cf. Ford 1987; von Bertalanffy 1968). It seems likely that an abstract organizational property that emerges in one may emerge in others. In the same way, it seems likely that principles underlying physical movement control (which also rely in part on principles of feedback) have something in common with principles embodied in higher mental functions (Rosenbaum et al. 2001a). For these reasons, the principle of feedback control seems useful as a conceptual heuristic.

Nonetheless, there certainly are many contexts in which the superstructure of feedback processes is quite unnecessary. Although we believe the ideas just described are important in principle, the global functions performed by discrepancy-reducing and discrepancy-enlarging loops are captured in the simpler terms *approach* and *avoidance*. These are concepts that also have a very long history in the analysis of behavior. Incentives draw behavior toward them and threats inhibit or even reverse such actions. Most of the rest of the chapter focuses on approach and avoidance processes.

2.2.2 Levels of Abstraction

Goals exist at many levels of abstraction. You can have the goal of being socially responsible; you can also have the goal of saving resources—a more restricted goal that contributes to being socially responsible. One way to save resources is to recycle. Recycling decomposes into other, more-concrete goals, such as placing empty bottles into containers and moving them to a pick-up location. All of these entail goals, values to be approached, but they exist at varying levels of abstraction.

It is often said that people's goals form a hierarchy (Powers 1973; Vallacher and Wegner 1987), in which abstract goals are achieved by attaining the concrete goals that help define them. Lower-level goals are attained by relatively brief *sequences* of action (formed from even more primitive subcomponents of motor control, e.g., Rosenbaum et al. 2001b). Sequences often have a self-contained quality, in that they run off fairly autonomously once triggered.

Viewed from the other direction, sequences of automatic acts can be organized into *programs* of action (Powers 1973). Programs are more planful than sequences, and require choices at various points. Programs, in turn, are sometimes (though not always) enacted in the service of *principles*—more abstract points of reference that provide a value basis for making decisions within programs or suggest that certain programs be undertaken or refrained from. What Powers (1973) called principles are roughly equivalent to what others call *values* (Schwartz and Bilsky 1990; Schwartz and Rubel 2005). The potential complexity does not stop even with values, however. Sets of values can coalesce to form a very abstract sense of desired (and undesired) self, or a sense of desired (and undesired) community.

All these classes of goals, from very concrete to very abstract, can in principle serve as reference points for self-regulation. When self-regulation is undertaken regarding a goal at one level, control presumably is simultaneously being invoked at all levels of abstraction below that one. Control is not necessarily being exerted at higher levels, however. Indeed, it is fully possible for a person to knowingly undertake an action that turns out to conflict with a higher-level goal. This creates problems when the person later attends to that higher goal.

2.2.3 Feedback Processes and Affect

The use of feedback control principles has also been extended to conceptualizing affect (Carver and Scheier 1990, 1998, 1999a, b). This extension applied the feedback concept somewhat differently. The argument was that the feeling properties that represent affect emerge from a feedback loop that runs in parallel to the behavior-guiding process, tracking how well the latter is doing its task. Thus, the input for the affect loop is some representation of the *rate of discrepancy reduction in the action system over time*.

This input is not sufficient to create affect, because a given rate of progress has different implications in different circumstances. Carver and Scheier (1998) argued that this input is compared to a reference value, as in any feedback system (cf. Frijda 1986, 1988). In this case, the reference is an acceptable or desired or intended rate of behavioral discrepancy reduction. As in other feedback loops, the comparison checks for deviation from the standard. If there is one, the output function changes.

The error signal in this loop (a representation of the discrepancy) is manifested subjectively as affect—positive or negative valence. If the sensed rate of progress is below the criterion, affect is negative. If the rate is high enough to exceed the criterion, affect is positive. If the rate is not distinguishable from the criterion, affect is neutral. Thus, feelings with a positive valence mean you are doing better at something than you need to or expect to, and feelings with a negative valence mean you are doing worse than you need to or expect to (for details, see Carver and Scheier 1998, Chaps. 8 and 9; 2013).

This two-layered viewpoint implies a natural link between affect and action. The affect loop has a direct influence on what occurs in the action loop. The idea of two feedback systems functioning in concert turns out to be common in control engineering (e.g., Clark 1996), where it permits devices to respond in a way that is both quick and stable, without undesired overshoots and oscillations (Carver and Scheier 1998, pp. 144–145). These properties seem similarly desirable in human experience.

The affect portion of Carver and Scheier's (1998, 1999a, b) viewpoint has a great many implications that are beyond the scope of this chapter (see Carver and Scheier 2013, for more complete treatment). We note a few here briefly.

The idea that affects of both valences can occur would seem true of both approach and avoidance systems. That is, both approach and avoidance have the potential to induce positive feelings (by doing well), and the potential to induce negative feelings (by doing poorly). But doing well at *approaching an incentive* is not quite the same experience as doing well at moving *away from a threat*. Thus, the two positives may not be quite the same, nor the two negatives.

Given this line of thought, and drawing as well on insights from Higgins (e.g., 1987, 1996) and his collaborators, Carver and Scheier (1998) posited two sets of affects, one relating to approach, the other to avoidance. The former arise from doing well versus poorly at gaining an incentive, the latter from doing well versus poorly at avoiding a threat. Thus, approach can lead to such positive affects as eagerness, excitement, and elation, and to such negative affects as frustration, anger, and sadness (Carver 2004; Carver and Harmon-Jones 2009). Avoidance can lead to such positive affects as relief and contentment (Carver 2009) and such negative affects as fear, guilt, and anxiety (Fig. 2.2)

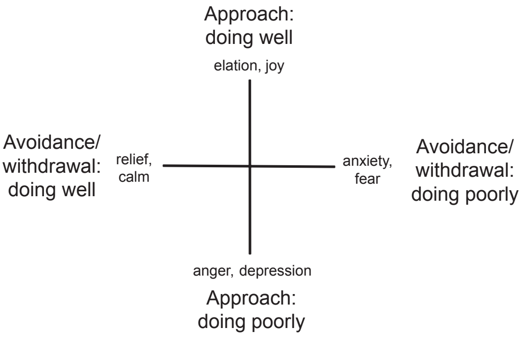

Fig. 2.2 Carver and Scheier's (1998) view of two orthogonal dimensions of self-regulatory function and examples of the affects that can emerge from them

A second issue is that the changes in behavior associated with negative and positive affect have an asymmetry: Negative affect implies a need for greater effort, whereas positive affect implies less need for effort than there had been. It has been argued that this asymmetry contributes to a system of priority management: the shifting from one goal to another as focal in behavior (Carver 2003; Dreisbach and Goschke 2004; Shallice 1978; Shin and Rosenbaum 2002; Simon 1967). Specifically, negative affect acts as a demand for higher priority (Simon 1967), and positive affect indicates that priority could be temporarily downgraded.

Another aspect of priority management concerns the idea that goals sometimes are not attainable and are better abandoned. Sufficient doubt about success in goal attainment creates reduction in effort and even giving up the goal itself (Carver and Scheier 1998, 1999a, b). This sense of doubt is accompanied by sadness or dysphoria. This issue comes up again later.

2.3 Impulse and Constraint

As we said at the outset, the view presented in the opening section has had adjustments and elaborations over the years. We turn now to an issue that induced some of those adjustments. A theme that has become prominent in many areas of psychology in recent years is the tension between impulse and constraint. This issue is by no means new.

It has been framed over many years in terms of concepts such as delay of gratification, planfulness, socialization, and id versus ego. The concept of impulsiveness is itself quite broad (e.g., Parker et al. 1993; Smith et al. 2007; Whiteside and Lynam, 2001), and the word is used in diverse ways in different contexts. But the core of the concept is that people often confront situations in which they can immediately follow an impulse or desire or they can overrule that impulse and evaluate more fully before acting.

Both impulse and constraint have valuable characteristics in the appropriate contexts (Block and Block 1980). When it is manifested as spontaneity, impulsiveness brings a sense of vigor and freedom to the human experience (e.g., Dickman 1990; Hansen and Breivik 2001). However, impulses can also create problems. Impulses can interfere with attainment of longer-term goals (e.g., spending for today rather than saving for the future). Impulses can lead to violation of social norms (Cooper et al. 2003; Lynam 1996) and thereby to interpersonal conflict. Being able to control impulsive reactivity thus is crucial to successful self-management (Vohs and Baumeister 2011).

What tips the balance between impulse and constraint? At least two mechanisms exist. One account of variability in impulsiveness rests entirely on the basic processes of approach and avoidance. The stronger the tendency to approach cues of incentives, the greater the likelihood of impulsive approach. If there are threat cues, though, the threat system becomes active, stifling ongoing approach. One might think of this stifling of approach as being an overruling of the approach motive by the avoidance motive, and thus representing constraint.

The competition between approach and avoidance is one starting point in thinking about impulse and constraint. But there are reasons to suspect that the competition between approach and avoidance is not the entire story. For example, in today's trait models of personality, the trait that is generally seen as reflecting approach—extraversion—and the trait that is generally seen as reflecting avoidance—neuroticism—are both distinct from the trait that reflects constraint—disinhibition versus constraint in Clark and Watson's (1999) three-factor model, or conscientiousness in the five-factor model (see also Depue and Collins 1999; Zelenski and Larsen 1999).

2.3.1 Dual-Process Models

A different response to constraint follows from what are often termed dual-process models of functioning. These models start with the idea that people process information in two somewhat distinct ways simultaneously. The two processing modes appear to use different aspects of the available information (Rudman et al. 2007). There is evidence that the two modes learn in different ways, and that the two patterns of learning create parallel influences on action that potentially compete with one another, thus requiring continuous arbitration (Daw et al. 2005; Otto et al. 2013).

What is often characterized as the more primitive mode of processing (sometimes called reflexive) is often (but not always) said to operate largely outside consciousness. The other mode (sometimes called reflective) is the symbolic processor of the rational mind. Some theorists stress the idea that the reflexive mode is best suited to contexts that are relatively unpredictable (e.g., Tops et al. 2010), because what it learns is actuarial patterns of associations which accumulate slowly but thoroughly (what some call model-free learning, e.g., Daw et al. 2005). In contrast, the reflective system is optimal in contexts that are relatively predictable, because what it learns is rules (what some call model-based learning), which can be realized suddenly and then be applied freely.

The idea of dual systems is by no means without controversy (e.g., Keren and Schul 2009; Evans and Stanovich 2013), and the many variations on this idea that have been posed by different theorists sometimes differ substantially from each other. For example, Braver (2012) discusses proactive and reactive control, and assumes that both modes use similar brain regions but in different patterns depending on task demands. Tops et al. (2010) also use the terms proactive and reactive, but instead tie these systems to different brain regions. For discussion of how two modes of processing can be instantiated within a single architecture, see Dayan (2008).

By now, this idea and variations on it have been taken up as a useful conceptual tool in many areas of psychology (Barrett et al. 2004; Kahneman 2011; MacDonald 2008; Rothbart et al. 2001, 2003; Evans and Stanovich 2013). A version of this viewpoint that has been particularly useful to us is from developmental psychology (Kochanska and Knaack 2003; Nigg 2000, 2003; Rothbart et al. 2001, 2003). This version posits basic approach and avoidance temperaments that act reflexively in the presence of incentive and threat cues, respectively. In acting reflexively, they are said to exert reactive control. Later to develop is a third temperament, often termed effortful control.

The label "effortful" conveys the sense that this is an executive, planful activity, entailing the use of cognitive resources to deter the tendency to react impulsively, though it is not intended to imply that the subjective experience necessarily feels like exerting effort. Effortful control relies on development of prefrontal brain areas (e.g., Durston et al. 2002a, b; Kochanska and Knaack 2003; Nigg 2003; Rothbart and Bates 1998). It is superordinate to approach and avoidance temperaments (e.g., Ahadi and Rothbart 1994; Clark 2005) and thus can countermand them (cf. Evans and Stanovich 2013). In that way, it permits control over reactive behavior.

Although restraint of approach impulses is the most obvious manifestation of this process, there are other potential manifestations that are equally important. Effortful control can also override what might be thought of as a reflexive tendency toward avoidance if the avoidance temperament is especially active. Thus, for example, with sufficient effortful control resources, a person can remain in a tension-inducing social situation rather than flee from it. If a person's approach temperament is weak or inactive, effortful control can override a reflexive tendency toward *inaction*. For example, it can get you to go exercise when you do not really want to. Thus, exerting effortful control can move a person toward either restraint or action, depending on what reactive response is being overcome.

This argument casts a somewhat different light on the concept of impulsiveness. In this view, what is impulsive is what is *reactive,* whether the outward display is of action or inaction. Impulsiveness as a concept has always been hard to pin down (Block 2002; Dickman 1990; Eisenberg 2002; Nigg 2000; Solanto et al. 2001; Stanford and Barratt 1992; White et al. 1994; Whiteside and Lynam 2001, 2003). It can take many forms, including jumping toward an incentive, being easily distracted by opportunities that arise while a current pursuit is ongoing, and reacting quickly to emotions. The aspect of impulsiveness that is emphasized here is that impulses are reactive: relatively reflexive responses to some stimulus in disregard of other considerations. The key, in this view, is that the action property represents a reactive, automatic association to the stimulus.

2.3.2 Dual-Process Models and Hierarchicality of Behavior

These kinds of ideas suggest a different way to think about the hierarchy of control that was first proposed by Powers (1973). We said earlier that programs of action entail decisions. They seem to be managed top-down, using planful, effortful processing. Planfulness is also a common characterization of behavior managed by the reflective system. It seems reasonable to map what Powers (1973) called program-level control (and even higher levels) onto the deliberative, reflective mode of functioning.

In contrast to this deliberative quality, what Powers (1973) termed sequences are well-learned action combinations that occur in a relatively automatic stream once they are triggered. Sequences (along with yet lower levels of control) are necessarily called up during the execution of programs. However, it seems reasonable to suggest that sequences can also be triggered more autonomously, without their being a subroutine of effort toward a higher goal (examples might include reaching to pick up a $10 bill you spotted on the ground and putting it into your pocket, or frowning and turning away when you see someone you dislike). Sequences may be triggered by the activation of strong associations in memory (the appearance of money as positive, the appearance of the other person as negative). In such cases, the operating characteristics would seem akin to those of the reactive mode of functioning.

In the past, it has often been noted that the level of control that is functionally superordinate can vary by situations and persons (e.g., Carver and Scheier 1998, 1999a). As we said earlier, it is easy to imagine cases in which a person is behaving according to a principle (e.g., a moral or ethical value), and it is easy to imagine cases in which the person is behaving according to a plan (what Powers, 1973, termed a program, because of its if–then properties). It is also easy, however, to imagine cases in which the person is acting impulsively and spontaneously, without regard to either principle or plan.

In making this case in the past, Carver and Scheier's emphasis generally focused simply on how sequences and plans differ. The literature of dual-process models raises the question of whether this differentiation is perhaps more important than had been realized. Perhaps Carver and Scheier (and others) underappreciated the extent to which lower self-regulatory structures can be triggered autonomously and their outputs enter the stream of ongoing action, without oversight from higher levels, and potentially even in conflict with values at higher levels.

This is one way the emergence of dual-process models has influenced our thinking. Another influence, which itself has a wide variety of implications, consists of an investigation of some of the biological underpinnings of the dual-process model.

2.3.3 Serotonergic Function and Dual-Process Models

A number of researchers have tried to understand roles played by different neurotransmitter systems in the management of behavior. One system that has been the subject of much investigation is the serotonergic system. In this section, we consider a potential role for serotonergic function in impulse and constraint.

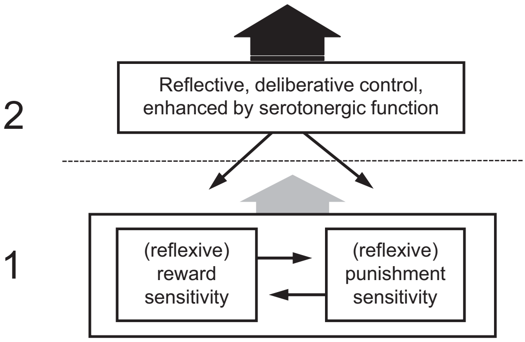

Fig. 2.3 Simplified description of dual-process model of behavior. The reflexive process (layer *1*) entails competition between reflexive approach and avoidance tendencies, yielding a resultant behavior tendency (*grey arrow*). The reflective process (layer *2*) may countermand that resultant, exerting its own influence on behavior (*black arrow*). We suggest that one effect of greater serotonergic function is to enhance the influence of the reflective system. (Adapted from Carver et al. 2008)

Human research on serotonergic function uses several methods, including acute tryptophan depletion and relating behavior to genetic polymorphisms that have independently been linked to serotonergic function (Manuck et al. 2006). A full review of the literature using these (and other) techniques to study serotonergic function in humans is well beyond the scope of this chapter. We will point to only a few select examples (for a broader, though dated, review, see Carver et al. 2008). This evidence appears to suggest that the serotonergic system functions (partly) to decrease reactivity and to increase constraint (Figure 2.3).

Some of the evidence comes from laboratory studies, in which tryptophan depletion, which temporarily reduces serotonin, appears to impair constraint over automatic emotional responses. As an example, consider a task in which specific cues are rewarded, and for which the response thus becomes habitual. Then the rules change such that this response is no longer rewarded. Tryptophan depletion impairs the ability to inhibit those responses after the rule changes (Cools et al. 2005; Park et al. 1994; Rogers et al. 2003).

Many studies have examined effects of tryptophan depletion on aggression. A study by

Cleare and Bond (1995) made a very important conceptual point in that regard. Participants were pre-assessed as being either high or low in aggression. Those high in aggressive tendencies became more aggressive after tryptophan depletion, but there was no effect for those low in aggressive tendencies. Similar results were reported by Finn et al. (1998). This suggests that effects of low serotonergic function on aggression are less about aggression per se and more about the release of existing habitual tendencies to be aggressive (see also Manuck et al. 2006; Spoont 1992). A later study (Bjork et al. 2000) further reinforced this point: In this case, tryptophan depletion led to greater aggressive response to provocation among men high in aggressiveness but had an opposite effect among those low in aggressiveness.

A good deal of research has also examined serotonin in adults with clinical conditions reflecting impulsive aggression (see Manuck et al. 2006). Lower serotonergic function has long been linked to history of fighting and assault (Coccaro et al. 1997), domestic violence (George et al. 2001), and impulsive aggression more generally (Coccaro et al. 1998; Cleare and Bond 1997).

The pattern of these findings (and others) appears consistent with the view that serotonergic pathways are involved in impulse control (Depue 1995; Depue and Collins 1999; Depue and Spoont 1986; Manuck et al. 2003; Soubrié 1986; Spoont 1992; Zuckerman 2005), particularly impulses that reflect strong emotions.

This pattern was characterized by Carver et al. (2008) in terms of the dual-process viewpoint described previously. Recall that the basic, reactive mode of functioning is said to be impulsive and highly responsive to strong emotions. The reflective mode is said to be planful and less reactive to immediate emotional cues. Joining these descriptions with the findings just described, it seems plausible that serotonergic function may shift the balance of influence between these two modes of functioning. That is, lower serotonergic function may increase the influence of the reactive system or decrease the influence of the reflective system.

2.3.4 Depression and Serotonergic Function

Now consider depression (see also Brinkmann and Franzen this volume). Depression is very different from the phenomena we have just been discussing, but depression is also linked to low serotonergic function. The facet scale called depression from trait neuroticism has been linked repeatedly to the serotonin transporter gene, the short allele being associated with higher scores. There is also evidence linking serotonergic function to clinically meaningful depression (for review, see Carver et al. 2008). Outcomes of meta-analyses of this literature have varied as a function of selection criteria. However, Uher and McGuffin (2010) found that the serotonin transporter polymorphism interacted with early maltreatment to predict vulnerability to depression in each of the 11 studies that used objective or interview measures of maltreatment (see also Caspi et al. 2010).

An earlier section linked low serotonergic function to impulsive reactions to emotional cues. The idea that high reactivity to emotions underlies impulsive violence, sensation seeking, and other externalizing problems is both intuitive and supported by a great deal of data (Cyders et al. 2009; Dick et al. 2010; Whiteside and Lynam 2003). Now, we are saying that low serotonergic function also implies vulnerability to depression, which is associated with lethargy and an absence of behavioral engagement (Sobin and Sackeim 1997). What could account for this very substantial difference in presentation?

To address this question we return to dual-process models, and to our working definition of impulsiveness. Dual-process models suggest that the reactive mode acts reflexively and is highly responsive to emotions. But these are "operating characteristics" of that mode of function. How the operating characteristics are manifested overtly depends on what emotions the person is experiencing and what reactive action impulse thereby is being triggered.

In most cases, emotions call for outward action of some sort. Eagerness promotes approach. Fear promotes avoidance. But intense sadness—the affective core of depression—calls for passivity (Frijda 1986). It is a *deactivating* emotion, a signal of failure. An over-responsiveness to emotion, applied to sadness, would promote behaviors that sadness ordinarily triggers. The behavior triggered by intense sadness is *in* action. Thus, depressed behavior often reflects passivity and apparent difficulty in initiating action.

Consistent with this, there is evidence that people in a sad mood evaluate tasks as requiring more effort than they are rated in the absence of the sad mood (Gendolla 2012). If success still seems possible despite the greater demand, people in sad moods actually mobilize more effort (reflected in stronger blood pressure responses) than those without a sad mood. But if demand is seen as being great enough to threaten success, sad people exert less effort than happy people, displaying a pattern much like fatigue (Brinkmann and Gendolla 2008; Gendolla 2012; see also Brinkmann and Franzen this volume).

Paradoxically, then, a single functional property—behavioral reactivity to emotion—can not only help release bursts of violence or acting out but may also help create essentially the opposite profile of behavior, in response to a different emotion.

This leaves two issues dangling. First, if people who are sensation seekers and people who are vulnerable to depression both have low serotonergic function, they must differ from each other in some other fundamental way. Second, the case that depression should be viewed as similar in this way to overtly impulsive behavior is thus far circumstantial. It depends entirely on findings concerning correlates of the serotonergic system. Is there any further evidence that this argument is tenable? We consider these questions in turn.

2.3.5 What Differentiates Impulsive Aggression and Sensation Seeking from Depression?

First, what other variable might underlie the great divergence between sensation seeking and depression? The most obvious candidate is the sensitivity of the approach system. When poor reflective oversight is combined with a very reactive approach system, the result is overt approach-related impulsiveness. When poor reflective oversight is combined with an unreactive approach system, the result is impulsive inaction: lack of effort toward potential rewards. In both cases, the effects of variation in level of basic incentive sensitivity (high and low, respectively) are amplified by the absence of effortful override.

Enhanced versus blunted approach motivation may be rooted in differences in dopaminergic function in certain brain areas. Dopaminergic pathways are believed to be critical in the engagement of goal-directed effort (Farrar et al. 2007; Salamone et al. 2007, 2005, 2006). A weakly functioning dopaminergic system yields less "wanting" for appetitive outcomes (Berridge 2007) and less engagement of effort in pursuit of them (Salamone et al. 2005, 2006, 2007). A range of evidence implicates deficits in dopaminergic function in depression (Dunlop and Nemeroff 2007).

2.3.6 Does Depression Relate to Impulsive Reactivity?

The second question is whether there is any direct evidence linking depression to over-reactivity to emotions or any other aspect of impulsiveness. There is. Three studies (Ekinci et al. 2011; Henna et al. 2013; Peluso et al. 2007) have associated a diagnosis of major depressive disorder (MDD) with self-reports of motor impulsivity on the Barratt Impulsiveness Scale (BIS; Barratt 1965); two of them (Ekinci et al. 2011; Henna et al. 2013) found a similar effect for attentional impulsivity.

The item content of the BIS makes it difficult to attribute impulsiveness to emotional versus nonemotional sources. But another recent study explored more explicitly the possibility that depression would be associated with reactivity to emotions (Carver et al. 2013). It employed a variety of questionnaires bearing on impulsiveness, and a subsample also completed a diagnostic interview for lifetime episode of MDD.

Of the scales administered, some were chosen to pertain to reflexive reactivity to emotions. Recall that the dual-process view does not distinguish emotional valences. People who are vulnerable to depression should have a general reactivity to emotion of diverse sorts, not just negative emotions. To ensure a test of this reasoning, the study included one scale that addressed impulsive behavioral reactions to emotions "in general," and another that assessed impulsive reactions to *positive* emotions in particular (the Positive Urgency Measure, PUM; Cyders et al. 2007).

The impulse-related questionnaires had previously been distilled to three underlying factors. Factor 1 (pervasive influence of feelings) reflects a broad tendency for emotions to reflexively shape the person's orientation to the world. Factor 2 (lack of follow-through) centers on the tendency to complete tasks versus being distracted and letting things go, with no obvious involvement of reacting to emotion. Factor 3 (feelings trigger action) centers on impulsive overt behavioral reactivity to emotions, including positive emotions. Persons diagnosed with MDD had higher scores on factors 1 and 3 than did persons with negative diagnoses, but there was no difference between groups on factor 2 (Carver et al. 2013). Importantly, these differences between groups were robust to several kinds of controls for current depressive symptoms and externalizing symptoms. Conceptually consistent with this finding is evidence that brain regions involved in emotions are over-responsive to positive social evaluations in depressed compared to nondepressed persons (Davey et al. 2011).

Longitudinal evidence also supports the importance of emotion-relevant impulsivity to depression. Smith et al. (2013) followed a group of fifth graders for a year, assessing diverse markers of psychopathology over time. They found that a measure of urgency (reflecting impulsive reactions to both negative and positive emotions) predicted increase in relative depression over that year, after controlling for a wide range of externalizing symptoms.

2.3.7 Transdiagnostic Vulnerability

The possibility that the broad spectrum of psychopathologies may be characterized by a more limited number of features that are actually transdiagnostic has been raised in a number of places in recent years (e.g., Harvey et al. 2004; Johnson-Laird et al. 2006). It seems worth asking whether an impulsive over-reactivity to emotions may be one such transdiagnostic feature (see also an argument made by Johnson-Laird et al. 2006, about the role of emotional over-responsiveness in psychopathology).

Some additional information is available on this question. The three factors described above have also been studied in other psychopathology-related contexts, albeit with nonclinical levels of symptoms. One of these studies (Johnson et al. 2013b) found that manic temperament, measured by the Hypomanic Personality Scale, correlated significantly with factor 3 after controlling for comorbid syndromes, but not to the other factors. Similar associations have been found between the PUM (a key contributor to factor 3) and both mania vulnerability (Giovanelli et al. 2013) and bipolar I diagnostic status (Muhtadie et al. 2014). Thus, reports of an over-responsiveness to positive emotions and emotions in general relates to mania vulnerability as well as to depression vulnerability.

Yet another set of analyses found associations between both emotion-reactivity factors and a wider range of problem behavioral tendencies, including anxiety, depression, suicidality, alcohol problems, aggressive tendencies, and borderline personality traits (Johnson et al. 2013a). As a group, these findings are consistent with the notion that an impulsive over-reactivity to emotions represents a feature common to a great many psychopathologies.

2.4 Summary and Conclusion

This chapter sketched the outlines of a view of the structure of self-regulation, based on the organizing principle of feedback control processes, as applied to goal striving and affective experience. We then considered this viewpoint in light of some more recent developments in psychology and related disciplines. In particular, the emerging salience of dual-process models of self-regulation provides an interesting tool to use in reexamining the difference between actions that are planful and deliberative and actions that are more spontaneous and seem to be triggered by cues of the moment, often cues that take the form of emotional reactions to stimuli. Earlier views recognized that such spontaneous executions of sequences of acts could take place if a higher level of control was not presently operative, but said little more than that about it. The dual-process view provides a more elaborated picture, at least providing some hints about why the autonomous triggering of spontaneous actions might occur.

In later sections of the chapter, we expanded on this idea to discuss one viewpoint on some of the biological underpinnings of the reflective–reflexive distinction. We suggested there that one role played by the serotonergic system (one role among many, we hasten to add) is to influence the balance between reflective and reflexive. This is an idea that is not without its controversies, but it is an idea we think worth exploring further.

The chapter then turned to an implication of this view of the serotonergic system which follows from the fact that low serotonergic function has been tied to depression vulnerability as well as vulnerability to externalizing problems. The position was put forward there that both of these classes of problems, and perhaps others as well, may be grounded partly in tendencies to overreact to situational emotional states, displaying the actions that follow from those emotions. Evidence that this tendency was related to diverse problematic tendencies was briefly reviewed. Although this is far from establishing the case, we think this idea, as well, is worth exploring further.

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Self-Regulation in an Evolutionary Perspective

3

Marco Del Giudice

3.1 Introduction

In this chapter, I situate self-regulation in an evolutionary perspective, and explore the implications of an evolutionary approach for the study individual differences in self-regulation. I begin with an overview of the self-regulation continuum, from simple control mechanisms with no explicit goal representation to deliberate, self-directed executive processes like those found in human adults. In particular, I highlight the central role of inhibition and future orientation in the emergence of complex self-regulatory abilities, and introduce the construct of impulsivity. In the next section, I review the two basic strategies of behavior control—feedback and feedforward control—and discuss their relative advantages and disadvantages from the standpoint of control theory. A central theme of the section is that self-regulation involves trade-offs at all levels—between speed and accuracy, robustness and flexibility, and so forth; organisms deal with those trade-offs by implementing multiple control systems that coexist in the brain and cooperate in the regulation of goal-directed behavior.

Next, I discuss how organisms shift the balance between feedback and feedforward control in a context- and task-dependent manner, and outline an ecological theory of control strategies. The goal is to understand how environmental and individual factors interact to determine the optimal self-regulation strategy in a given context. I then go on to show how the same principles can be employed to understand stable individual differences in control strategies and impulsivity (characterized as "coping styles" in the biological literature), and review some potential evolutionary explanations of adaptive individual variation. Finally, I introduce the framework of life history theory, discuss how it provides a unifying perspective on individual differences in self-regulation, and conclude by critically examining the association between life history strategies and self-regulation in humans and nonhuman animals.

3.2 Self-Regulation: An Overview

3.2.1 The Self-Regulation Continuum

The term "self-regulation" has many possible meanings, and definitions vary across authors and research areas. While the existence of multiple definitions can be confusing, the different kinds of self-regulation described in the literature can be easily understood as regions on a continuum going from comparatively simple and mindless control mechanisms to complex, hierarchical, and deliberate mental processes.

In the broadest sense, the concept of self-regulation applies to all forms of goal-directed behavior (e.g., Carver and Scheier 2011; Hofmann

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et al. 2012; Tops et al. 2010). It is important to realize that, by this definition, self-regulation does not require goals to be explicitly represented by the individual organism, even if the goal may be clearly discernible by an outside observer. When a bacterium moves toward higher concentrations of glucose by chemotaxis, its behavior is regulated by a clever system of feedback control that alternates straight-line swimming and random tumbling. The *objective* goal of this behavior is obvious to an external observer—moving the bacterium toward glucose—even if the bacterium itself has no internal representation of the reason for its behavior; in fact, the bacterium does not even need to represent the direction in which it is swimming (Bechhoefer 2005).

In Daniel Dennett's terminology, such real but unrepresented goals can be understood as "free-floating rationales" (Dennett 2009). Even in very simple organisms, natural selection tracks the causal regularities that affect survival and reproduction, since organisms that—for whatever reason—are better at exploiting the causal structure of their environment are usually also better at surviving and reproducing. As a result of this selection process, evolution equips organisms with machinery that supports effective goal-directed performance (e.g., chemotaxis) with no need for the individual organism to possess any representation of the underlying goals and causal properties.

As organisms evolve more sophisticated nervous systems, goals and reasons may begin to be actively represented, even if only partially and implicitly. For example, the firing rate of a neuronal group may implicitly encode the expected amount of food in a given direction of space. By gradual accumulation of function, evolution has provided humans with a remarkable ability to explicitly represent their goals (or at least some of them), communicate them to conspecifics, and employ those representations to build detailed plans as well as mental scenarios of their own behavior and that of other people (see Dennett 2009).

Self-regulation in the narrow sense concerns a subset of behaviors—broadly defined to include cognitive operations in addition to body movements—whose main function is to change the probability of later behaviors by the same organism (see Barkley 2001). Some scholars refer to narrow-sense self-regulation as *self-control* (e.g., Carver and Scheier 2011; Hofmann et al. 2012). The basic component of narrow-sense self-regulation is *inhibition*—the ability to override impulses and responses that conflict with current goals. Thus defined, inhibition does not require explicit goal representations, although it does require the existence of multiple interacting control systems within the same organism. Simple forms of inhibition can take place in absence of a control hierarchy; for example, control systems A and B—each equipped with their own goals—may reciprocally inhibit one another whenever their activation level crosses a certain threshold. Of course, when self-regulation processes become hierarchically organized (e.g., Carver and Scheier 2011; Filevich et al. 2012; Kopp 2012), higher-order systems may acquire the ability to flexibly inhibit lower-order systems in the service of higher-order goals. In the self-regulation literature, inhibition is usually framed in the context of hierarchical control systems (e.g., Carver and Scheier 2011; Filevich et al 2012).

At the far end of the continuum is the family of *executive functions*, an even narrower subset of regulatory processes that—in their most elaborate form—are only possessed by adult humans. Executive functions stand out because of their deliberate self-directedness (Barkley 2001), and permit extremely high levels of flexibility and strategic planning (Diamond 2013; Miyake et al. 2000). The standard taxonomy of executive functions includes *inhibition* (deliberate overriding of dominant or prepotent responses), *updating* (constant monitoring and rapid addition/deletion of working memory contents), and *shifting* (switching flexibly between tasks or mental sets). A broader, biologically plausible taxonomy of executive functions advanced by Barkley (2001) also includes *affective self-regulation* and *generativity* (the ability to mentally generate new combinations of behavioral units).

On the surface, executive functions look like a heterogeneous collection of cognitive processes. What they all share is a common theme of *future orientation*. In different ways, executive processes contribute to detach behavior from immediate, short-term goals in order to maximize the long-term benefits for the individual (discussed in Barkley 2001; Denckla 1996). Executive functions can serve multiple adaptive roles including vicarious learning, delayed reciprocity in social exchanges, flexible tool use, and self-defense against social manipulation. In adults, executive functions are usually covert (e.g., silent self-talk), possibly as an adaptation to social competition (see Barkley 2001, for a detailed treatment).

3.2.2 Impulsivity

Both conceptually and empirically, inhibition and future orientation play a central role in the self-regulation continuum. Together, they allow the emergence of the full range of executive functions deployed by adult humans. Inhibitory functions allow individuals to interrupt ongoing actions, delay prepotent responses, and reduce attentional and motor interferences. Inhibition is a precondition for all other forms of executive control, and is required to protect ongoing executive processes from external and internal interferences (Barkley 2001). Consistent with this view, psychometric studies show that inhibition can be regarded as the "general factor" of executive functioning, as it accounts for most of the shared variance between different executive abilities (Miyake and Friedman 2012).

The concept of future orientation can be understood in more rigorous terms as a function of time discounting (or delay discounting). In a nutshell, time discounting quantifies the extent to which preferences are affected by delays in the presentation of rewards. High discount rates are revealed by a strong preference for smaller immediate rewards over larger, delayed ones. Future orientation is reflected in low discount rates, and covaries with inhibitory abilities in both humans and nonhuman species (see Coppens et al. 2010; DeYoung 2011).

Behavioral disinhibition and present orientation can be seen as partially overlapping facets of a broader trait—*impulsivity*. Impulsivity is arguably the most important dimension of individual variation in self-regulation, and can be described as the tendency to act without deliberation and without consideration of future consequences (Carver 2005; DeYoung 2011). The construct of *effortful control* is symmetrical to that of impulsivity, and refers to the ability to inhibit dominant responses while taking into account the long-term consequences of actions (see Rothbart 2007).

In much psychological literature, impulsivity is treated by default as a dysfunctional, maladaptive aspect of personality and behavior. However, some authors have stressed how impulsivity can also bring important advantages, including the ability to make quick decisions and seize on unexpected opportunities (Block 2002; Dickman 1990). The adaptive potential of impulsivity has been examined in greater detail by evolutionary biologists.[1] A wealth of empirical and theoretical findings demonstrate that—depending on ecological circumstances, the structure of the environment, and the nature of specific tasks—present orientation and impulsive decision making can often be highly adaptive, leading individuals to maximize the benefits of behavior in key areas such as mating, foraging, and exploration (e.g., Chittka et al. 2009; Coppens et al. 2010; Daly and Wilson 2005; Green and Myerson 1996; Sih and Del Giudice 2012; Stephens et al. 2004).

3.3 Two Strategies of Behavior Control

Self-regulatory processes may reach a remarkable degree of sophistication and differentiation, especially in socially complex organisms like

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[1] In evolutionary biology, *adaptive* and *maladaptive* denote the effects of traits and behaviors on fitness, that is, the differential replication of genes in subsequent generations. In psychology and the social sciences, the same terms usually denote the subjective and/or social desirability of a trait or behavior. Traits that promote health, subjective well-being, and mutually rewarding social relations are viewed as adaptive, whereas socially undesirable, distressing, or health-damaging traits are viewed as maladaptive. Since natural selection promotes reproductive success rather than happiness or health, biologically adaptive traits may or may not be socially desirable or conducive to health and well-being.

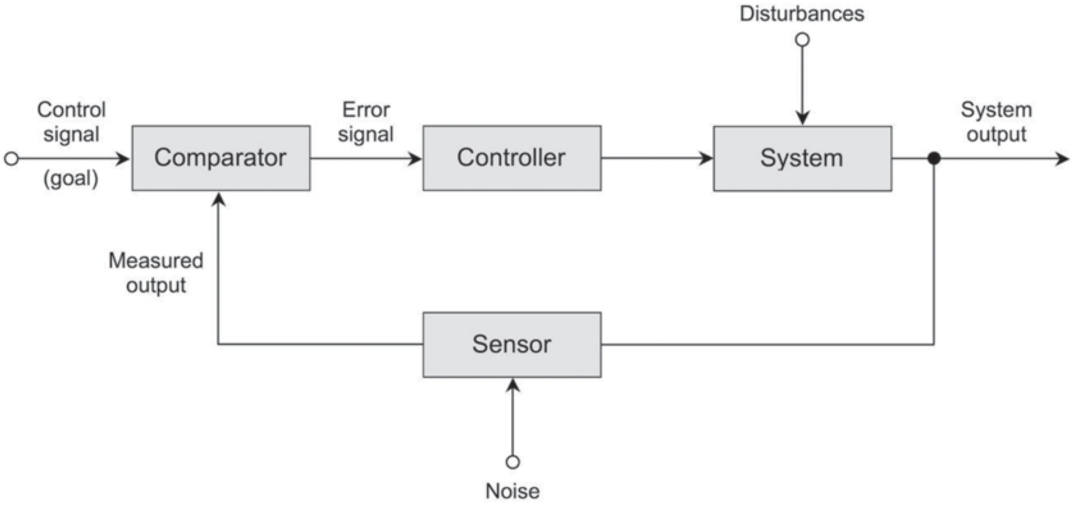

Fig. 3.1 Schematic representation of a feedback (closed-loop) control system

humans (Barkley 2001). However, their internal logic ultimately boils down to two basic strategies of behavior control—*feedback control* and *feedforward control*. Feedback and feedforward controllers are the building blocks of all regulatory systems, and their characteristics and limitations have been worked out in detail in the field of mathematical control theory (see Albertos and Mareels 2010; Bechhoefer 2005). In this section, I provide a brief overview of feedback and feedforward systems from the standpoint of control theory.

3.3.1 Feedback Control

In feedback or closed-loop control, the current goal (or *control signal*) is compared with the actual state of the system (i.e., the system's *output*), and an *error signal* is obtained as a result. For example, the goal of a bird chasing a fly may be that of getting as close as possible to the fly; the perceived distance between the bird and the fly at any given moment would then constitute the error signal. The error signal is used to generate a goal-directed action, which alters the state of the system (the bird may change speed and/or trajectory). However, other causal factors (*disturbances*) may be acting on the system at the same time; for example, the fly may suddenly turn, or a change in wind speed may affect the bird's trajectory. The joint effect of goal-directed actions and disturbances determines the system output, which is then measured and compared to the current goal, closing the control loop (Fig. 3.1). The critical feature of a feedback controller is that it tracks the system output in real time, progressively narrowing the gap between the goal and the state of the world through moment-to-moment self-correction.

As a rule, the system output is not *directly* available for comparison but has to be estimated or measured in some indirect way, for example, through sensory organs and related neural pathways. Measurement processes—broadly defined to include sensory processes and the associated neural computations—inevitably introduce some error (or *noise*) in the feedback loop. Indeed, feedback systems face a fundamental trade-off between tracking speed and the ability to reject unwanted noise. If the output is measured with higher temporal resolution—thus increasing the ability to track rapid changes in the state of the system—more irrelevant noise will enter the feedback channel and get mixed up with the useful information. Conversely, effective filtering of unwanted noise inevitably reduces the tracking speed of a control system (Bechhoefer 2005).

A powerful way to employ feedback controllers is to nest multiple feedback loops within one another, yielding a *feedback cascade*. In this type of hierarchical arrangement, the inner control

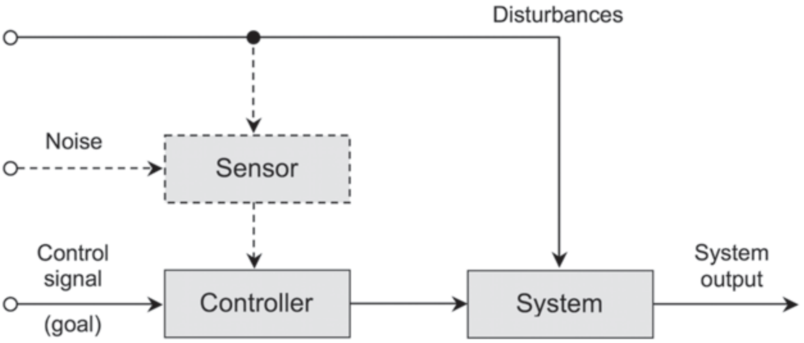

Fig. 3.2 Schematic representation of a feedforward (open-loop) control system. A feedforward controller may employ information about past and current conditions to predict the future state of the system (*dashed box* and *arrows*)

loop regulates a lower-order variable (i.e., pursues a lower-order goal) in order to simplify the control actions performed by the controller in the outer loop (Albertos and Mareels 2010). Nested feedback loops allow a complex control task to be split into smaller modular tasks, and permit high levels of flexibility and accuracy. For these reasons, feedback cascades are very popular in cognitive and neuropsychological models of self-regulation (see Carver and Scheier 2011; Filevich et al. 2012; Kopp 2012). A classic application of feedback loops is the TOTE model advanced in 1960 by Miller and colleagues. A TOTE unit (acronym of *Test-Operate-Test-Exit*) is an abstract feedback controller that executes an iterative "plan" until its goal is reached. In this model, the hierarchical plans that control an organism's behavior are implemented by cascades of nested TOTE units working at different levels of abstraction (Miller et al. 1960).

The main strength of feedback control lies in its ability to respond to unknown or unanticipated disturbances. More generally, feedback control has an intrinsically self-correcting nature; for this reason, it does not require an accurate preexisting model of the system in order to function properly. However, feedback systems are also highly sensitive to noise and rely on accurate measurement of system output, which may or may not be available in a given situation. Another crucial limitation of feedback control is that it depends on the ability to track real-time changes in the system. Sensory processing, neural computation, inertia in the system, and so forth introduce delays and response lags in the feedback loop. As the overall delay increases, the performance of feedback control deteriorates rapidly; beyond a certain threshold, delays in the feedback loop may destabilize the system and lead to erratic, uncontrolled behavior (Albertos and Mareels 2010; Azuma and Hirose 2008; Bechhoefer 2005).

3.3.2 Feedforward Control

While feedback control is a ubiquitous and powerful strategy, it also has important limitations. As deftly put by Albertos and Mareels (2010), "driving a car by feedback only would equate to driving using information only from the rear view mirror" (p. 213). In other words, feedback controllers can only respond to disturbances and changes in the system once they have occurred, but are unable to *anticipate* them. Returning to the car analogy, imagine a driver trying to keep her car on track by only looking in the rear view mirror. Every time the road turns, the car begins to veer off course; the backward-looking driver then notices the deviation in the mirror and responds by steering the car back on its trajectory (with some unavoidable delay). A forward-looking driver would see the turn approaching and could begin the steering movement in advance, resulting in a much smoother trajectory.

When disturbances can be anticipated (or ignored altogether), feedforward or open-loop systems may become highly effective means to control the behavior of a system. In feedforward control, the goal is combined with a model of the system that may also include the predicted effects of future disturbances; the results of this computation are then used to guide behavior, with no further feedback about the state of the system (Fig. 3.2). For example, when a chasing bird gets close enough to the fly, it may "dive" toward the prey with a rapid anticipatory motion based on (a) the predicted position of the fly in the next fraction of a second and (b) a model of the motor actions required to reach that position at the right time.

The simplest forms of open-loop control may skip the prediction step entirely; many protective reflexes—for example, retracting one's hand when it touches a hot object—are based on simple, "ballistic" open-loop mechanisms (see Albertos and Mareels 2010). More complex instances of feedforward regulation may involve simulation of future events, strategic planning, and integration of preexisting knowledge about the rules that govern the system, the likelihood of potential outcomes, and the influence of contextual variables.

Just like feedback control, feedforward control also has both strengths and weaknesses. To begin with, feedforward control permits extremely fast execution once an action sequence is initiated. Other advantages of feedforward systems include their insensitivity to noise, their greater dynamic stability, and the fact that they do not require accurate, real-time measurement of the system output. On the other hand, feedforward regulation often requires an accurate model of the system, and enough information about the current state of the system so that future disturbances can be successfully predicted. Most crucially, feedforward systems—regardless of their complexity—are unable to respond to unanticipated events that occur while the planned action is unfolding (Albertos and Mareels 2010; Bechhoefer 2005).

3.3.3 Combining Feedback and Feedforward Control

It is apparent from the preceding discussion that feedback and feedforward systems have largely complementary sets of advantages and disadvantages. As a result, the design of self-regulation strategies involves a number of important trade-offs—between speed and accuracy, flexibility and robustness, predictive ability and computational simplicity, and so forth. The standard engineering solution to these trade-offs is to combine feedback and feedforward elements in the same control system, in order to exploit the strengths of both strategies and compensate for their weaknesses (Albertos and Mareels 2010; Bechhoefer 2005). For example, the predictive estimates employed in feedforward control can be used to compensate the delays introduced by feedback loops and make the system more resistant to sensory noise (see Wolpert and Ghahramani 2000).

There is considerable evidence that the brain controls behavior through the joint action of multiple control systems based on complementary principles (e.g., Tucker et al. 1995; Wolpert and Ghahramani 2000; Wolpert et al. 2003). Control subsystems employing the same or different strategies can be combined in many different ways; in particular, hierarchical arrangements of higher- and lower-order controllers—as in feedback cascades—can achieve remarkable levels of speed, accuracy, and flexibility (e.g., Albertos and Mareels 2010; Carver and Scheier 2011; Filevich et al. 2012). In addition, feedback and feedforward processes can be combined *sequentially* in time to increase behavioral flexibility and optimize learning. When a feedforward controller needs an accurate model of the system, feedback loops can be employed in the learning phase to build, update, and refine such a model—effectively "training" the feedforward controller and enhancing its future performance (this is known as *feedback-error learning*; see Wolpert and Ghahramani 2000). For example, an initial phase of feedback control may facilitate slow, systematic exploration of a novel environment (Sih and Del Giudice 2012); the context model built in the learning phase can then be used to make quick, effective decisions guided by feedforward processes.

3.4 The Ecology of Control Strategies

While the overall performance of a control system can be improved by a mixture of feedback and feedforward processes, the optimal combination between the two strategies may change—sometimes dramatically—across different contexts and tasks. For example, Azuma and Hirose (2008) simulated a neural network performing a complex control task (riding a bicycle without falling) with different amounts of delay in the perception–action loop. As the delay increased, feedback control became more and more unstable and the optimal strategy shifted to feedforward prediction (see Sect. 3.3). From a biological standpoint, brains should possess the ability to shift the balance between feedback and feedforward control depending on the current task and environmental conditions. Moreover, there is no reason why strategic flexibility should be limited to motor tasks: The general principles of feedback and feedforward control—and the resulting trade-offs—apply to all kinds of goal-directed behavior, from simple motor actions to complex social interactions (e.g., Carver and Scheier 2011; Wolpert et al. 2003).

In the remainder of this section, I combine the principles of control theory with insights from evolutionary biology to derive some initial predictions about the ecology of control strategies. In order to understand how optimal strategies may vary across environments, the standard focus on control performance has to be supplemented with careful consideration of the organism's needs and priorities.

In general, whether a strategy is biologically adaptive in a given context does not only depend on its performance in terms of speed and accuracy but also on the overall cost–benefit balance with respect to an individual's fitness. A slower and/or less accurate strategy may be adaptive if it increases the organism's chances of successful survival and reproduction. Furthermore, the costs and benefits of a strategy in a given environment may vary dramatically between different individuals (for example, between males and females, old and young, well fed and starving). Since environmental *predictability* has been singled out as a key determinant of the adaptiveness of control strategies (e.g., Tops et al. 2010), I will center my analysis on the distinction between predictable and unpredictable environments.

3.4.1 Unpredictable Environments

When the local environment is unpredictable and subject to sudden changes, feedback strategies have two important advantages over feedforward strategies. First, feedback control tracks the environment in real time, enabling flexible behavioral adjustment in response to changing conditions; and second, it works even when it is difficult or impossible to construct an accurate model of the environment (see also Tops et al. 2010). The benefits of feedback control are especially critical when an individual's goal is to prevent and/or avoid potential dangers in the environment. However, the preventive effectiveness of feedback strategies is greatest when dangerous events can be anticipated based on warning cues; since feedback processes are intrinsically backward-looking, they cannot successfully prevent events that occur too abruptly.

When the environment reaches very high levels of unpredictability, the potential benefits of feedback control decrease while the costs of continued vigilance increase accordingly. In such environments, it may be more advantageous to embrace unpredictability rather than attempt to control it—in other words, some individuals may shift from a risk-averse strategy focused on harm prevention to a high-risk strategy involving competition, bold exploration, and so forth (see Del Giudice et al. 2011; Ellis et al. 2012). Individual characteristics that favor risk taking in unpredictable environments include sex, dominance status, and physical conditions. In particular, the males of most species—including humans—face stronger mating competition and more variable reproductive outcomes than females (see Geary 2003; Kokko and Jennions 2008). The result is stronger sexual selection for competitive traits such as risk taking, dominance seeking, and physical aggression (see Archer 2009; Cross et al. 2011; Wilson et al. 2002).

By definition, risky decisions face individuals with unpredictable outcomes, as they may result in large gains as well as heavy losses (see Frankenhuis and Del Giudice 2012). When individuals engage in high-risk courses of action, the immediate feedback they receive can be irrelevant or even misleading. In an all-out fight with a dangerous opponent, the best strategy is usually to keep fighting no matter what rather than backing down after the first blow. More generally, high-risk strategies often require outright *insensitivity* to threats and dangers to work successfully. For extreme risk takers, informational insulation from signals of threat can be an asset, not a weakness (Del Giudice et al. 2011; Korte et al. 2005). Thus, it can be adaptive for them to suppress the activity of feedback control systems and rely on open-loop, "ballistic" strategies that deliberately ignore the immediate consequences of one's actions.

3.4.2 Predictable Environments

In predictable environments, feedforward strategies offer several potential benefits including robustness, decision speed, and enhanced sequential planning capabilities. It is important to keep in mind that open-loop self-regulation can take various forms that differ in their complexity and in their relation with impulsivity. First, there is the ballistic, impulsive sort of open-loop regulation involved in high-risk strategies. At moderate levels of complexity, feedforward control is driven by habits and rigid, inflexible behavioral routines (see Coppens et al. 2010). When coupled with detailed context models, however, open-loop control may enable careful, deliberate, future-oriented planning, which in turn requires active inhibition of competing short-term goals.

While all these modes of self-regulation imply a primacy of feedforward control, they differ widely in their functional implications. The most complex forms of feedforward regulation require a host of dedicated cognitive adaptations for planning and mental simulation, and might only make sense in long-lived species with complex social structures such as humans (Barkley 2001). Moreover, the human ability to use language to transmit knowledge about the environment permits vicarious learning on an unprecedented scale, and maximizes the power of self-regulation based on explicit rules and expectations.

While feedforward control may function especially well in predictable environments, it is not necessarily the optimal strategy for all individuals. When harm prevention is a high priority it may be adaptive to shift to feedback strategies, which as a rule are better suited for dealing with unforeseen events—including dangerous ones. Closed-loop strategies sacrifice some of the speed and robustness of open-loop strategies in exchange for enhanced protection from harm. For example, higher female investment in offspring production and parental is expected to select for stronger risk aversion and harm avoidance in females (Archer 2009; Campbell 1999; Cross et al. 2011). As a result, females should have a stronger tendency than males to rely on feedback control strategies even in predictable and comparatively safe contexts.

The superior ability of feedback control to deal with unexpected changes in the environment does not apply only to dangerous events. Closed-loop systems respond quickly to all sorts of novel circumstances, including the emergence of unforeseen *opportunities* (Sih and Del Giudice 2012). While feedforward strategies are more robust, they cannot adjust to unexpected events—regardless of their positive or negative quality—and tend to suppress sensory input that does not conform to predictions (Tops et al. 2010; Tops and Boksem 2010). Thus, an abundance of potential opportunities may tip the balance in favor of feedback strategies even in predictable environments.

Even more generally, feedback control may be adaptive in stable, predictable contexts because it supports systematic learning. As noted by Sih and Del Giudice (2012), feedforward strategies are associated with fast but shallow learning styles; in addition, they make it difficult to update one's cognitive models once they are formed because of their limited self-correction abilities. In contrast, stimulus-driven processes favor slower but more careful and systematic learning, and are associated with increased cognitive and behavioral flexibility—including the ability to quickly unlearn rules and associations that are no longer valid (Coppens et al. 2010). Thus, feedback strategies may be highly adaptive when the task is to learn the structure of a predictable environment with high accuracy and resolution. Once a sophisticated model of the environment has been constructed through feedback-driven exploration (Wolpert and Ghahramani 2000), it can be exploited by feedforward control systems to enable quick and accurate decision making. Developmentally, individuals growing up in predictable contexts may go through an initial phase of predominantly closed-loop regulation and increasingly shift toward open-loop control as they learn and mature.

3.4.3 Delayed Outcomes

In many important domains of behavior, the consequences of an action can only be evaluated at some distant point in the future. Accepting or rejecting a mate, deciding how many offspring to raise, choosing a nest site or a territory, stocking food reserves for the winter—what all these decisions have in common is that their outcomes take a long time to become manifest. When decisions affect subsequent generations, their consequences may even extend beyond the lifespan of a single individual. When outcomes are delayed beyond a certain point, feedback control is simply not an option; while self-correction may be possible in the long term (e.g., building a new nest in the next breeding season), the only viable strategy in the short term is to base actions on feedforward models.

On the face of it, the last statement might seem paradoxical: How can an individual build a model of something it has never experienced before (and may never experience again)? The answer is, *it does not have to*. When fitness-relevant decisions recur over many generations, evolution can be expected to equip organisms with built-in implicit knowledge about the causal structure of the system (see Cosmides and Tooby 1994). Such knowledge can inform model-based planning—thus enabling feedforward behavior control—even in cases where individual learning is difficult or impossible. From another perspective, feedback does not occur at the individual level but rather at the *population* level, as a consequence of natural selection—successful decision rules are retained (as individuals who make good decisions reproduce more) while unsuccessful ones are weeded out. This argument can be generalized to decisions in unstable and/or unpredictable contexts. While unpredictability makes it difficult to build a model of the environment, an organism may still rely on evolved feedforward strategies designed to maximize fitness in unpredictable conditions. As discussed above, such strategies may often involve high levels of impulsivity and risk taking.

3.4.4 Defensive Responses

A final topic to consider is the regulation of defensive responses. Shudo et al. (2003) developed a mathematical model to investigate optimal response strategies to unpredictable danger. In the model, a potentially dangerous event occurs, but assessing the actual severity of the danger takes a certain amount of time. Feedforward strategies are directly triggered by the event and immediately start a ballistic defensive response; in contrast, feedback strategies respond to the *consequences* of the event and adjust the strength of the response to the actual level of danger, thus maximizing control accuracy.

Shudo and colleagues found that optimal response strategies always include a feedforward component. Mixed strategies can be favored if uncertainties in danger estimation are very large and delays in the feedback loop are sufficiently small; however, pure feedback control is never optimal. A similar logic applies to defensive reflexes such as hand retraction or the blink reflex (Sect. 3.3). These results suggest that even individuals who rely on feedback strategies to prevent danger may suddenly switch to feedforward control after a dangerous event has occurred, in order to mount a quick and effective response.

3.5 From Control Strategies to Coping Styles

As detailed in the preceding sections, the trade-offs of behavior control explain both the existence of multiple control systems in the brain and the ability to shift between different strategies in a context- and task-sensitive way. The same trade-offs are likely to underlie the existence of stable individual differences in self-regulation styles. In the biological literature, patterns of individual differences in self-regulation are usually characterized as *coping styles,* as they emerge most reliably in response to stressful challenges involving unpredictable and/or potentially threatening events (Koolhaas et al. 1999).

The basic distinction in the biological literature is that between *reactive* and *proactive* coping styles. Reactive individuals show a primacy of feedback control; they are behaviorally flexible, high in cue dependency, and engage in thorough exploration of novel environments. Reactive individuals also tend to be shy, fearful, nonaggressive, risk-averse, future-oriented, and low in general activity. On the contrary, proactive individuals show a primacy of feedforward control; they are low in cue dependency, show rigid, inflexible behavioral routines, and are quick but superficial explorers. Proactive individuals also tend to be active, bold, aggressive, risk-prone, and impulsive (Coppens et al. 2010; Koolhaas et al. 1999, 2007; Réale et al. 2010; Sih and Del Giudice 2012). Of course, the existence of stable coping styles does not mean that individuals are rigidly tied to a fixed control strategy regardless of the current situation. Instead, contextual and state-dependent variation in control strategies usually coexists with *average* differences in preferred strategy across individuals.

Individual differences in coping styles along the proactive–reactive axis have been documented in a broad range of species, including (but not limited to) primates, pigs, rodents, birds, and fish (see Carere et al. 2010; Koolhaas et al. 1999; Réale et al. 2010). The concept of coping styles overlaps significantly with those of *behavioral syndromes, behavioral types,* and *personality types*. Accordingly, there is a growing tendency to regard those labels as practically synonymous (e.g., Coppens et al. 2010; Sih and Del Giudice 2012; for a different perspective see Uher 2011).

3.5.1 The Evolution of Coping Styles

Why should members of the same population display stable individual differences in coping styles? Evolutionary biology provides several potential answers to this question; here I review some of the most common alternatives (see Wolf et al. 2013, for in-depth discussion). To begin with, small initial differences in individual conditions may be amplified and stabilized by self-reinforcing cycles if conditions and behavior are reciprocally connected. For example, larger individuals of a species could afford to explore more boldly because they are less threatened by predators. Bolder exploration may enable them to find more food, thus becoming even larger, and so on (see Luttbeg and Sih 2010; Sih and Del Giudice 2012).

Alternatively, individual differences may result from *adaptive developmental plasticity* (West-Eberhard 2003; Schlichting and Pigliucci 1998). Developmental plasticity is the ability of an organism to produce distinct phenotypes when exposed to different environments throughout its ontogeny. Since different control strategies are adaptive in different contexts (Sect. 3.4), individuals may have evolved the ability to respond to early cues—for example, cues indicating that the environment is unpredictable, or that adult social competition is going to be especially intense—by adjusting their behavioral phenotype so as to match the predicted environmental conditions. As a result, individuals growing up in different conditions will go on developing different coping styles, possibly in interaction with individual variables such as sex, competitive ability, and so forth.

While developmental plasticity depends on early environmental inputs, there is ample evidence that coping styles also reflect genotypic differences between individuals (reviewed in Carere et al. 2010; van Oers and Sinn 2013). Adaptive genotypic differences can be maintained in a population for a number of distinct reasons. First, the costs and benefits associated with different coping styles may result in the same average fitness (*selective neutrality*). Second, genotypic differences may be maintained by *frequency-dependent selection* if the fitness of a given phenotype depends on its relative abundance in the population relative to other phenotypes. For example, proactive individuals may enjoy high reproductive success when a population is mostly composed of reactive individuals, but *not* when most other members of the population are also proactive. Third, spatial and temporal variation in environmental conditions and the associated selective pressures (*fluctuating selection*) may favor the maintenance of polymorphic alleles (see Del Giudice 2012; Wolf et al. 2013). Studies of bird and mammal populations have provided initial evidence that selection on coping styles does indeed fluctuate across space and time, creating the conditions for the maintenance of adaptive genotypic variation (see Dingemanse and Réale 2013).

Finally, unpredictable environmental fluctuations may favor the evolution of *diversified bet hedging*. In bet-hedging strategies, each individual randomly develops one out of two or more phenotypes through a stochastic "switch" mechanism. Diversified bet hedging spreads the risk of reproductive failure across a genetic lineage, since at least some individuals will end up with a well-matched phenotype regardless of the state of the environment. Specifically, bet hedging reduces average individual fitness in the short term, but enhances the long-term reproductive success of the lineage by decreasing fitness variance across generations (see Starrfelt and Kokko 2012). It should be noted that bet hedging, developmental plasticity, and genotypic variation are not mutually exclusive alternatives; in fact, they can coexist in various combinations and proportions depending on the structure of environmental fluctuations, the costs of plasticity, and other ecological factors (see Wolf et al. 2013).

3.6 A Life History Perspective on Self-Regulation

3.6.1 Life History Strategies

Life history theory is a branch of evolutionary biology dealing with the way organisms allocate time and energy to the various activities that comprise their life cycle (see Ellis et al. 2009; Hill and Kaplan 1999; Kaplan and Gangestad 2005; Stearns 1992). All organisms live in a world of limited resources; for example, the energy that can be extracted from the environment in a given amount of time is intrinsically limited. Time itself is a limited good; the time spent by an organism looking for mates cannot be used to search for food or care for extant offspring. Since all these activities contribute to an organism's evolutionary fitness, devoting time and energy to one will typically involve both benefits and costs, engendering trade-offs between different fitness components. For example, there is a trade-off between bodily growth and reproduction because both require substantial energetic investment, and thus producing offspring reduces somatic growth. Natural selection favors organisms that schedule developmental tasks and activities so as to optimize resource allocation. Different allocation decisions result in different *life history strategies*.

The critical decisions involved in a life history strategy can be summarized by the fundamental trade-offs between *current* and *future reproduction,* between *quality* and *quantity of offspring,* and—in sexual species—between *mating* and *parenting effort* (see Ellis et al. 2009; Kaplan and Gangestad 2005). By delaying reproduction, an organism can accumulate resources and/or "embodied capital" (including skills and knowledge), thus increasing the quality and fitness of future offspring; however, the risk of dying before reproducing increases concomitantly. When reproduction occurs, the choice is between many offspring of lower quality and fewer offspring of higher quality. While intensive parental investment is a powerful way to increase the embodied capital (and long-term prospects) of one's descendants, the fitness gains accrued through parenting must be weighed against the corresponding reduction in mating opportunities.

Different life history strategies solve these problems in different ways by determining how organisms allocate effort among fitness-relevant traits. The same framework can be employed to describe life history differences between species and between individuals of the same species (Réale et al. 2010).

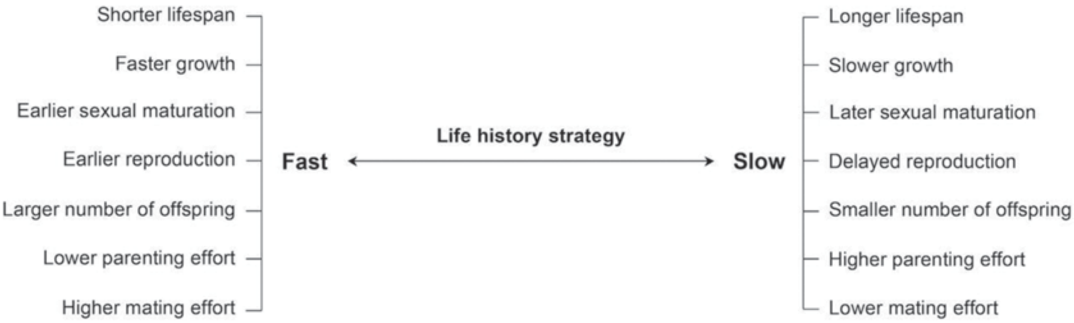

Fig. 3.3 The fast–slow continuum of life history variation

3.6.2 The Fast–Slow Continuum of Life History Variation

Because life history trade-offs are not functionally independent of one another, differences in life history strategies between and within species show a general pattern of trait covariation. Specifically, slow growth and late reproduction correlate with long lifespan, high parental investment, fewer offspring of higher quality, and low juvenile mortality. Conversely, fast growth and early reproduction correlate with high juvenile mortality, short lifespan, larger numbers of offspring, and reduced parental investment in each. This is commonly referred to as the *fast–slow continuum* of life histories (Sæther 1987; see Ellis et al. 2009; Fig. 3.3).

The fast–slow continuum has profound implications for the organization of behavior. A short lifespan, higher mortality, and early reproduction make it optimal to discount future rewards and to favor short-term gains over long-term benefits; future-oriented behavior is only favored in the context of slow strategies. Furthermore, organisms betting on future reproduction must maximize their chances of surviving and remaining healthy. This is best obtained through risk aversion—that is, avoidance of variable rewards in favor of surer outcomes, even at the price of a lower average payoff.

In most organisms, individual life histories are determined by a combination of genetic and environmental factors. Indeed, life history strategies often exhibit a remarkable degree of developmental plasticity. The key dimensions of the environment that affect the development of life history strategies are *resource availability, extrinsic morbidity–mortality,* and *unpredictability,* as signaled by observable cues (see Ellis et al. 2009; Kuzawa and Bragg 2012). Energetic stress causes the developing individual to shift toward a slower life history strategy; this translates into development of a more energy-sparing phenotype, including slower growth, delayed sexual maturation, and low fecundity. Extrinsic morbidity–mortality constitutes external sources of disability and death that are relatively insensitive to the adaptive decisions of the organism. Environmental cues indicating high levels of extrinsic morbidity–mortality cause individuals to develop faster life history strategies. Faster strategies in this context—a context that devalues future reproduction—function to reduce the risk of disability or death prior to reproduction. Moreover, high extrinsic morbidity–mortality means that investing in parental care has quickly diminishing returns, which favors reduced parental investment and offspring quantity over quality.

In addition to average levels of extrinsic morbidity–mortality, unpredictable *variation* in environmental conditions over time and space also regulates life history development. On the timescale of human development, variable and unpredictable contexts tend to entrain faster life history strategies, thus acting in the same direction of environmental harshness (e.g., Belsky et al. 2012; Brumbach et al. 2009; Ellis et al. 2009). In summary, dangerous and unpredictable environments promote the development of fast life history strategies; conversely, safe and predictable environments tend to shift development toward slow life histories.

3.6.3 Life History Strategies and Individual Differences in Self-Regulation

In recent years, it has become apparent that life history theory offers a unifying perspective on individual differences in self-regulation (Del Giudice in press; Kruger et al. 2008; Réale et al. 2010; Sih and Del Giudice 2012; Wolf et al. 2007). The logic of fast life history strategies promotes a focus on current rewards, a steep discounting of the future, and a tendency to take risks (especially in males). As a consequence, individual differences in impulsivity can be expected to overlap to a large degree with the fast–slow continuum of life history variation. This hypothesis is supported by a large amount of data showing that fast life history traits systematically correlate with higher impulsivity, both in humans and nonhuman animals (e.g., Kruger et al. 2008; Réale et al. 2010; Wang et al. 2009; reviewed in Del Giudice in press).

In many nonhuman species, the association between impulsivity and life history strategies extends to individual differences in coping styles. Studies of coping styles in nonhuman animals show that feedforward regulation—characterized by reduced flexibility, low cue dependency, and quick but superficial exploration—is systematically associated with boldness and impulsivity in proactive, fast life history individuals. In contrast, feedback regulation—characterized by increased flexibility, cue dependency, and slow but thorough exploration—clusters with shyness and low impulsivity in reactive, slow life history individuals (Biro and Stamps, 2008; Careau et al. 2009; Carere et al. 2010; Coppens et al. 2010; Koolhaas et al. 1999; Réale et al. 2010). Sih and Del Giudice (2012) recently argued that the association between feedforward regulation, impulsivity, and fast life histories may be explained by a general trade-off between avoiding risk and acquiring larger rewards (the *risk–reward trade-off*). This argument converges with theoretical models advanced by Stamps (2007) and Wolf et al. (2007) in suggesting that basic life history trade-offs may underlie the structure of personality and cognition in nonhuman animals.

While the association between feedforward regulation and impulsivity has been replicated in various species (though with exceptions and qualifications; see Réale et al. 2010), there are reasons to doubt the generality of this pattern, at least where humans are concerned. As discussed in Sect. 2.4, feedforward control can take many forms, ranging from simple and inflexible strategies to complex, highly structured strategies oriented toward long-term goals. My argument is that the association between feedforward regulation and impulsivity described in the animal literature only applies to simpler forms of feedforward control—ballistic responses and rigid, inflexible routines.

Indeed, the more sophisticated forms of deliberate, future-oriented feedforward control are associated almost by definition with *low* impulsivity. The fact that most species do not engage in the kind of long-term planning typical of human adults may explain the apparent consistency of the animal literature, in which impulsivity is almost invariably associated with traits that indicate a primacy of feedforward regulation.

The idea that feedforward control can be associated with both high *and* low impulsivity is both theoretically plausible and consistent with the empirical data. For example, there is considerable evidence that motor inhibition can be achieved through reactive, stimulus-driven processes but also through proactive anticipatory processes; moreover, the two kinds of inhibition rely on partially distinct neural pathways (Aron 2011). In the same vein, Tops et al. (2010) made an important distinction between *proactive impulsivity,* arising from a lack of feedback control on behavior, and *reactive impulsivity,* in which behavior is directly controlled by immediate emotional stimuli (see also Tops and Boksem 2010). In a longitudinal study of executive functions in children, self-restraint in a delay of gratification task—a prototypical measure of future orientation—was associated with higher inhibition and *reduced* shifting ability, the latter being a key correlate of feedforward regulation (see Miyake and Friedman 2012).

In humans, slow life history strategies may often involve a combination of effortful control (low impulsivity) and predominantly feedforward regulation, as indicated by reduced shifting ability and low dependency on immediate cues. Intriguingly, individuals who develop in safe, predictable environments may show an initial primacy of feedback regulation (supporting thorough, systematic learning; Sect. 3.4) followed by a developmental shift toward increased feedforward control. This prediction is consistent with the idea that slow life histories entail higher investment in embodied capital, including accumulation of knowledge and skills.

At the opposite end of the life history continuum, individuals who engage in high-risk behavioral strategies may develop a pattern of impulsivity coupled with relatively inflexible feedforward control. Because the costs and benefits of risk taking differ systematically between the sexes, males should be more likely to develop a bias toward feedforward regulation in response to danger and unpredictability. In line with this prediction, human males consistently display more risk taking than females, even if sex differences in impulsivity are very small (Cross et al. 2011).

In sum, the structure of individual differences in self-regulation is likely more complex than currently acknowledged in the coping styles literature. While simpler forms of feedforward control may be functionally associated with impulsivity and risk taking, feedforward regulation can also be employed in the service of long-term goals and may require high levels of active inhibition. So far, this distinction has not been explored in the animal literature on coping styles; it is therefore unclear whether it only applies to humans or may extend to other species as well.

Conclusion

Self-regulation is a biological property of living organisms, and can only be fully understood in the light of evolution. In this chapter, I approached the topic from a theoretical vantage point, leaving aside the issue of how self-regulatory processes are implemented at the neurobiological level. I started my analysis from the basic concepts of control theory, and showed how the logic of feedback and feedforward control can be combined with insights from evolutionary biology to outline an ecological theory of control strategies. I then discussed how life history theory offers a general framework for understanding individual differences in impulsivity and coping styles, and concluded with a critical examination of the relation between life history strategies and self-regulation in humans. In particular, I argued that, at least in humans, a primacy of feedforward control may be associated not only with fast life history strategies and high levels of impulsivity but also with *slow* life history strategies and high levels of effortful control.

In total, I hope I have shown how an evolutionary perspective can enrich the study of self-regulation by fostering integration across levels of analysis and suggesting new, testable predictions to guide empirical research.

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Self-Regulatory Strength: Neural Mechanisms and Implications for Training

4

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4.1 Introduction

> Exhausted with fatigue…the sailor on a wreck throws himself down to rest. But hardly are his limbs fairly relaxed, when the order "To the pumps!" again sounds in his ears. Shall he, can he, obey it? Is it not better just to let his aching body lie, and let the ship go down if she will? So he lies on, till, with a desperate heave of the will, at last he staggers to his legs, and to his task again.
>
> William James, *The Principles of Psychology* (1890/1950, p. 562)

When considering this sailor's plight, one can easily draw parallels to the common experience of a battered will in the face of life's relentless stream of demands and responsibilities. While human beings possess the capacity to exert self-control in the service of long-term goals, health, and well-being, failure is common and appears in many domains—from eating and drug-seeking behaviors to pathological gambling and infidelity in relationships (Baumeister et al. 1994). In the case of the aforementioned sailor, without "a desperate heave of the will," failure is imminent and probably would mean that he would go down with the ship.

A predominant theory that has yielded many investigations of how and when people experience self-regulation failure is the limited resource or strength model of self-control (Baumeister and Heatherton 1996). The strength model proposes that the capacity to exert self-control draws upon a limited resource that, when reduced, increases the likelihood of giving in to unwanted and often unhealthy behaviors. By this reasoning, the capacity to regulate one's behavior is likened to a muscle, which can become fatigued with overexertion. Following this overexertion, there is a lack of self-regulatory resources that prevents people from carrying out tasks that requires effortful cognitive and attentional control.

Since the strength model was originally proposed, a large body of behavioral work has generated supportive evidence of the model. Specifically, this line of research has identified many instances in which people show a conspicuous lack of self-regulatory strength and resources, what is commonly known as depletion. When people are in a depleted state, they are more likely to experience self-control failure across domains. Despite these established depletion effects, it is still not fully understood how exactly depletion exhausts self-regulatory capacity and

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which attendant cognitive processes are affected. Researchers in social and cognitive neuroscience have begun to tackle this issue by examining putative neural mechanisms for how self-regulatory strength is weakened by depletion, resulting in self-control failure. In doing so, they have begun to identify independent brain markers of the underlying cognitive processes impacted by depletion manipulations.

In this chapter, we first review supporting evidence from behavioral studies for the strength model. These studies have well established the means by which depletion weakens self-regulatory capacity and compromises future attempts at self-control. Next, we review recent investigations of the brain bases of self-regulatory strength and depletion. These investigations have given rise to three neurobiological explanations. The first account focuses on the idea that resource depletion disrupts top-down control processes within the prefrontal cortex (PFC) that are broadly associated with planning and regulation of behavior. A second account suggests that depletion may compromise the self-regulatory capacity through potentiation of the brain's emotion and reward circuitry. The third account draws upon the first two by suggesting that, depending on the demands in a given self-control context, depletion can undermine the regulatory functioning in the PFC, as well as potentiate emotion and reward systems.

We then explore the possibility of whether people can improve their self-regulatory strength and capacity, both in the short and long term by incorporating certain brain markers as an index to track training effects. We conclude with a roadmap suggesting future studies to assess domain-general versus domain-specific accounts of self-regulatory strength, as well as the extent to which training effects might cut across domains.

4.2 Behavioral Studies of Self-Regulatory Strength and Depletion

After the strength model was first proposed in the mid-1990s, experimental psychologists set out to identify the various ways people experience self-regulatory depletion. Among the first, laboratory manipulations of depletion used thought suppression, an act presumably requiring strenuous mental effort. Specifically, Muraven and colleagues (Muraven et al. 1998) found that after participants actively suppressed thoughts about a white bear (see Wegner et al. 1987), they were less likely to persist on a difficult, unsolvable anagrams task. The researchers interpreted this effect as support for the limited resource account of self-regulation failure, with the thought suppression task depleting resources that would otherwise be allocated for persistence in a later task or for resisting the temptation to quit that task. This finding challenges folk theories and self-help programs that instruct people to ignore or suppress undesirable thoughts and emotions.

Other forms of suppression also seem to tap self-regulatory resources. For example, suppressing stereotypes predicts poor task performance on subsequent tasks (Gordijn et al. 2004). Additionally, inhibiting the physical expression of emotions (e.g., stifling one's laughter) also produces reliable depletion effects (Baumeister et al. 1998; Schmeichel et al. 2003; Vohs and Heatherton 2000).

In addition to thought and emotion suppression, there are several other means by which self-regulatory capacity is reduced, compromising future self-control attempts. In the domain of judgment and decision making, Vohs and associates (Vohs et al. 2008) conducted a set of studies revealing that the engaging decision-making processes and making autonomous choices deplete self-regulatory resources. Depletion effects also appear in and impact social behaviors. For example, the act of socially conforming is depleting (Kahan et al. 2003), as is being the target of prejudice (Inzlicht et al. 2006; Johns et al. 2008). As a social perceiver, managing impressions of others is a depleting act (Richeson et al. 2003; Vohs et al. 2005).

By the mid- to late 2000s, researchers across separate labs had implemented multiple methodologies and manipulations to test the strength model of self-regulation. Around that time, Hagger and colleagues (Hagger et al. 2010) carried out a meta-analysis that found that the evidence supported the strength model, and that this model served as the best explanation of depletion effects as compared to other competing models (e.g., motivation-based theories).

In addition to confirming the validity of the strength model over and against other theories, self-control researchers sought to identify physiological substrates of self-regulatory strength and depletion. One prominent body of research has identified circulating levels of blood glucose as a potential biomarker of self-control (Gailliot et al. 2007). As glucose becomes depleted after successive self-control attempts, failure becomes more likely. By this reasoning, ingestion of glucose should reverse the short-term effects of depletion.

Before being implicated in self-regulation, glucose had previously been associated with cognitive benefits and enhancements. For example, early work by Benton et al. (1994) demonstrated that glucose ingestion improved attention and memory (inferred from faster reaction times). More recently, Parent and others (Parent et al. 2011) conducted a careful double-blind study to test the effects of blood glucose (vs. placebo) on memory processes. They found that elevated glucose levels facilitated memory encoding in the hippocampus, and that this was predictive of subsequent episodic recall. Furthermore, Smith and colleagues (Smith et al. 2011) reviewed the literature on ingested glucose's effects on memory and cognitive performance, noting consistent effects across populations (younger and older adults, and those with clinical syndromes that have accompanying cognitive impairment). They also observed that the biggest benefit was in the domain of verbal episodic memory, with glucose enhancing memory in young adults but only in contexts with increased cognitive demands (i.e., dual tasking). Consequently, researchers reasoned that glucose-mediated improvements in memory may appear in self-regulatory attempts following depletion. This glucose account has generated some debate, and interested readers should consult thoughtful rejoinders by Beedie and Lane (2012), Kurzban (2010), and Sanders et al. (2012).

4.3 Proposed Neural Mechanisms Underlying Self-Regulatory Strength and Depletion

Despite these behavioral studies providing ample evidence for the strength model and identifying glucose as a potential biomarker of self-regulatory strength, the underlying neural mechanisms of depletion—namely in terms of how it negatively impacts self-control—remained elusive. Thankfully, with the spatial resolution afforded by modern brain-imaging techniques (e.g., functional magnetic resonance imaging, fMRI), researchers can localize brain regions associated with self-regulatory strength and depletion. In addition to shedding light on general mechanisms, these regions and their activation patterns can serve as markers to help identify those individuals who are especially prone to depletion effects and self-control failure. Moreover, this brain-marker approach to understanding individual differences in self-regulatory strength may help clinicians who aim to develop individualized self-control training programs.

In this section, we consider the following three neural mechanisms of depletion that give rise to strained efforts to exert self-control: (1) compromised executive functioning in PFC, (2) increased impulse strength due to enhanced reward processing, and (3) an interplay between compromised executive functioning and increased impulse strength. These mechanisms can be likened to theories that conceptualize self-control as a struggle between desires and impulses on the one hand, and inhibitory forces on the other (Heatherton and Wagner 2011; Hofmann et al. 2009). Even Freud had a similar idea with his metaphor of the rider and his horse representing the ego and id, respectively (Freud 1923). Accordingly, one can compare the first mechanism (compromised executive functioning) to an incompetent rider, or the second mechanism (increased impulse strength) to a giddy and intractable horse.

4.3.1 Depletion Compromises Executive Functioning

The first mechanism was inspired by social neuroscience research and proposed that the self-regulatory resource that depletion taps and "drains" with repeated use consists of executive functions supported by regions in the PFC, such as the dorsolateral prefrontal cortex (DLPFC) that previously had been implicated in working memory processes. This account assumes that if someone completes a task that places strong processing demands on executive functioning, then performance on a subsequent task that requires self-control will diminish, presumably because both tasks draw from the same "pool" of executive functions. Additionally, the extent to which the first task depletes and weakens executive functioning should predict the magnitude of impaired performance in the second task.

Richeson and colleagues (Richeson et al. 2003) prompted the initial development of this account by conducting an fMRI study in which they measured neural correlates of self-regulatory depletion following a face-to-face interracial exchange (i.e., white participants, black confederates). They identified two regions, DLPFC and anterior cingulate cortex (ACC), that were activated in response to black faces and were correlated with implicit racial bias. Both regions had been linked with dissociable executive functions, with the DLPFC involved in cognitive control and the ACC responsible for detecting conflict between competing neural representations (MacDonald et al. 2000). In addition to DLPFC and ACC activity associated with implicit bias, participants who showed greater recruitment of these two regions also showed more self-regulatory depletion following an interracial exchange—as measured by Stroop interference (Stroop 1935). Richeson and coworkers concluded that the executive functions supported by DLPFC and ACC, presumably due to detecting (ACC) and inhibiting (DLPFC) implicit racial bias, were depleted and not available to be recruited during the Stroop task. In this way, more activation of DLPFC and ACC served as an index of depleted (i.e., non-available) resources and predictive of poorer task performance (i.e., higher Stroop interference; see Richeson et al. 2003, Fig. 3).

More recent studies lend support to this account of executive functions in the PFC serving as a key brain basis of self-regulatory strength and depletion. Hedgcock et al. (2012) conducted an fMRI study to investigate the neural correlates of depletion by testing whether self-regulatory capacity was compromised based on a two-stage model of self-control (Hedgcock et al. 2012). This model characterizes self-control as proceeding first by way of conflict identification (e.g., "This cake is tempting but I have to follow doctor's orders and stick to my diet"), followed by an implementation stage in which a person attempts to regulate behavior (e.g., "I am going to put the cake away and eat something else instead"). As mentioned, there are regions in the PFC that are associated with these two stages: the ACC for conflict identification and DLPFC for implementation, respectively. Hedgcock and colleagues found that participants showed diminished activity in the right middle frontal gyrus (a subregion within DLPFC) after prior exertion of attentional control. They interpreted this reduced DLPFC activity as a likely neural correlate of depletion, potentially indicative of weakened self-regulatory capacity.

In the emotion domain, Wagner and Heatherton (2013) found that participants who became depleted after completing a taxing attention-control task (adapted from Gilbert et al. 1988; Schmeichel et al. 2003) showed diminished communication between the ventromedial prefrontal cortex (VMPFC) and the amygdala upon viewing negatively valenced affective stimuli (Wagner and Heatherton 2013). The depleted group also exhibited greater activity in the amygdala in response to these negative stimuli, and one possible interpretation of this is that without top-down, regulatory "supervision" by the VMPFC, amygdala reactivity becomes exaggerated.

4.3.2 Depletion Increases Impulse Strength

A second account lays out another route by which depletion affects self-regulatory strength. This account claims that whenever a person's capacity to exercise self-control is compromised (e.g., during depletion), a key precipitating factor that leads to failure may be amplified activity associated with bottom-up reward and emotional processing—giving rise to increased impulse strength. Initial behavioral work suggests this possibility. Schmeichel and others (Schmeichel et al. 2010) conducted a set of studies revealing that the exercise of self-control increases approach motivation and attention to rewarding stimuli. More recently, Vohs and colleagues (Vohs et al. 2012) conducted a comprehensive set of field and in-lab studies showing that prior exertions of self-control led to heightened subjective feelings of emotion and desire. The authors claimed that depletion causes a broad shift in cognitive processing, from chronic monitoring and restraint-based processing to more evaluative processing, in turn weakening self-regulatory capacity. In fact, this seems to be a prevalent phenomenon that people experience in daily life (Hofmann et al. 2012).

Taken together, these findings allowed social brain scientists to make predictions about post-depletion neural activity in response to rewarding sensory cues, especially in populations that are more prone to depletion effects. For example, those who chronically restrain their eating tend to overeat when in a depleted state (Hofmann et al. 2007; Vohs and Heatherton 2000), but it remained unclear as to how depletion changed dieters' processing of food cues so as to drive overconsumption.

In recent neuroimaging work, Wagner and colleagues (Wagner et al. 2013) sought to address this issue by investigating the effects of depletion on neural responses to appetizing food images in dieters. They found that depletion affected the brain's reward and value systems, as indicated by increased activation in the orbitofrontal cortex (OFC), which has reciprocal connections with subcortical reward-related regions, namely the ventral striatum (Wagner et al. 2011).

This heightened reward activity that dieters show when depleted may also drive approach behaviors and bias eating decisions. Lopez and colleagues (Lopez et al. submitted) found that dieters showed a marked bias in their computer mouse trajectories during a food preferences task that was specific to appetitive, unhealthy foods. This bias was characterized by direct trajectories when dieters chose unhealthy foods and more curved trajectories towards unhealthy foods when healthy foods were chosen—presumably indicative of partial attraction to those unhealthy foods (cf. Spivey and Dale 2006).

Taken together, all of these findings converge on the idea that an important feature of self-regulatory depletion is an increase in reward value and impulse strength. Such an increase supports recent work by Vohs and colleagues (Vohs et al. 2012) showing that depletion leads to a global shift in evaluative processing and attendant increases in desire and impulse strength.

4.3.3 Depletion Affects both Executive Functioning and Impulse Strength

A third account proposes that in some instances, depletion may impact both bottom-up emotion and reward systems as well as top-down control processes. In their balance model, Heatherton and Wagner (2011) suggest that self-regulation failure occurs whenever the balance is "tipped" in favor of those brain areas associated with emotion and reward processing (Heatherton and Wagner 2011). As Heatherton and Wagner argue, this can happen in a bottom-up fashion, such as during exposure to tempting cues (for eating, see Jansen 1998), but it can also happen when functions associated with regulating thoughts and behavior are temporarily impaired, such as during alcohol consumption (Volkow et al. 2008).

For instance, Wagner and associates (in press) reported findings that might best be conceptualized as a "broken link" of communication between inferior frontal gyrus (IFG; an area associated with self-control of motor behaviors, Aron et al. 2004) and two reward-related regions, OFC and ventral striatum, during exposure to food cues. This broken link implies that monitoring and control functions in the PFC may no longer reach brain regions associated with reward, allowing evaluative processing to take over and drive up the intensity of an impulse (cf. Vohs et al. 2012). This broken link has also been observed in the emotion domain. Wagner and Heatherton (2013) found that, following depletion, there was a different pattern of communication between PFC and the amygdala (a key region involved in emotion processing; Wagner and Heatherton 2013).

Additional studies are needed to investigate how prefrontal regions communicate and connect with emotion and reward systems, and how individual differences in this connectivity might predict self-control success (and/or failure). Even so, the evidence coming in thus far suggests that a brain-based account of self-regulatory strength and depletion likely implicates both bottom-up processing of appetitive and affective stimuli (which may give rise to increased subjective feelings of desire and impulse strength; e.g., Vohs et al. 2012; Wagner and Heatherton 2013) and top-down control processes in the PFC (e.g., Hedgcock et al. 2012). Indeed, future behavioral and neuroimaging investigations may benefit from studying the interplay between these rapid, reward-related responses and more effortful, regulatory processes (e.g., see iterative reprocessing model in Cunningham and Zelazo 2007; Wiers et al. 2013). And while we have presented these mechanisms separately for explanatory purposes, we believe all three are valid since they describe likely routes by which depletion can weaken one's capacity to exert self-control.

4.4 Improving Self-Regulatory Strength in the Short and Long Term

In addition to identifying the neural underpinnings of self-regulatory strength and the instances in which people succeed and fail in their self-control attempts, it is equally, if not more, important to consider whether the capacity to self-regulate can be improved. And if this is possible, then there should be identifiable neurobiological markers that index improvement.

As we discussed earlier in this chapter, glucose has been proposed as a possible biomarker of self-regulatory strength, which may be used to index training effects. As mentioned before, the glucose account has been challenged, with some citing the metabolic properties of how the brain consumes glucose (Kurzban 2010). Others have claimed that merely rinsing with carbohydrates is sufficient to reverse depletion effects and propose that the act of rinsing triggers striatal dopamine pathways and signals future, anticipated reward (Kringelbach 2004; Molden et al. 2012). Neuroimaging techniques are well suited to identify the precise neural mechanisms underlying these reversal effects, especially as to whether glucose ingestion (versus rinsing) differentially affects activity in subcortical reward systems and/or regulatory regions in PFC. Positron emission tomography (PET) in particular may be useful to test whether glucose metabolism increases during depletion and predicts subsequent self-control failure (see Heatherton and Wagner 2011, Box 2). Unlike fMRI, which measures blood-flow dynamics in terms of how the brain utilizes oxygen, PET detects and measures radiopharmaceuticals that emit positrons as they circulate in the blood stream and brain. These chemicals act as markers of brain metabolism, with the amount of a marker's uptake indicative of the metabolic demands from nearby brain regions. One of these chemical markers commonly used in PET is flurodeoxyglucose (18 F), which means that the use of glucose-PET methods could determine if certain brain regions show especially high glucose uptake in the context of a depleting task (vs. a baseline task), and whether this uptake is a reliable marker of depletion and self-control failure.

An additional body of research has considered biological markers of self-regulation in the peripheral nervous system that may serve as targets of improving self-regulatory strength in the short term. For example, with PFC implicated in successful self-control, and since subregions within PFC have been shown to regulate autonomic nervous system (ANS) activity (Groenewegen and Uylings 2000), investigators have measured

ANS-specific processes in self-regulatory contexts.

Segerstrom and Nes (2007) collected heart rate variability (HRV) data while participants were instructed to eat certain foods and refrain from eating others. The group that had to exert the most self-regulatory effort (i.e., eat carrots in the presence of chocolate and cookies) showed the greatest HRV compared to the other groups who did not need to engage in self-control. Participants with higher baseline HRV also tended to persist longer in a subsequent anagrams task. From these findings, Segerstrom and Nes concluded that HRV can serve as a valid physiological marker of self-regulatory strength. The implication is that current/state-based HRV serves as an index of available self-regulatory capacity at the moment, while more tonic/trait-based HRV might predict successful self-control across multiple attempts and contexts.

Another important line of work has utilized other cardiac-related measures as independent biomarkers of effort during tasks with varying difficulty. Gendolla and Richter (2010) review studies showing that cardiac reactivity changes in response to self-involvement and task difficulty. These two factors are undoubtedly present and relevant in self-control contexts since these situations require active monitoring of one's own behavior (self-involvement) and place strong demands on self-regulatory strength (task difficulty). Moreover, these cardiac reactivity effects have been documented using multiple measures and across task domains. For example, preinjection period and systolic blood pressure track with difficulty of a memory task (Richter et al. 2008), and prior exertion during a difficult arithmetic task leads to depletion effects as measured by several cardiovascular responses (Wright et al. 2003). Wright and colleagues (2008) extended this finding, showing that blood pressure was modulated by the level of mental fatigue, both for a regulatory task that required response inhibition (i.e., a Stroop task) and a nonregulatory (arithmetic) task (Wright et al. 2008)—supporting the idea that these cardiovascular biomarkers are domain general and therefore relevant in self-regulatory task settings. In this volume, Gendolla and Silvestrini summarize more recent empirical work highlighting the role of motivational processes and their automatic effects on physiological activity (e.g., preinjection period) and task performance.

Collectively, these cardiovascular effects are consistent with the idea that PFC activity—in of itself a likely brain marker of self-control—modulates downstream autonomic activity in the periphery. But future studies should confirm this by employing multi-method paradigms (e.g., electroencephalography (EEG) coupled with recording cardiac reactivity) to identify central–peripheral nervous system interactions, specifically in self-regulatory contexts.

The studies discussed so far in this section highlight physiological correlates of self-regulatory strength and how they might be used as a barometer by which individuals can monitor and potentially improve their self-control on a moment-by-moment basis. These correlates consist of peripheral nervous system processes that become active when people flexibly exert self-control in response to contextual and task-based features. This knowledge is critical for our understanding of the biological substrates of self-regulatory strength, but whether tonic self-regulatory strength can be trained and increased over time is another crucial question. Indeed, this question may hold the most clinical import in populations for whom self-control failure is the norm rather than the exception.

Initial behavioral investigations of self-control training have yielded some promising effects in multiple domains. Muraven (2010) found that smokers who practiced self-control (either by avoiding tempting foods or squeezing a handgrip) for 2 weeks prior to quitting smoking showed higher abstinent rates and were less likely to relapse (Muraven 2010). Also in the smoking domain, Kober and colleagues (Kober et al. 2010) trained smokers to implement a self-control strategy that consisted of focusing on the long-term, negative health consequences of smoking. This strategy was effective in reducing the craving for cigarettes, and an fMRI study by the same group identified a neural mechanism (i.e., a pathway between the PFC and the ventral striatum) that underlies regulation of craving (Kober et al. 2010).

Another study by Hui and others (Hui et al. 2009) administered a training protocol consisting of a Stroop task and mouthwash rinse task, both of which require exercising inhibitory control. Those who completed this training (compared to weak and no training groups) performed better at in-laboratory self-control tasks and engaged in more frequent health behaviors in daily life (e.g., dental care and hygiene). Another study applied self-control training to the regulation of aggressive behaviors (Denson et al. 2011). In this case, the training protocol consisted of a manual regulation task in which participants were instructed to use their nondominant hand in a number of common, everyday activities (e.g., teeth brushing, opening doors, etc.). This training was effective in reducing aggression, specifically among those with high levels of trait aggression. Presumably, this subset would be most amenable to training, since they had the relatively weakest (trait-level) self-regulatory strength to begin with and therefore could show the greatest improvement in self-control.

These findings across behavioral domains are consistent with Baumeister and Heatherton's (1996) strength model of self-control, in that these training effects reflect self-regulatory capacity that can be strengthened with repeated use and practice over longer time intervals (this strengthening is to be distinguished from short-term self-regulatory fatigue; Baumeister and Heatherton 1996, p. 3). While these effects are encouraging and suggest that people can indeed improve their self-control of a wide range of behaviors, less is known about the neurobiological substrates of training, especially the following: which brain regions support successful self-control, whether these regions undergo structural and/or functional changes during training, and the extent to which these changes may persist over time.

First, it is important to consider whether there are reliable brain regions that are linked with successful self-control, since these regions would most likely be indices of self-regulatory capacity as it improves during training. In a neuroimaging study, Berkman et al. (2011) investigated the neural predictors of self-control of smoking by measuring event-related activity during a go/no-go response inhibition task and then had participants report on their daily smoking behaviors for several weeks following initial fMRI scan. They found that the IFG moderated the relationship between reported craving and subsequent smoking in everyday life, such that greater IFG recruitment in the no-go versus go task attenuated the relationship between craving and subsequent smoking (see Fig. 4 in Berkman et al. 2011). The authors interpret these findings as evidence for neural markers of self-regulatory capacity, since greater activation predicted successful control of craving that led to decreased smoking.

This study's methodology represents a recent development in how researchers analyze neuroimaging data (termed the "brain-as-predictor" approach; Berkman and Falk 2013), which treats brain activation as an independent variable within a model to predict behavioral outcomes of interest (Bandettini 2009; Berkman and Falk 2013). A recent study that also used this approach found that IFG activity associated with successful response inhibition modulated resistance to food desires in everyday life (Lopez et al. In Press). Not surprisingly, participants who resisted the desire to eat frequently gave in to temptations to eat, but critically those participants who showed greater IFG recruitment while inhibiting prepotent responses in a go/no-go task were even less likely to act upon their impulses to eat. The study's authors interpreted this finding as possibly indicative of a state–trait interaction, with successful self-control most likely when participants actively resisted desires in the moment (state) and showed overall higher IFG recruitment (trait) associated with response inhibition.

These two studies, which predicted outcomes in different behavioral domains, both identified inhibition-related IFG activity as a crucial individual difference supporting self-control success in daily life. The fact that IFG has been implicated in regulating smoking and eating behaviors represents preliminary evidence for a brain-based model of training self-control proposed by Berkman et al. (2012). Their model builds on the strength model of self-regulation and makes the prediction that an intervention intended to increase self-regulatory strength (or inhibitory control) in one domain (e.g., motor control) should show transfer effects in other domains, such as emotion regulation. For example, if people were trained to increase their motor control via a standard response inhibition task, then they should show improvements in their working memory capacity and/or ability to control their emotions.

This is in line with a key tenet of the strength model, namely that self-regulatory capacity draws from a domain-general resource that impacts many types of behavior. With regard to the two studies discussed above, the IFG may be an appropriate neural target of self-control training. And even though the IFG might activate most robustly during inhibitory control tasks, these tasks can be the primary component of a training regimen for improving self-control of a wide range of behaviors. That is, while "cold," cognitive control is being trained up, training effects may translate to the domain of "hotter," appetitive and addictive behaviors like eating, smoking, and drug use. From this line of reasoning, an outstanding question arises: For those individuals who do not tend to activate IFG during a response inhibition task, can training facilitate and increase IFG recruitment? Moreover, would such increases predict successful outcomes during, for instance, the control of food or drug cravings?

Thus far, empirical forays into the neural correlates of successful self-control have converged on the PFC, specifically the IFG, as being a reasonable target of self-control training. Given how important self-control is for life outcomes (e.g., Mischel et al. 1988) and its special role in theories of the self (Higgins 1996), however, it seems likely that there are multiple, diverse brain regions that support self-control—and therefore would be implicated in self-control training. For example, research by Hare and associates (Hare et al. 2009; Hare et al. 2011) has shown that the VMPFC is a key player in evaluative processing, with increased VMPFC activity associated with poorer self-control. With this in mind, the VMPFC may also serve as a neural marker of self-control training regions.

4.5 Final Considerations for Improving Self-Regulatory Strength

The prospect of improving people's self-regulatory strength, whether in the short or long term, should be grounded in brain-based accounts. These accounts make specific predictions about how depletion alters cognitive processing and impacts self-regulatory strength. Accordingly, we sketch out some final avenues of research that we believe will be particularly fruitful as the social brain sciences continue to mature throughout the twenty-first century.

First, we propose that future studies should ultimately aim to categorize subpopulations of individuals who experience repeated self-regulation failure but by different means. That is, by employing various neuroimaging techniques, researchers can identify those for whom self-regulation failure is triggered by (1) higher reward sensitivity and/or impulse strength generated by emotion and reward systems, (2) impaired functioning in the PFC, or (3) disconnection between prefrontal areas and emotion and reward systems. These three scenarios correspond to the routes by which depletion compromises self-regulatory capacity and precipitates failure we have discussed throughout this chapter. For example, for those with impaired top-down functioning, a training regimen consisting of multiple sessions of inhibitory control practice might be appropriate. Or, in the case of someone who is hypersensitive to cues that signal reward and subsequently experiences overwhelmingly strong impulse strength, an intervention that involves an implicit learning or reconditioning task might make the most sense.

Another promising line of research that we hope will develop further is the brain-as-predictor approach (Berkman and Falk 2013). Specifically, we believe that state–trait interactions in populations that are prone to self-regulation failure should be explored to determine whether there are reliable neural predictors of failure in everyday life (e.g., post-depletion reward activity in dieters; Wagner et al. 2013).

Conclusion

Science has begun to uncover the brain bases of human beings' remarkable but precarious capacity to regulate thoughts, emotions, and behaviors. This capacity has undoubtedly been paramount to the continued survival of our species. In fact, some have theorized that evolutionary pressures in the past selected for neural systems that utilized and expended energy to give rise to a stable sense of self, as well as flexible cognitive processes that allowed for self-regulation of behavior to adhere to group norms and preserve one's standing within a group (Baumeister et al. 2007; Heatherton 2011). With the advent of modern neuroimaging, scientists now have the opportunity to observe the live workings of the brain—not only as people attempt to exercise this self-regulatory capacity but also when this capacity is taxed and weakened by depletion.

We offered perspectives on how and why brain-imaging studies can extend and inform behavioral studies of self-control. One major aim of brain studies will be to provide independent markers of the depleting effects of engaging in self-control. We reviewed three neural accounts of self-regulatory depletion, and then we considered potential ways that self-regulatory strength can be improved, in both the short run with several physiological indices of interest and the long run, where we hypothesized that brain systems might be amenable to change following self-control training.

Brain science offers new perspectives on an old and perplexing problem—why is it so easy to fail at self-control? And why are some people more likely to fail at self-control than others? We have little doubt that investigations of the neural mechanisms of self-regulation will continue, as more methodologically sophisticated, interdisciplinary work takes place across the social brain sciences and continues to illuminate the neurobiological mechanisms that govern behavior.

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The Muscle Metaphor in Self-Regulation in the Light of Current Theorizing on Muscle Physiology

5

Michael Richter and Joséphine Stanek

5.1 Introduction

In the last two decades, the strength model of self-regulation or self-control, respectively, (e.g., Baumeister 2002; Baumeister et al. 2000, 2007; see also Lopez et al. in press) has exerted a considerable impact on self-regulation research and theorizing. The model conceptualizes self-regulation as the capacity to alter one's own behavior (e.g., Baumeister 2002; Baumeister and Vohs 2007) and postulates that controlling behavior (for instance, overriding a habitual response) requires resources or energy, respectively. Resources that are mobilized to regulate behavior are supposed to be consumed in the regulation process and need to be restored. According to the strength model of self-regulation, all kinds of self-regulatory activity draw on the same resources. Performing a self-regulatory action should thus reduce the amount of resources that are available for subsequent self-regulation. Given that the model predicts that self-regulation efficiency is a direct function of the amount of available resources, performing a task that requires self-regulation should lead to decreased performance in subsequent tasks that rely on self-regulation. This effect is called ego-depletion effect and most of the empirical work on the strength model of self-regulation has focused on it (see Hagger et al. 2010, for a recent review of the empirical research on ego depletion).

When presenting the strength model of self-regulation, authors have repeatedly likened self-regulation to muscle activity arguing that self-regulation resembles a muscle—the muscle metaphor. The ego-depletion effect should resemble muscle fatigue—the decrease in muscle performance after sustained physical exercise that is restored after rest. Self-regulation and muscle activity should both require energy resources, and the depletion of these resources should underlie both the ego-depletion effect and muscle fatigue. The strength model of self-regulation also claims that self-regulation can be trained and strengthened like a muscle. Repeatedly performing self-regulatory tasks should lead to higher self-regulation capacities and better performance in tasks that require self-regulation.

In this chapter, we will take a closer look at the physiological foundation of the muscle metaphor. After an introduction to muscle functioning, we will discuss the two key elements of the muscle metaphor. We will elaborate on resource depletion as the cause of muscle fatigue, and we will discuss training effects on muscle strength.

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We will show that the muscle metaphor relies on a simplistic concept of the muscle that does not adequately reflect the current state of research and theorizing in muscle physiology. We will also elaborate on how self-regulation research and theorizing may benefit from the physiological research on muscle work.

5.2 Muscle Work

5.2.1 Muscle Structure

Skeletal muscles contain bundles of parallel muscle cells, the muscle fibers.[1] Muscle fibers are mainly composed of cylindric myofibrils that extend the entire fiber length. Each myofibril is surrounded by a sarcoplasmic reticulum and consists of order arrangements of the proteins actin and myosin as well as other proteins that have a structural function or are involved in muscle action. The proteins form sarcomeres that lie in series and constitute the basic contractile unit of the muscle (see Fig. 5.1 for a schematic representation of muscle composition). Each sarcomere is limited by two sheets of structural proteins (Z proteins) running transversely across the fiber (Z line). Thin myofilaments composed of two helically coiled actin filaments and attached tropomyosin and troponin molecules project at right angles from the Z lines towards the sarcomere center. Thick myosin filaments lie in the center of the sarcomere paralleling the actin myofilaments. Actin and myosin filaments overlap but at rest the actin filaments do not reach the central region of the myosin filaments. Actin and myosin filaments build a hexagonal structure so that each myosin myofilament is surrounded by six actin filaments and each actin element is surrounded by three myosin filaments. The myosin molecules consist of a long tail and a globular head that projects towards the actin filaments. Both the myosin heads and the actin filaments contain binding sites for one another, but at rest the myosin–actin binding is prevented by tropomyosin and a troponin subunit (troponin-I) that block the binding site on actin (see Fig. 5.2).

5.2.2 Muscle Contraction

Muscles are innervated by alpha motor neurons originating from the central nervous system. Each alpha motor neuron innervates many muscle fibers. The electrical stimulation of the motor neuron causes an action potential at all innervated muscle fibers. The generated action potential propagates over the sarcolemma and enters into the muscle cell via a system of transverse tubules. The transverse tubules system is linked to the sarcoplasmic reticulum—the cell's store of calcium ions (Ca^{2+}). An action potential that is spread by the transverse tubules systems leads the sarcoplasmic reticulum to release the stored Ca^{2+} into the cytoplasm. The released Ca^{2+} binds to a troponin subunit (troponin-C) causing a structural change of tropomyosin that exposes the myosin-binding site on actin. Given that myosin–actin binding is no longer prevented, the myosin head attaches to actin and pivots. This "power stroke" causes a sliding of the actin filament towards the center of the sarcomere. Figure 5.3 displays this process.

In the default state—when myosin–actin binding is prevented by troponin-I—adenosine diphosphate (ADP) and inorganic phosphate (P_i) are bound to the myosin head. When the myosin head connects to actin—building a so-called cross-bridge—both are removed. After its power stroke, the myosin head stays connected to actin until the binding of adenosine triphosphate (ATP) to the myosin head causes another structural change that separates the myosin head from actin. The enzyme myosin ATPase then splits ATP to ADP and P_i that remain connected to the myosin head. The energy that is made available by this ATP hydrolysis is transferred to the myosin head causing the head to pivot back into its resting state. The sequence described above is called cross-bridge cycling and continues as long as Ca^{2+} binds to troponin-C—removing the blocking of myosin–actin binding—and as long

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[1] Good general introductions to muscle physiology can be found in Brooks et al. (2005), McArdle et al. (2010), Scott (2008), Sahlin et al. (1998), Sherwood (2010), or Westerblad et al. (2010).

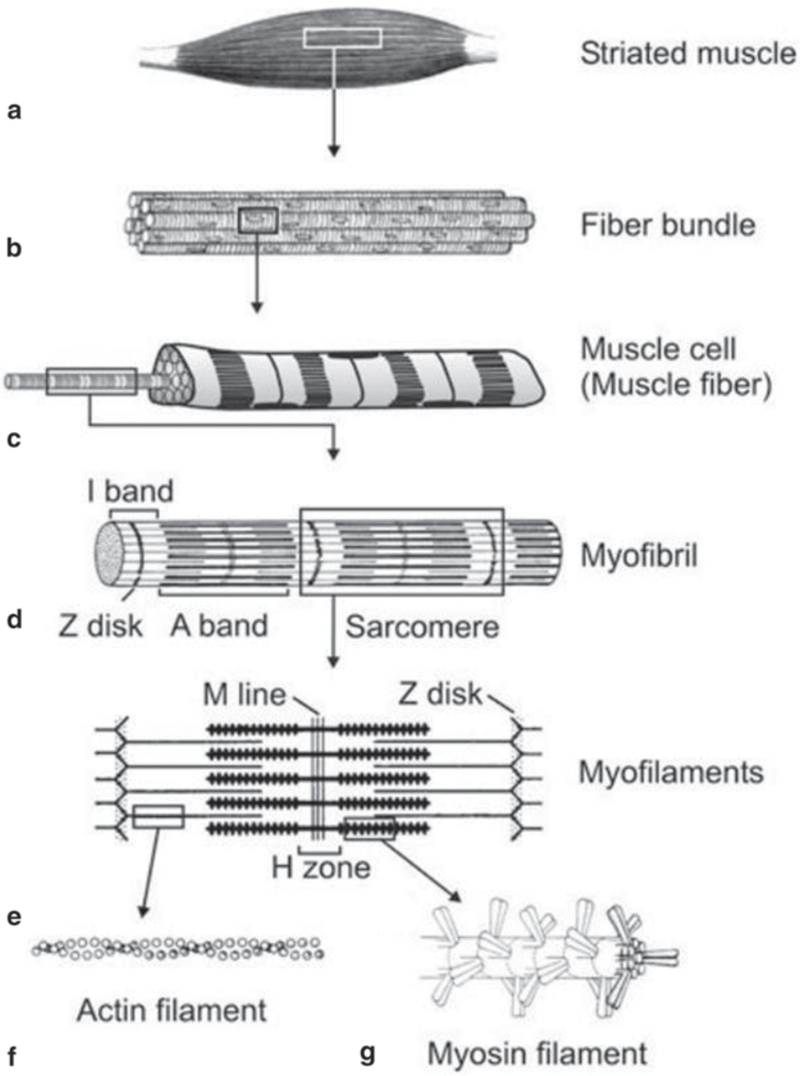

Fig. 5.1 Composition of skeletal muscle tissue. (From Functional anatomy of muscle: Muscle, nociceptors and afferent fibers by S. Mense, 2010, published in *Muscle pain: Understanding the mechanisms* by S. Mense and R.D. Gerwin, pp. 17–48. Copyright by Springer. Reprinted with permission)

as there is enough ATP to disconnect myosin and actin. The shortening of the sarcomeres caused by the repetitive cycling of myosin heads shortens the muscle fiber and creates force.

The membrane of the sarcoplasmic reticulum contains ATP-driven Ca^{2+} pumps that continuously pump Ca^{2+} from the cytoplasm into the sarcoplasmic reticulum. When the stimulation of the muscle ceases, that is, when there are no longer action potentials that lead the sarcoplasmic reticulum to release Ca^{2+} into the cytoplasm, cytoplasmic Ca^{2+} concentration quickly drops due to the activity of the pump. Due to the low cytoplasmic Ca^{2+} concentration, Ca^{2+} no longer binds to troponin-C and the tropomyosin–troponin complex changes back to its initial configuration blocking the myosin-binding site on actin. Given that myosin heads can no longer connect to actin, muscle contraction ends.

5.2.3 Energy Metabolism

ATP is the immediate energy source of muscle contraction; that is, it is the only energy source that muscle cells can directly use for contraction.

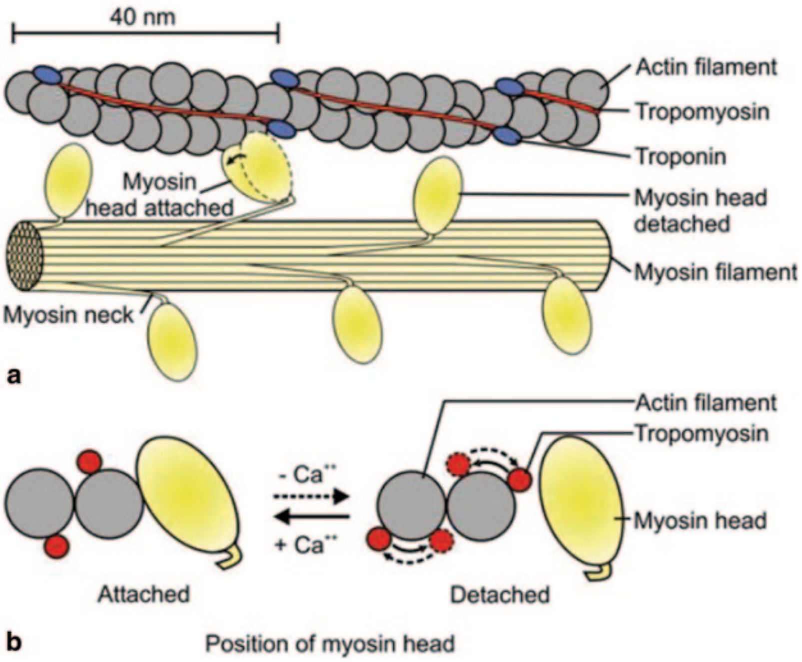

Fig. 5.2 Actin–myosin interaction. (From Functional anatomy of muscle: Muscle, nociceptors and afferent fibers by S. Mense, 2010, published in *Muscle pain: Understanding the mechanisms* by S. Mense and R. D. Gerwin, pp. 17–48. Copyright by Springer. Reprinted with permission)

Other energy-rich compounds (e.g., glucose, fatty acids) need to be broken down and their energy needs to be transferred to ATP before it is available to muscle cells. In skeletal muscle fibers, ATP is mainly used for cross-bridge cycling, pumping Ca^{2+} back into the sarcoplasmic reticulum, and the activity of the Na^+–K^+ pump that restores the cell's resting membrane potential after an action potential (e.g., Homsher 1987; Kushmerick 1983). ATP is stored in muscle cells and releases energy when hydrolyzed by the enzyme adenosine triphosphatase (ATPase) to ADP and P_i ($ATP + H_2O \leftrightarrow ADP + P_i + H^+ +$ energy + heat). Given that the amount of stored ATP is low—it would enable only a maximal contraction for one or two seconds—ATP has to be continuously restored. Three buffer systems—the phosphagen system, glycolysis, and oxidative phosphorylation—continuously resynthesize ATP to prevent ATP depletion. The buffer systems differ regarding the rate of ATP resynthesis and the total amount of ATP that they can produce. All three systems contribute to ATP resynthesis, but their relative importance varies with the duration and intensity of exercise (e.g., McArdle et al. 2010). At the onset of high-intensity exercise, most ATP comes from the phosphagen system, whereas glycolysis is the major source of ATP after approximately 30 s of exercise. After a minute of exercise, most ATP stems from oxidative phosphorylation.

5.2.3.1 The Phosphagen System

The phosphagen system constitutes the fastest way to resynthesize ATP (it may produce approximately 2.6 mmol s^{-1} kg^{-1} of ATP, Greenhaff et al. 2004). It comprises three main reactions. The creatine kinase reaction produces ATP by converting phosphocreatine (PCr), adenosine diphosphate (ADP), and a proton (H+) to ATP and creatine (Cr). The adenylate kinase reaction also resynthesizes ATP. It converts two ADP molecules to one ATP and one adenosine monophosphate (AMP) molecule. While the adenylate kinase reaction produces ATP, the amount of restored ATP is low compared to other sources of ATP resynthesis. The reaction plays a major role in removing ADP to keep the ATP/ADP ratio high, which is essential for ATP hydrolysis. Moreover, the produced AMP stimulates glycolysis by activating enzymes that are crucial for the rate of glycolysis. The third phosphagen reac-

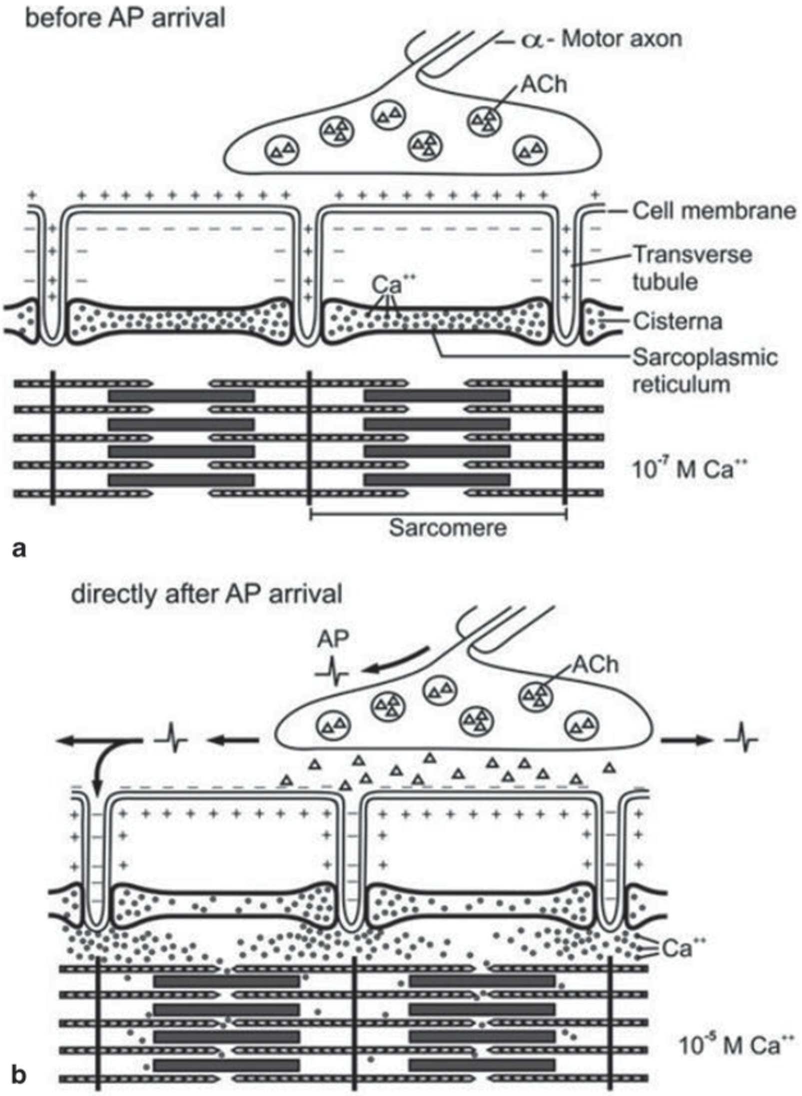

Fig. 5.3 Excitation–contraction coupling. (From Functional anatomy of muscle: Muscle, nociceptors and afferent fibers by S. Mense, 2010, published in *Muscle pain: Understanding the mechanisms* by S. Mense and R. D. Gerwin, pp. 17–48. Copyright by Springer. Reprinted with permission)

tion, the AMP deaminase reaction, does not produce ATP. It converts AMP and H_2O to ammonia (NH3) and inosine monophosphate (IMP). The AMP deaminase reaction removes AMP, which speeds up the adenylate kinase reaction and restores by this means a high ATP/ADP ratio. The phosphagen system—mainly the creatine kinase reaction—enables the muscle to rapidly regenerate a high amount of ATP. However, the amount of PCr stored in muscle fibers is relatively low and would only last for a contraction of a couple of seconds if it was the only source of ATP regeneration.

5.2.3.2 Anaerobic Glycolysis

Anaerobic glycolysis provides a second way to regenerate ATP. Its ATP turnover rate (approximately 1.4 mmol s^{-1} kg^{-1} of ATP, Greenhaff et al. 2004) is lower than that of the phosphagen system but higher than the turnover rate of oxidative phosphorylation. During glycolysis, blood glucose and muscle glycogen—glycogen is the stored form of glucose—are broken down to pyruvate yielding two molecules of ATP per molecule of glucose. Pyruvate is a substrate for oxidative phosphorylation. However, mitochondria need oxygen to produce ATP from pyruvate.

If pyruvate production exceeds the capacity of the mitochondria to take up pyruvate, pyruvate is transformed to lactate via the lactate dehydrogenase reaction (pyruvate + NADH + H+ ↔ lactate + NAD+). This prevents the accumulation of pyruvate, which would inhibit glycolysis. The production of lactate also helps glycolysis by regenerating NAD+, which is an essential substrate for glycolysis. Lactate production also delays metabolic acidosis—a potential cause of muscle fatigue—by contributing to metabolic proton buffering (e.g., Tiidus et al. 2012).

5.2.3.3 Oxidative Phosphorylation

Oxidative phosphorylation (synonyms are cellular oxidation, mitochondrial respiration) refers to the mitochondrial regeneration of ATP from macronutrients like carbohydrates, fat, or amino acids. Three major steps are involved in this process. First, the fuel molecules are broken down to acetyl-CoA. Second, acetyl-CoA is degraded in the citric acid cycle (synonyms are tricarboxylic acid cycle or Krebs cycle) in several steps. In this process, electrons in the form of hydrogen atoms are transferred from the substrates to coenzymes (nicotinamide adenine dinucleotide, NAD+, and flavin adenine dinucleotide, FAD) resulting in the generation of CO_2. Third, the electrons are transferred from the reduced coenzymes (NADH and $FADH_2$) to oxygen in the electron transport chain. This releases energy that is used to regenerate ATP from ADP and P_i.

In the oxidative phosphorylation of glucose (and glycogen), glucose is first broken down in anaerobic glycolysis to pyruvate that then enters the mitochondria where it is converted to acetyl-CoA. The complete oxidation of carbohydrates is relatively slow (e.g., approximately 0.68 mmol s^{-1} kg^{-1} of ATP for muscle glycogen, Greenhaff et al. 2004), but it is more efficient than anaerobic glycolysis (it produces 32 molecules of ATP per glucose molecule). The energy that the stored carbohydrates can provide (approximately 2000 kCal) exceeds the energy that is available from the phosphagen system. The largest source of potential energy (between 50.000 and 100.000 kCal) constitutes triaglycerols, stored fat. Most triaglycerol is stored in adipose tissue and can be hydrolyzed to yield one glycerol molecule and three fatty-acid molecules. Glycerol and fatty acids are transported in the blood to the muscle where glycerol serves as substrate for glycolysis to generate pyruvate that is converted to acetyl-CoA. Fatty acids are transformed in the mitochondria to acetyl-CoA in a process called beta-oxidation. Acetyl-CoA then enters the citric acid cycle to produce ATP as described above. The regeneration of ATP via oxidative phosphorylation of triaglycerol is very slow (0.24 mmol s^{-1} kg^{-1} of ATP for fatty acids, Greenhaff et al. 2004), but one molecule of triaglycerol may produce 460 molecules of ATP (19 ATP from glycerol breakdown, 441 ATP from the fatty-acid molecules). Amino acids only play a significant role in exercise exceeding 1 h (e.g., Poortmans 2004). In long-lasting exercise, they may provide up to 6 % of the total expended energy. Amino acids contribute to ATP regeneration by serving as intermediates in the citric acid cycle or by being converted to pyruvate or acetyl-CoA. The specific metabolic pathways as well as the amount of regenerated ATP depend on the type of amino acid.

5.3 The Muscle Metaphor

5.3.1 Resource Depletion as a Cause of Muscle Fatigue

We will now take a closer look on how the muscle metaphor fits with the mechanisms described above. One key element of the muscle metaphor is that both muscle fatigue and decreased self-regulation efficiency are supposed to result from the depletion of energy resources. The muscle metaphor thus suggests that the decline in muscle performance after sustained exercise is due to a lack of energy. Given that ATP is the direct source of energy for muscle contraction, one might wonder if ATP depletion is the cause of muscle fatigue.

Empirical studies provided mixed evidence for this hypothesis. Some studies found no decrease in ATP concentration even if maximal muscle force was considerably reduced (e.g., Allen et al. 2002; Baker et al. 1993) or observed slight decreases in ATP that did not parallel the decrease in maximal muscle force (e.g., Baker et al. 1994; Dawson et al. 1978). Other studies provided positive evidence by demonstrating strong associations between decreased ATP availability and force decline (e.g., Karatzaferi et al. 2001), particularly, when looking at local ATP concentrations (e.g., Westerblad et al. 1998). It is of note that the reduced maximal force associated with decreased ATP concentration is not supposed to reflect a lack of energy available for muscle concentration. It has been attributed to decreased Ca^{2+} release from the sarcoplasmic reticulum resulting from reduced ATP concentrations (e.g., Allen et al. 2008; Westerblad et al. 1998). Given that the force-generating cycling of cross-bridges relies on the unblocking of myosin–actin binding sites by Ca^{2+}, a reduction in released Ca^{2+} results in less cross-bridge cycling and less force. The inhibiting effect of reductions in ATP on Ca^{2+} release seems to constitute a protection mechanism that reduces the energy consumed by cross-bridge cycling and reuptake of Ca^{2+} by the sarcoplasmic reticulum and prevents further decreases in ATP. Such a protection mechanism makes sense in the light of the serious consequences of complete ATP depletion. Given that ATP is the general energy source of the muscle cell, decreased ATP availability seriously impairs the cell's functioning, and leads to muscle rigor and cell death (e.g., MacIntosh et al. 2012; MacIntosh and Shahi 2011).

What about the energy systems that restore ATP? Do they show signs of depletion? One may speculate that these systems become depleted being no longer able to resynthesize ATP at a rate that is high enough to maintain a high-force level. As discussed above, the PCr system allows the muscle to restore ATP at a higher rate than the other systems. Thus, depletion of PCr stores could significantly slow down ATP resynthesis and the reduced ATP availability might lead to decreased force. The empirical evidence regarding the relationship between PCr depletion and force decline is mixed. Several studies showed that PCr concentration declines in parallel to declining maximal force at the onset of exercise and that PCr stores can become completely depleted (e.g., Sahlin et al. 1987). However, other studies cast doubt on the role of PCr depletion as a causal agent of muscle fatigue. They showed that PCr and maximal force during exercise and recovery can be dissociated (Fitts and Holloszy 1976; Saugen et al. 1997) and that PCr stores can still be very high even when participants are completely exhausted (e.g., Sahlin et al. 1992).

There is some evidence for associations between falling muscle glycogen and blood glucose concentrations and fatigue during long-lasting, high-intensity exercise (e.g., Callow et al. 1986; Chin and Allen 1997). However, there are other studies showing that this relationship only holds for a certain range of exercise intensity. If exercise intensity is low or very high, glycogen concentration and fatigue are dissociated (e.g., Saltin and Karlsson 1971). Furthermore, there is also evidence suggesting that reductions in muscle glycogen do not automatically lead to reduced ATP resynthesis (Baldwin et al. 2003) challenging the hypothesis that a lack of energy underlies the observed relationship between reductions in glycogen concentration and muscle fatigue. Depletion of triaglycerol, stored fat, has not been discussed as a major cause of fatigue. This is not surprising given that the amount of triaglycerol stored in adipose tissue provides enough energy to run more than 30 marathons.

To sum up, there is some evidence that the availability of ATP and of substances that are used to restore ATP can be reduced after sustained physical exercise and that these changes may parallel muscle fatigue. However, there is also evidence that questions the hypothesis that energy depletion is a major cause of fatigue and evidence for complete depletion of energy resources is sparse. The depletion of energy resources is only one among several factors that have been discussed in the physiological literature as a cause of muscle fatigue (see Allen et al. 2008; Fitts 1994; Gandevia 2001; Sahlin et al. 1998; Westerblad et al. 1998, 2010, for reviews). Muscle contraction involves several steps and an impairment of any of these steps may lead to a decreased muscle performance. Muscle fatigue resulting from events localized in the cerebral cortex (e.g., impaired descending output to motor neurons) or in the spinal cord (impaired alpha motor neuron firing, suboptimal recruitment) is called central fatigue. Peripheral fatigue refers to impairments that take place in the muscle itself. Factors causing peripheral fatigue include metabolic inhibition of cross-bridge cycling, impairment of excitation–contraction coupling, and impaired neuromuscular transmission. Metabolic factors that have been extensively discussed in the physiological literature as significant causes of muscle fatigue are the accumulation of inorganic phosphate (P_i), lactate, and hydrogen ions (H^+).

P_i is the product of the breakdown of PCr. High levels of P_i seriously impair muscle functioning by reducing the force produced by cross-bridges, decreasing myofibrillar sensitivity to Ca^{2+}, and reducing the amount of Ca^{2+} released by the sarcoplasmic reticulum (e.g., Allen et al. 2008; Westerblad et al. 2002, for reviews). The major causal role of P_i in muscle fatigue is further supported by the close relationship between P_i concentration and muscle fatigue during exercise and recovery (e.g., Fitts 1994). The accumulation of lactate produced by anaerobic glycolysis has also been suggested as a major cause of muscle fatigue. However, recent research calls this hypothesis into question (e.g., Allen et al. 2008) and recent reviews of muscle fatigue do not consider lactate accumulation to be a major cause of fatigue. Anaerobic glycolysis also increases H^+ concentration and decreases muscle pH. Increases in H^+ inhibit the enzyme phosphofructokinase reducing the rate of glycolysis, decrease myofibrillar Ca^{2+} sensitivity, reduce ATPase activity, impair cross-bridge functioning, slow down maximal shortening velocity of muscle fibers, and inhibit Ca^{2+} uptake and subsequent Ca^{2+} release by the sarcoplasmic reticulum (e.g., Fitts 1994, 2004; Westerblad et al. 2010, for reviews). All these factors considerably impair muscle functioning and lead to decreased maximal force. However, researchers recently started to question the importance of the slight reductions in pH observed in fatigued muscles suggesting that accumulation of H+ plays a minor role for human muscle fatigue (e.g., Westerblad et al. 2002, 2010).

In the preceding paragraphs, we have presented some of the factors and mechanisms that have been discussed in the physiological literature as causal agents of muscle fatigue. Despite decades of research on muscle fatigue, physiologists do not agree regarding the factors that cause fatigue and the relative importance of these factors (Fitts 1994). It is obvious that the muscle metaphor does not adequately reflect the physiological work on muscle fatigue and the controversy among researchers. By suggesting that there is agreement that energy depletion is the cause of muscle fatigue, the muscle metaphor overstates the role of depletion, overstates the degree of agreement among muscle physiologists, and neglects the variety of factors that seem to play a role in muscle fatigue. Depletion of energy resources may be a factor involved in muscle fatigue but it is neither the sole nor the major cause of muscle fatigue. Moreover, it is important to note that the muscle metaphor's depletion hypothesis conflicts with current ideas that many metabolic changes that cause muscle fatigue constitute protection mechanisms that prevent depletion (e.g., MacIntosh & Shahi 2011, 2012). Muscle fatigue may not be due to resource depletion but protect against it.

5.3.2 Training Effects on Muscle Strength

The muscle metaphor also suggests that repeatedly performing self-regulatory activity leads to increases in self-regulation efficacy like a muscle becomes stronger with repeated muscle exercise (e.g., Baumeister 2012; Baumeister et al. 2006, 2007). The muscle metaphor thus implies that repeatedly exercising a muscle leads to increased muscle strength. We will provide two examples that demonstrate that this constitutes a strong simplification of the complex relationship between muscle exercise and muscle adaption. First, muscle-training effects depend on the principle of overloading (McArdle et al. 2010). Only if the muscle is stimulated by repeated exercise at an intensity level that is higher than the normal exercise intensity level, adaptions will occur. Simply stimulating the muscle at a low intensity will not result in any significant changes. Second, the specific effects of training depend on the type of exercise as well as on the intensity, frequency, and duration of the exercise (e.g., Brooks et al. 2005; McArdle et al. 2010). Not all types of muscle training lead to increases in muscle strength.

Training types may be classified into endurance and resistance training. Endurance training is characterized by a high-activation frequency of motor units and a modest load that the muscle contracts against (e.g., cycling, jogging). The specific effects of endurance training depend largely on the energy systems that are used during training. Training of the aerobic system increases, among others, mitochondria number and size, the number of enzymes involved in oxidative phosphorylation, the muscle's capacity to oxidize fatty acids, the capacity to oxidize carbohydrates during maximal exercise, and the size of slow-twitch muscles (e.g., Brooks et al. 2005; Holloszy and Coyle 1984; McArdle et al. 2010). Training of the anaerobic system increases anaerobic substrate (ATP, PCr, muscle glycogen) levels, the amount and activity of the enzymes that control anaerobic glycolysis, and the capacity to tolerate higher blood–lactate levels (e.g., Brooks et al. 2005; McArdle et al. 2010). Endurance training also leads to an increase in maximum blood flow to the activated motor units as well as an increased performance of the capillary system. The adaptions induced by endurance training basically allow the muscle to perform longer.

Resistance training refers to exercise that is characterized by a high load that the muscle has to contract against (e.g., weight lifting). It results among others in an increase in the cross-sectional area of the muscle (mainly due to increases in the cross-sectional area of individual muscle fibers), an improved capacity for motor unit recruitment, and an increased motor neuron firing efficiency (e.g., Fry 2004; Kraemer et al. 1996). The main effect of resistance training on muscle performance is an increase in maximal muscle force.

As is evident from this brief review, muscle training is a complex topic and training a muscle may lead to different outcomes depending on the type of training. The muscle metaphor's hypothesis that muscle strength increases as a function of repeated exercise inadequately represents the complex relationship between different types of muscle training and various effects on muscle performance.

5.3.3 The Utility of the Muscle Metaphor

In the preceding sections, we have sketched the mechanisms that underlie muscle work, muscle fatigue, and training effects on muscle performance. It should have become evident that muscle activity is a highly complex process and that there is still a controversy regarding the involved mechanisms. The muscle metaphor that is used in the literature on the strength model of self-regulation does not adequately reflect this complexity and controversy of current theorizing on muscle functioning. It relies on a simplistic idea of the muscle that conflicts in part with the physiological evidence.

The crucial question is whether the simplified model of muscle functioning that is implied by the muscle metaphor constitutes a problem. One reason for using a metaphor is to provide an analogy that facilitates the comprehension of a new subject by transferring information from a known subject to the new subject (Boyd 1993). The muscle metaphor could help people that are not familiar with the strength model of self-regulation to understand the model. Imagine a physiologist who is an expert in muscle physiology but knows nothing about the strength model of self-regulation. When she learns that self-regulation resembles a muscle, she will transfer the knowledge that she has about muscle physiology to self-regulation. She probably would expect that theorizing about self-regulation involves ideas about different energy systems that restore a primary energy compound (like the PCr system, anaerobic glycolysis, and oxidative phosphorylation restore ATP), a detailed model on how self-regulation relates to task performance (like the physiological model of muscle activation and contraction), a whole bunch of variables that are discussed as causes of self-regulatory failure (like the variety of variables that are discussed as causes of muscle fatigue), and predictions regarding the specific effects of different self-regulation trainings on various performance parameters (like the specific effects of different types of muscle trainings). When she then learns about the predictions of the strength model of self-regulation, she will be confused by the fact that the model does not refer to the elements that she was expecting. It is obvious that her prior knowledge about muscle physiology would not help her to understand the strength model of self-regulation.

What about a person who is not familiar with the literature on muscle functioning? The muscle metaphor would not be of any help because this person could not apply the metaphor. Given that she has no prior knowledge about the muscle that could be transferred and facilitate the understanding of the strength model of self-regulation, the muscle metaphor would be useless. However, one might argue that everyone has some knowledge about muscle functioning that could be used. It is likely that everyone has gone through the experience that after intense physical exercise, muscle performance declines. People could draw on this knowledge to benefit from the muscle metaphor. However, even in this case the muscle metaphor relies on an oversimplification. Muscle fatigue can only be observed when maximal performance is assessed. If one does not have to exert one's maximum force, one will not observe fatigue effects (e.g., Allen et al. 2008). If one only has to perform at a submaximal level, one will be able to perform for a long time without any signs of fatigue. Imagine that you and your friend are asked to run 1 km. You have to run at your maximum speed, whereas your friend has to walk the kilometer at a speed of 1 km/h. Directly after the first task, both of you have to walk 2 km at a speed of 2 km/h. Even though you will be certainly more exhausted than your friend after the first task, there will be no performance differences between both of you in the second task. Both of you will easily manage to walk the 2 km in 1 h. The muscle metaphor neglects that muscle fatigue effects require the exertion of maximal performance in the second task. It simply suggests that performing high-intensity muscle exercise reduces performance in a second task, independent of the intensity of muscle activity that is required in the second task. Thus, people may have some personal experience regarding muscle functioning that may help them to understand some of the predictions of the strength model of self-regulation. However, their personal experience may also contradict the model's predictions—like in the example presented above—and hamper the understanding of the model.

It seems that the muscle metaphor's utility for facilitating the understanding of the strength model of self-regulation is limited. Unfortunately, using the muscle metaphor in self-regulation research leads to two serious problems. First, given that it does not adequately reflect current physiological thinking about muscle functioning, self-regulation researchers who present the muscle metaphor in their own scientific work are at risk of misrepresenting physiological knowledge. We think that scientists should aim at presenting knowledge from other domains as precisely and correctly as possible and avoid unwarranted simplifications. There is hardly a good reason why self-regulation researchers should inadequately present physiological knowledge in their own research. Second, we are afraid of the impact that the muscle metaphor will have on self-regulation researchers' thinking about the muscle. Individuals who do not have much knowledge about muscle physiology—and most self-regulation researchers probably do not know much about this topic—will adopt the idea that self-regulation resembles a muscle and will infer from the strength model's predictions to muscle work. For instance, they will adopt the idea that muscle fatigue is due to resource depletion and probably repeat this incorrect statement in their own work. Thus, the muscle metaphor may lead self-regulation researchers to develop incorrect representations of muscle functioning. Given the limited utility of the muscle metaphor and the discussed problems, we are wondering if the strength model on self-regulation would not be better off without the muscle metaphor. We are convinced that the model itself is strong enough to get along without the inadequate muscle analogy.

5.4 What Self-Regulation Researchers Can Learn from the Physiological Research on Muscle Functioning

Even if we think that the muscle metaphor is inadequate, we nevertheless feel confident that self-regulation researchers may benefit from the work on muscle physiology. The physiological research may provide a useful model that demonstrates how focused research on the mechanisms that underlie an effect may lead step by step to a deeper understanding of the effect. It also highlights that it is not the effect itself that merits scientific inquiry but the detailed understanding of the mechanisms that underlie the effect. Physiologists do not conduct extensive research on the effect that sustained muscle exercise results in decreased maximal muscle force. They are more interested in examining the causal mechanisms that underlie this phenomenon developing more and more sophisticated models of muscle fatigue. Self-regulation researchers still seem to be more interested in demonstrating ego-depletion effects instead of examining in detail the mechanisms that underlie the effect. In the light of more than 100 studies that have demonstrated ego-depletion effects—Hagger et al. (2010) already included 83 studies in their meta-analysis—this focus on replicating ego-depletion effects does not seem to be warranted. Furthermore, we doubt that such a focus fosters our understanding of ego-depletion effects and self-regulation.

There are nevertheless exceptions. A couple of researchers have discussed and examined mechanisms that should underlie the ego-depletion effect. For instance, Baumeister and colleagues suggested resource depletion as underlying mechanism (e.g., Baumeister 2002; Baumeister et al. 2000). Gailliot et al. (2007) postulated that glucose would be the resource that becomes depleted after self-regulatory efforts. Baumeister and colleagues recently speculated that the strategic conservation of resources may also play an important role (e.g., Baumeister 2012; Baumeister et al. 2007). A similar view was expressed by Beedie and Lane in their resource-allocation model of self-control (Beedie and Lane 2012). Further examples constitute Molden and colleagues' suggestion that ego-depletion effects are due to a lack of motivation (Molden et al. 2012), Job and colleagues' idea that subjective beliefs about the availability of resources are crucial (Job et al. 2010), Kaplan and Berman's attention restoration model that postulates that the depletion of voluntary, directed attention causes the ego-depletion effect, Tops and colleagues hypothesis that ego depletion reflects the protective inhibition of self-regulation and motivation (see Chap. 6), Inzlicht and Schmeichel's proposition that shifts in motivation and attention cause the ego-depletion effect (Inzlicht and Schmeichel 2012), or Wright's research that suggests that at least some ego-depletion effects might be due to feelings of fatigue (e.g., Wright et al. 2013).

These developments are steps in the right direction but, compared to theorizing on muscle functioning, current theorizing on ego depletion is still not very sophisticated and lacks important details. For instance, many central concepts like self-regulation, resources, or motivation are not well defined, which prevents from crucial empirical tests. Current models also do not include testable predictions on how self-regulation impacts performance or on how resources, glucose, motivation, attention, or subjective beliefs are translated into performance.

We agree with Inzlicht and Schmeichel (2012) that it is time to stop replicating one and the same effect and to start exploring the mechanisms that underlie the ego-depletion effect. The research on self-regulation would greatly benefit from empirical research and theorizing that focuses on the "black box" between "high self-regulatory effort in task 1" and "reduced performance in self-regulation in task 2." Researchers should aim at building models that define the central variables in a specific manner, provide detailed mechanisms that explain how self-regulation affects task performance, and postulate testable mechanisms that explain why and under which conditions exerting self-regulation in one task leads to decreased performance in subsequent tasks. Given that the central outcome that all models try to explain is task performance, every model that does not include specific predictions regarding the determinants of task performance would be incomplete. The physiological research on muscle activity may provide a guiding model for the development of these models. Knowledge about current physiological research and theorizing on muscle work would at least prevent researchers from using muscle analogies that may seem to be convincing at first sight but that inadequately reflect current theorizing on muscle functioning.

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Protective Inhibition of Self-Regulation and Motivation: Extending a Classic Pavlovian Principle to Social and Personality Functioning

6

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6.1 Introduction

During the 1950s, a group of Russian researchers led by Ivan Pavlov made a striking discovery (Nebylitsyn 1972; Nebylitsyn and Gray 1972; Pavlov 1955; see Mehrabian 1995). The researchers exposed the participants to a succession of discrete stimuli increasing in intensity (e.g., a series of tones that progressively increased in volume, or pain stimuli of increasing strength). Participants initially displayed more physiological arousal (defined by depression of the cortical alpha rhythm, enhanced response magnitudes in skin conductance, pupil dilation, and/or peripheral vasoconstriction) with each increase in stimulus intensity. However, at some point in the series, this trend was reversed: With each increase in stimulus intensity, participants displayed *less* physiological arousal. Pavlov and his associates theorized that these observed decreases in arousal were driven by a mechanism of the nervous system to protect itself against an overload of stimulation. They therefore referred to this mechanism as *protective inhibition* (also known as transmarginal inhibition).

Since Pavlov's (1955) pioneering work, the principle of protective inhibition has been invoked to explain a number of psychophysiological patterns, such as an onset of fatigue during strenuous exercise, loss of concentration during periods of intense mental activity, and the daily wakefulness–sleep cycle (Levin 1961). At least in theory, protective inhibition could also be relevant to understand phenomena that are of interest to social and personality psychologists, such as self-regulation and social motivation. However, as far as we know, the principle of protective inhibition has never been applied to social phenomena, while it has had only a limited influence on personality psychology (by influencing Eysenck's theory of extraversion; Eysenck 1970). Our goal in this chapter is to change this situation. In particular, we suggest that protective inhibition is a fundamental psychophysiological principle that limits the expenditure of a wide variety of motivational, social, and self-regulatory resources. As such, the principle of protective inhibition has broad implications for understanding social motivation and self-regulation, because protective inhibition predicts individual differences and changes in expenditure of resources over time and as a function of perceived coping resources.

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In what follows, we begin by discussing research on protective inhibition within the classic Pavlovian tradition. Next, we outline a model of protective inhibition in self-regulation and motivation (PRISM). We then review how the PRISM model may help to understand a wide range of social and personality phenomena that involve the expenditure of motivational and self-regulatory resources, such as ego depletion (Baumeister et al. 1998; see Chap. 4), effort mobilization (see Chaps. 18 and 19), coping with stress (e.g., Seery et al. 2013), and regulation of cortisol and effort in depression (see Chap. 22). Finally, we consider some additional ways in which the PRISM model may further advance our understanding of the biobehavioral foundations of self-regulation.

6.2 The Pavlovian Tradition of Protective Inhibition

The principle of protective inhibition was first discovered in experiments on individual differences in arousability and the orienting response. Novel, emotionally significant, salient (e.g., intense, varied, complex, dense, surprising, moving), and unpredictable stimuli induce a temporary pattern of physiological, attentional, and behavioral changes (the orienting response), which decreases with repeated exposures to the same stimulus ("familiarity effect" or "habituation"; Maltzman and Raskin 1965; Sokolov 1960, 1963). The orienting response was first described by the Russian physiologist Ivan Sechenov (1863), and baptized by Ivan Pavlov, who also referred to it as the "Что это такое?" or "What's that?" reflex. The orienting response involves a range of physiological changes, including depression of the cortical alpha rhythm, increases in skin conductance responses, heart rate slowing, pupil dilation, cephalic vasodilation, and peripheral vasoconstriction. Together with behavioral changes, including increased muscular tension and turning one's head toward the stimulus, the total set of changes that make up the orienting response facilitate the appraisal of the stimulus. The orienting response may display many generalized features across evocative conditions, even though its specific somatic responses may vary somewhat between contexts (Berntson et al. 1992; Sokolov 1963).

6.2.1 Acute Protective Inhibition

As discussed in the beginning of this chapter, subsequent experiments by Pavlov and his associates discovered the mirror image of the orienting response in the form of protective inhibition, which entails a lessening of physiological arousal with increasing stimulus intensity (Nebylitsyn 1972; Nebylitsyn and Gray 1972; Pavlov 1955; see Mehrabian 1995). Protective inhibition is different from habituation, as the former rises with increasing stimulus intensity, whereas the latter rises with increasing stimulus familiarity. The shift from increased arousal towards protective inhibition of physiological arousal is graphically depicted in Fig. 6.1: Initially, arousal responses increase as stimulus intensity increases; however, beyond some point in the series (the threshold of protective inhibition), arousal responses decrease steadily with progressively more intense stimulus presentations.

Subsequent research revealed strong and consistent negative correlations between the individual response magnitudes in the orienting response paradigm and the level of stimulus intensity that elicited arousal decrements in the protective inhibition paradigm (Nebylitsyn 1972). That is, more easily arousable participants (categorized according to their response magnitudes in the orienting response paradigm) showed lower thresholds of protective inhibition. In response to novel or intense stimuli (not involving sudden increases in intensity large enough to produce a startle reflex), arousable persons show larger amplitudes of arousal and slower habituation of arousal to baseline or resting levels. Moreover, when individuals are exposed to a closely spaced succession of high-intensity events, more arousable persons initially manifest generally higher levels of arousal. However, with prolonged exposure, more arousable persons tire faster (see Mehrabian 1995). These observations had a formative

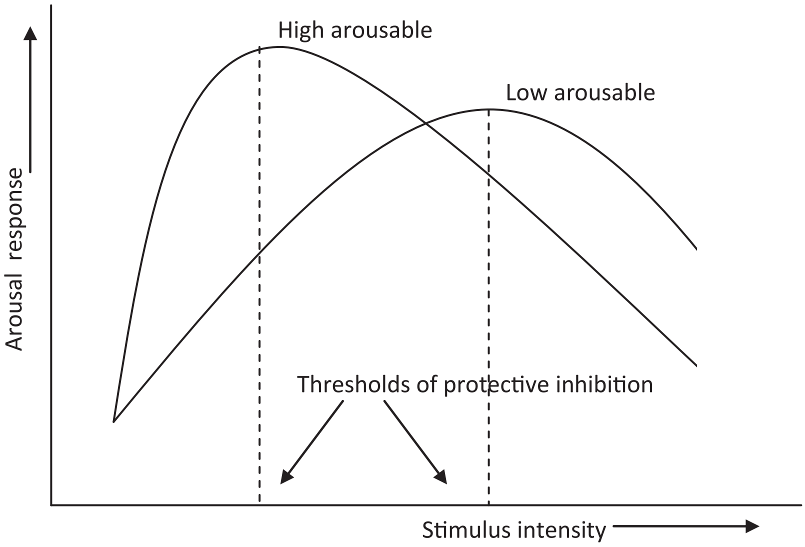

Fig. 6.1 Theoretical *curves* illustrating results from the protective inhibition (PI) paradigm. In the PI paradigm, participants were exposed to a succession of discrete stimuli increasing in intensity. Initially, arousal responses increased as stimulus intensity increased; however, beyond some point in the series (the threshold of PI), arousal responses decreased steadily with progressively more intense stimulus presentations. Moreover, more arousable persons initially manifest generally higher levels of arousal but lower thresholds of PI

influence on Eysenck's (1970) personality theory of extraversion, which he related to individual differences in arousability.

In the Pavlovian tradition, protective inhibition refers to the nervous system overload and consequent decrements in the nervous system response (i.e., diminishing arousal responses). However, protective inhibition may also increase behavioral avoidance of intense, high-arousing stimuli, i.e., increase a drive to withdraw (Tops et al. 2009). For instance, when confronted with an approaching stranger, infants at first watch the stranger soberly, with a brief heart rate deceleration (orienting response) followed by a slower, larger acceleration. When the heart rate acceleration is near peak, the infants avert their gaze and heart rate declined, after which the infants returned their gaze to the stranger once again (Waters et al. 1975). When intense stimuli cannot be, or are not, avoided behaviorally, they may trigger physiological mechanisms of protective inhibition.

Findings that protective inhibition facilitates behavioral withdrawal suggest that protective inhibition is related to other mechanisms that limit the enactment of basic biological appetitive approach "drives" or "needs" by increasing satiety, aversion, and a drive to withdraw (Tops et al. 2009). For example, imagine that you are eating a delicious but copious meal. Initially, your senses are filled with sensory pleasures of viewing and then tasting an array of culinary delights. As you continue eating, however, two things happen: First, there is a diminishing marginal benefit to the delicious tastes; second, you start to feel full—uncomfortably so. Early in your meal, there are no negative effects, but as you keep stuffing yourself, a threshold is crossed, and negative effects start to appear. In addition, unlike the pleasurable effects, which are diminishing, the negative ones are growing in magnitude. Similar processes may regulate other forms of need fulfillment, like drinking and sex, and the seeking of environmental stimulation and novelty (Mehrabian 1995; Zuckerman 1979). Through crying or protesting when put to bed unsatisfied, the need or hunger for stimulation is one of the first needs demonstrated by infants. Protective inhibition regulates limitless stimulation seeking and prevents overstimulation by increasing an opposing drive to withdraw from further stimulation, similar to the satiety and eventually aversion that follow eating and overeating.

6.2.2 Cumulative Protective Inhibition

Pavlov's theory of protective inhibition has been applied both to acute arousal responses ("acute protective inhibition") and to the accumulation of costs of the mobilization of physiological resources over multiple orienting responses ("cumulative protective inhibition"). It thus appears that there is a limit or that there are incremental costs to arousal responses and the mobilization of physiological resources. Cumulative protective inhibition may occur when sustained periods of high arousal are evoked by high levels of physical activity and/or mental alertness. Two common examples are onset of fatigue during strenuous exercise or loss of concentration during periods of intense mental activity (Levin 1961). The daily wake–sleep cycle is the most common example of cumulative protective inhibition (Levin 1953, 1961), with sustained periods of wakefulness, leading to physical and mental fatigue and an extended period of sleep (which is a low-arousal state).

Oswald (1962) has pointed out that extreme stress and hyperarousal can paradoxically lead to sleep as a provoked reaction. For example, in the face of intense noxious stimulation (e.g., the sounding of a loud horn), newborns amazingly will fall asleep after a few presentations (Tennes et al. 1972). Also, following surgical procedures (e.g., circumcision), they enter a period of deep sleep. Such mechanisms may protect vulnerable infants from overstimulation in the absence of more mature coping mechanisms. This protective mechanism may lay the groundwork for later, more sophisticated psychological defenses (Spitz et al. 1970). Among adult patients with narcolepsy, high arousal states such as during anger, shame, fear, surprise, orgasm, or laughter can trigger sleep or cataplexy (a sudden and transient episode of a loss of muscle tone accompanied by a full conscious awareness, similar to sleep paralysis while falling asleep or on waking). Levin (1953) suggested that sleep in narcoleptic patients may occur in any situation in which they suppress the impulse to escape from danger. These sleep or cataplexy attacks, as well as fatigue, following high arousal have been explained in terms of Pavlovian protective inhibition (Levin 1953, 1961).

Similarly, migraine (head/neck pain) attacks often follow or are exacerbated by stress and fatigue, and involve muscle weakness and hypersensitivity to light, sound, smells, and taste-driving withdrawal from strong stimulation (Hedborg et al. 2011; Sacks 1985). Sensory excitability of this type may precede the onset of headache, and, in general, is characteristic of the early portions of the migraine attack. It is often followed by a state of sensory inhibition or indifference for the remainder of the attack (Sacks 1985). Similarly, states of anxiety and emotional hyperarousability are common in the early portions of the attack and states of apathy, withdrawal, and depression for the remainder of the attack. This depression entails a sense of utter hopelessness and permanence of misery reaction that is disproportionate in relation to the relative short-lived and familiar nature of the attack, but may reflect a perception of lack of resources. Attacks often occur during borderline stadia of sleep. Sacks (1985) theorized that migraine and cataplexy attacks involve mechanisms of protective inhibition originating from hibernation and tonic immobilization and freezing responses in animals, enabling the animal to avert or become less accessible to danger.

In short, protective inhibition in the Pavlovian tradition refers to inhibition of arousal to prevent physiological damage from either acute overstimulation or accumulation of stimulation over time. Individuals who tend to show higher arousal responses and less habituation also tend to have a complementary lower threshold of protective inhibition.

6.3 Protective Inhibition of Self-Regulation and Motivation

To date, Pavlov's protective inhibition principle has been applied mostly in relation to mobilization of resources by the anticipation of urgency or the need to process novel stimuli (Mehrabian 1995). However, repeated mobilization of physiological resources also involves the costs of actually having to meet challenges and perform tasks. This neglected aspect of cumulative protective inhibition may form an important conceptual bridge between protective inhibition and contemporary theories of coping with stress, effort mobilization, and resource conservation.

6.3.1 Protective Inhibition and Conservation of Resources

The notions of predictability and controllability are central to understanding which challenges trigger a physiological stress response (Sapolsky 2005). Physiological responses to challenge take one of two forms: *Reactive* homeostatic responses arise to changes in physiological variables, which already occurred or were not predicted, and *predictive* homeostatic responses emerge in anticipation of predictably timed challenges (Moore-Ede 1986; Romero et al. 2009; cf. Landys et al. 2006). When a challenge or task is perceived as predictable and controllable, because coping resources are perceived to be sufficient (e.g., enough muscle strength), predictive homeostasis is maintained, and the task may not be experienced as effortful. By contrast, situational novelty (e.g., Hasher and Zacks 1979; Shiffrin and Schneider 1977) and unpredictability of cognitive operations (Ackerman 1987; Fisk and Schneider 1983) require effortful processing and can trigger reactive physiological responses that potentially incur health costs (Romero et al. 2009). For instance, reactive homeostatic control may decrease less urgent predictive homeostatic regulation (e.g., circadian variation in appetite), causing "somatic neglect" (Koole et al. 2014).

Predictability allows for stimuli and contexts to become familiar and for the habituation of orienting responses and reactive control as predictive control takes over (familiarity effect; Maltzman and Raskin 1965; Sokolov 1960, 1963). By contrast, if habituation does not take place (e.g., due to unpredictability), then reactive control needs to be bound by another mechanism. For this reason, and because reactive control reduces predictive homeostatic regulation of the internal milieu, such cognitive control requires the momentary tracking of physiological costs and resources and is experienced as effortful (Tops et al. 2013). The experience of effort is hence an adaptive motivational mechanism that limits the (re-)initiation and prolonged performance of tasks that demand reactive control, stimulating a drive away from the current task, towards alternative, more rewarding options, especially when there are insufficient perceived benefits, threats, or resources to compensate for the physiological costs of reactive control (Boksem and Tops 2008; Tops et al. 2013).

At this point, some form of cumulative protective inhibition may come into play, which arises during a prolonged period of dealing with stressors. Cumulative protective inhibition serves to decrease the accumulation of costs of physiological arousal by decreasing further stimulation. To decrease stimulation, protective inhibition (a) increases a drive to withdraw (Tops et al. 2009), (b) decreases the perceived level of coping resources one possesses at the moment, and (c) decreases the motivation to mobilize resources by increasing the subjective effort and aversiveness of reactive control (Tops et al. 2013). In other words, cumulative protective inhibition increases the weight of costs or effort and decreases the hedonic weight in effort–reward or cost–benefit processing (Boksem and Tops 2008).

6.3.2 PRISM

We refer to the aforementioned processes of lowering motivation to mobilize resources as "protective inhibition of self-regulation and motivation" (PRISM). This limitation of the (re-)initiation of effortful tasks may relate to the construct of "ego depletion," which has been widely researched within social and personality psychology (see Hagger et al. 2010, for a review and meta-analysis). Ego depletion refers to the idea that effortful self-control draws upon a limited pool of mental resources that can be used up (Baumeister et al. 1998; see Chap. 4). However,

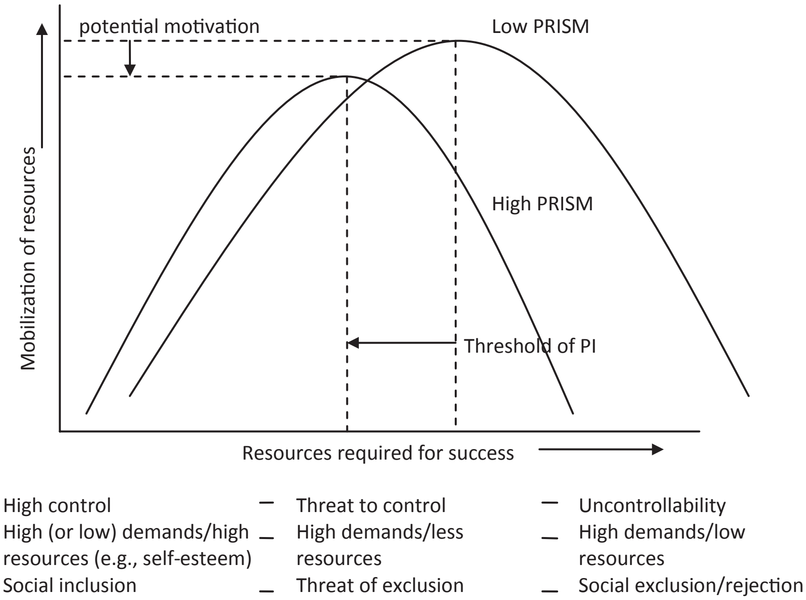

Fig. 6.2 Illustration of the effects of protective inhibition of self-regulation and motivation (PRISM). Theoretical *curves* are drawn to represent individuals who are not or barely affected by PRISM (*low PRISM*) and individuals who are affected by PRISM (*high PRISM*). The arrows show the effects of an increase in PRISM. See the text for explanation

we do not think that PRISM depends on the actual depletion of a limited pool of resources. Instead, PRISM involves a protective mechanism that, following reactive control, temporarily shifts motivation and attention towards a behavior that does not require reactive homeostatic control and preferably involves recuperation (cf. Inzlicht and Schmeichel 2012).

A host of studies support the idea that the mobilization of resources is guided by a resource conservation principle. For instance, motivational intensity theory (Brehm and Self 1989) asserts that resource mobilization should be proportional to the difficulty of a performance challenge (i.e., proportionally to implicit perceptions of the amount of resources needed to successfully cope with a challenge), so long as success appears possible and worthwhile (i.e., within the range of "potential motivation"), and low where success appears impossible or excessively difficult, given the benefit that it can accrue (see Chaps. 18 and 19). PRISM adds a dynamic element to the motivational intensity theory, which entails a decrease in the potential motivation (i.e., the maximal amount of resources one is willing to mobilize to confront a given challenge) in response to prolonged effort expenditure. We assume that PRISM and potential motivation are implicit processes acting through the level of subjective effort, resistance, and anhedonia or lethargy.

It is important to point out that the PRISM model uses a slightly different terminology compared to the motivational intensity theory. In particular, recent formulations have defined effort mobilization as the recruitment of resources for carrying out instrumental behavior (Gendolla and Wright 2009). In the PRISM model, we prefer the term "resource mobilization" over "effort mobilization," because it is easier to see how resource mobilization relates to the other elements of the model, such as the perceived level of coping resources, and the level of resources that is required for success (Fig. 6.2). Moreover, PRISM increases subjective effort, which is not directly related to the objective effort or resource mobilization. Because of the important role of subjective effort in the PRISM model, it might cause confusion if we used the term effort mobilization.

6.4 Controllability, Social Resources, and PRISM

The processes proposed by our PRISM model are closely tied to resource mobilization and conservation. In line with Sacks (1985), who proposed that protective inhibition originated from hibernation and tonic immobilization and freezing responses in animals, PRISM may be related to the conservation–withdrawal response, characterized behaviorally by immobility and low levels of aggression (Engel and Schmale 1972). As we already noted, a systematic and well-validated conceptual framework for mobilization is provided by motivation intensity theory (Brehm and Self 1989). In this section, we use the framework of motivation intensity theory to PRISM processes, to illuminate the dynamic aspects of the PRISM model.

In the previous section, we saw that motivation intensity theory assumes that resource mobilization is proportional to perceptions of the amount of resources needed to successfully cope with a challenge, so long as success appears possible and worthwhile (Brehm and Self 1989). Furthermore, resource mobilization should be indexed and constrained by the perceived availability of resources. This means that resource mobilization is constrained by perceived controllability, defined as the perception of having sufficient resources to successfully cope with a challenge, success that appears possible, and, in practice, success that does not appear excessively difficult, given the benefit that it can accrue.

Figure 6.2 illustrates the theoretically predicted effects of PRISM. The different curves represent individuals who are weakly affected by PRISM (low PRISM) and individuals who are strongly affected by PRISM (high PRISM). PRISM decreases the potential (justified) motivation, i.e., the maximum amount of resources mobilized for a goal, by decreasing the importance of success or the value of the incentive, by decreasing the perceived amount of resources available to a person, and by increasing subjective effort. When the amount of resources that is required for success is lower than the potential motivation, the amount of resource mobilization follows the required resources. However, when the amount of mobilized resources reaches the level of potential motivation, resource mobilization drops. Because PRISM decreases potential motivation, it causes resource mobilization to drop at a lower level of required resources. The above can also be expressed in terms of controllability. First, as the level of potential motivation and available resources is approached, there is increasing resource mobilization with increasing threat to control. This is followed by a drop in resource mobilization and disengagement when the perception of uncontrollability becomes increasingly clear and equivocal.

PRISM decreases potential motivation by increasing subjective effort, thereby increasing subjective costs and resistance during performance. For instance, PRISM increases lethargy or anhedonia by offsetting rewarding activities with increased feelings of aversion and resistance associated with the required mobilization of resources. However, high subjective costs during performance are likely, through learning experiences, to also increase anticipated subjective costs. In other words, high-PRISM individuals are more likely to avoid starting performance on a task and to refrain from mobilizing resources because of anticipated high costs. Although individuals differ in their perceptions of the amount of resources required for success, most studies manipulate or measure objective parameters of, e.g., task difficulty. For this reason, we put the objective required amount of resources on the *x*-axis in Fig. 6.1, comparable to the objective stimulus intensity in the protective inhibition paradigm (Fig. 6.1). The increased perceptions of the amount of resources required for the success of high-PRISM individuals is shown in the leftward shift and lower maximum of their curve relative to the low-PRISM curve (cf. Chap. 19).

Because we believe that PRISM is potentially applicable to a broad range of human behaviors, we use a broad definition of resources. Examples of resources are physical condition, physiological energy resources, quality of the environment, time, money, skills, and social resources such as level of support, inclusion and status, and the trustworthiness of the people around you. Social resources are important sources of control in human life. For instance, it has been proposed that humans possess a “sociometer” to keep track of the level of social support in the environment, having the experience of a certain level of self-esteem as readout (Leary et al. 1998). Hence, the level of social resources, such as social support or inclusion versus exclusion, should influence the perceptions of controllability and hence the likelihood and magnitude of resource mobilization in response to challenges in social situations.

Notice that the inverted U-shaped function in Fig. 6.2 and individual differences in PRISM do not only show up in conditions of very high required resources or with individuals who show very high PRISM effects. Similar patterns may be found under conditions that combine a lower range of required resources with lower potential motivation as in conditions that combine a higher range of required resources with higher potential motivation. The potential motivation is determined by both the task and the level of PRISM, and we assume that PRISM decreases the potential motivation at all levels of task importance and incentives. From this, it follows that effects of PRISM can be observed both in psychologically healthy samples and among samples with psychological disorders, and in response to both subtle and large task challenges.

6.5 Empirical Examples of PRISM

Although many predictions can be derived from the PRISM model (e.g., Tops et al. 2008), we restrict the present discussion to two core predictions here. Specifically, in Sect. 6.5.1, we discuss examples of the inverted U-shaped relationship between the size of the challenge and the amount of resource mobilization (Fig. 6.2). We discuss this relationship also in Sect. 6.5.2, where we focus on the hormone cortisol that is a modulator of resource mobilization. The PRISM model predicts that this relationship is moderated by people's perceived level of resources, and that PRISM decreases this level of resources in response to prolonged resource mobilization, especially when prior efforts were unsuccessful at bringing rewards. Finally, in Sect. 6.5.3 we discuss examples of PRISM that involve low perceived levels of social resources that cause the crossing of the threshold of protective inhibition.

6.5.1 Inverted U-shaped Relationships

Inverted U-shaped relations are widely found in psychological research (Grant and Schwartz 2011). For instance, there are inverted U-shaped relations between the levels of (especially uncontrollable) stress-related neuromodulators and functioning of the prefrontal cortex (Arnsten 2009). Similar patterns have also been found in humans in the amplitude of an emotional arousal-related event-related potential (the late positive potential; de Rover et al. 2012). More generally, individuals high in anxiety tend to have elevated neural responses to mild or moderate threats but paradoxically lower responses to high-intensity threats, suggesting an inverted U-shaped relation between anxiety and threat responding (see Maresh et al. 2013). The Yerkes–Dodson law, a widely cited century-old principle, states that the relationship between arousal and behavioral performance can be linear or curvilinear (inverted U-shaped), depending on the difficulty of the task (Yerkes and Dodson 1908). Although protective inhibition may be involved in some of the former relationships, in the case of the Yerkes–Dodson law notice that arousal is represented on the *x*-axis, as an independent variable, whereas the protective inhibition pattern puts arousal on the *y*-axis, as a dependent variable. Moreover, the mobilization of resources that is modulated by PRISM relates differentially to both arousal and performance.

A curvilinear effort function that is largely compatible with PRISM also characterizes the cardiovascular responses reflecting resource mobilization as a function of task difficulty in the chapters by Wright and Agtarap (Chap. 19), Gendolla and Silvestrini (Chap. 18), and Silvia (Chap. 20). These results have been obtained in the framework of Brehm's motivational intensity theory (Brehm and Self 1989). The PRISM model incorporates elements of the motivational intensity theory, but adds individual differences in a number of parameters of the model (cf. Silvia, Chap. 20), and dynamic processes over time affecting potential motivation and the perceived level of resources (cf. Wright and Agtarap, Chap. 19, who focus on ability as an example of perceived resources).

Also within the framework of the motivational intensity theory, combined with other theories, Brinkmann and Franzen (Chap. 22) found evidence that depressed mood leads to higher perceived task difficulty (i.e., perception of a larger amount of resources required to successfully complete the task), which leads to higher resource mobilization for easy tasks (requiring a relatively smaller amount of resources) but to disengagement (i.e., protective inhibition) for difficult but still possible tasks because of the perception that those tasks require too much resources to successfully complete. This result fits well with the PRISM model (Fig. 6.2). A similar inverted-U shaped pattern was found in the amplitude of an event-related potential (feedback-related negativity) suggesting high resource mobilization followed by protective inhibition as a function of individual differences in the intensity of depressed mood (Tucker et al. 2003; cf. Tops et al. 2006).

6.5.2 Inverted U-shaped Patterns of Cortisol

U-shaped patterns and evidence for an association between depression and PRISM are also found in studies of the hormone cortisol, which is the end product of the hypothalamic–pituitary–adrenal cortex axis. Cortisol has a main function in the mobilization of resources (e.g., blood glucose levels) to meet the demands of challenges, no matter whether those challenges are pleasurable (e.g., your favorite sports) or unpleasant (e.g., an experimental stress test; Sapolsky et al. 2000; Tops et al. 2006; Tops and Boksem 2008). Compared to the other regulators of resource mobilization, such as the catecholamines (e.g., adrenalin) and the sympathetic nervous system, cortisol is stronger involved in challenges that are not resolved immediately, but are anticipated to require more or less extended mobilization of resources. This involvement in longer-duration mobilization processes may make cortisol an especially suitable measure to study PRISM, which takes place after accumulated resource mobilization over time. The cortisol awakening response (CAR; i.e., the typical temporary increase in cortisol within 30 min after awakening), which may reflect the mobilization of resources for meeting the challenges of the coming day, appears especially sensitive to PRISM (Tops et al. 2008). Supporting the sensitivity of the CAR to PRISM, in a meta-analysis the CAR was positively associated with job stress and general life stress; it was negatively associated with fatigue, burnout, or exhaustion (Chida and Steptoe 2009).

Consistent with PRISM, Engert et al. (2010) reported that the cortisol response of healthy adults to a social evaluative challenge displayed an inverted U-shaped pattern as a function of perceived social resources (early-life maternal care and self-esteem) and/or possibly chronic distress. Specifically, cortisol responses were low in the high maternal care, higher in the medium care, and low in the low maternal care group. The low maternal care group displayed increased levels of depression and anxiety and decreased self-esteem, while the high-care group displayed the highest self-esteem. The medium- and high-care groups were similar in terms of depression, anxiety, and self-esteem, which is not surprising in light of recent work that revealed an inverted U-shaped pattern, such that some cumulative lifetime adversity is associated with optimal well-being. For instance, relative to a history of either no adversity or nonextreme high adversity, a moderate number of adverse life events has been associated with less negative responses to pain and, while taking a test, to a cardiovascular response pattern that was interpreted to reflect positive perceptions of the level of resources relative to demand (Seery et al. 2013). Both the results of Engert et al. (2010) and Seery et al. (2013) are consistent with the theory that, whereas a moderate amount of challenge increases the mobilization of resources for active coping, potentially increasing the level of perceived resources and control (e.g., by increasing skills or support networks), accumulation of high adversity increased PRISM (Fig. 6.2).

In a large study ($n = 1378$) of participants with a lifetime depression and/or anxiety disorder and healthy participants, the CAR displayed an inverted U-shaped pattern as a function of symptom scores of past-week general distress, anhedonic depression, and anxious arousal: Both low- and high-symptom scores were associated with a lower CAR (Wardenaar et al. 2011). High-symptom levels may have triggered protective inhibition. The curved associations seemed to be generalizable across the complete spectrum of healthy participants and current and remitted patients and replicated findings in a smaller sample (Veen et al. 2011). In another large longitudinal study of a high-risk focus sample ($n = 351$), cortisol responses to a social evaluative challenge at age 16 displayed an inverted U-shaped pattern as a function of the chronicity of depressive problems, with recent-onset depressive problems predicting an increased cortisol response, and more chronic depressive problems as a blunted response (Booij et al. 2013). The results of this study suggest that depressive problems initially increase cortisol responses to stress, but that this pattern reverses when depressive problems persist over prolonged periods of time, and there is accumulation of high resource mobilization, increasing PRISM.

As a whole, the above shows that PRISM explains reliable patterns in the mobilization of resources by cortisol that have been found in large studies, and that often defied prediction and explanation in the original studies.

6.5.3 Interactions Between PRISM and Social Resources

PRISM may further be triggered by social exclusion, as evidenced by increased emotional numbing and lethargy (Twenge et al. 2003) and reduced pain sensitivity (DeWall and Baumeister 2006) among excluded individuals. Such findings lend credence to our interpretation that PRISM often involves a low perceived level of resources (or a perceived level of resources relative to the required level of resources) that causes the crossing of the threshold of protective inhibition. PRISM, after social exclusion, also affects cortisol levels. Female (but not male) participants who first experienced a social exclusion manipulation showed blunted cortisol responses to a social evaluative challenge (Weik et al. 2010). Possibly depending on prior experiences and baseline perceived level of resources, the social exclusion manipulation may have been associated for some female participants with feelings of actual exclusion, i.e., social uncontrollability, associated with hopelessness and PRISM (Fig. 6.2).

In an unpublished analysis of data from one of our studies ($n = 57$ healthy female participants), we included scores on a trait measure of fear of negative social evaluation and contingent self-esteem (self-esteem that is dependent on the approval of others, the same measure that predicted PRISM in Tops et al. 2008) and a trait measure of loneliness in a regression analysis predicting donations made to a good cause in the presence of the experimenter. The two trait measures were mutually positively correlated ($r = 0.31, p < 0.02$). The results showed that, while high scores of trait fear of negative social evaluation predicted higher donations (partial $r = 0.36$, $p < 0.01$), trait loneliness predicted lower donations (partial $r = -0.40$, $p < 0.01$). Moreover, fear of negative social evaluation predicted more intense self-reported state feeling of being observed, guilt, and uneasiness, while trait loneliness tended to relate negatively to those feelings but predicted more intense state loneliness, feeling excluded, and fatigue during the session. The PRISM model explains these results in terms of increased mobilization of resources in relation to fear of negative social evaluation, which is associated with concerns about losing social resources (threat of exclusion), and intensified attempts to prevent this loss (Fig. 6.2). By contrast, loneliness is associated with feelings of actual exclusion, i.e., social uncontrollability, associated with hopelessness and PRISM.

Social rejection has been found to increase positive emotions, cognition, and memories among people high in self-esteem and low in depression (DeWall et al. 2011), which may reflect the mobilization of resources and motivation of active coping aimed at repairing social inclusion. This response is not seen among individuals low in self-esteem or high in depression, who may have the perception of having too few resources to successfully bring about social inclusion. The neuropeptide oxytocin, is believed to be involved in mobilization of resources of social support, partly by facilitating interpersonal trust and positive social perceptions when confronted with a challenge (Tops et al. 2013). A recent study found that oxytocin administration (relative to placebo) increased self-perceived trust in participants reporting a negative mood response following social rejection, but not in those whose mood state was euthymic (Cardoso et al. 2013). Notice that although negative mood was activated, which may *motivate* support and inclusion seeking and avoidance of exclusion, positive prosocial mood such as trust was also activated, which may facilitate support seeking (Tops et al. 2013). This result suggests that oxytocin induces more active coping among individuals who are motivated to mobilize resources, but not among individuals who feel deprived of control and resources.

6.6 Neural Mechanisms of PRISM

In Sect. 6.3, we suggested that PRISM may help to prevent damage accumulating from reactive homeostatic control. We assume that predictive and reactive homeostatic control are part of more general predictive and reactive action control systems (PARCS; Tops and Boksem 2012; Tops et al. 2013). In this section, we discuss neurological evidence that the reactive control system implements the different elements of PRISM: (a) it keeps track of physiological and social coping resources and generates a feeling state that reflects the perceived level of resources, (b) it generates a feeling state of increased subjective effort which increases with duration of reactive control, and (c) it is involved in the inhibition of motivation, perhaps by increasing the subjective effort and aversiveness of reactive control. Reflecting the integrating nature of the PRISM model, the evidence is heterogeneous, pertaining to, for instance, physiological and social resources and the process of anhedonia that is typically studied in relation to depression. On the other hand, PRISM also provides some level of integration to the heterogeneity of functions that have been ascribed to the brain areas involved.

6.6.1 The Feeling of Resources

Evidence from neuroimaging and neurophysiology supports our thesis that reactive control systems translate information about action costs and resources into a motivational feeling of subjective effort. Reactive control areas include the anterior insula (AI) and inferior frontal gyrus (IFG). As a control area of the reactive system and ventral orienting attentional system, the right IFG/AI regulates emotional arousability and orienting responses in the light of limitations imposed by the costs of reactive resource mobilization and level of perceived resources. Through its reciprocal connections with autonomic and visceral centers of the nervous system such as the hypothalamus (Carmichael and Price 1995), the AI has been proposed to be involved in the monitoring and regulation of peripheral resources such as glucose levels (Allport et al. 2004), muscle condition (Craig 2003), autonomic activation and perception of heart beat (Critchley et al. 2004), and the processing of aversive bodily states (Paulus and Stein 2006). Connecting such monitoring functions to the regulation of resource mobilization, good heartbeat perceivers show a more finely tuned behavioral self-regulation of physical load than poor heartbeat perceivers (Herbert et al. 2007).

Brain areas involved in reactive control keep track of physiological and social coping resources and generate a feeling state that reflects the perceived level of resources. AI activity is associated with positive and negative affective arousal states. Craig (2008, 2009) reviewed evidence to suggest that, in the AI/IFG, an integrated representation is formed of the global emotional moment that is also informed by interoceptive information such as glucose levels and the condition of muscles. Classical work showed that affective arousal states carry resource information (physiological resources such as glucose levels, as well as social resources) and are associated with implicit perceptions of coping abilities, power, and self-esteem (Thayer 1989). Similarly, Morris (1999) stated that mood appears to be sensitive to the adequacy of resources given current levels of demand.

In humans, social resources are very important, which may explain why, especially in insecure or narcissistic individuals, the state level of self-esteem follows perceptions of how one is appraised by the social environment (Leary et al. 1998). Monitoring trustworthiness of others and how one is appraised by others in the current social environment is essential to the momentary monitoring of social resources, and the net continuous output of such a process may determine the experienced state level of power and self-esteem. Given the importance of social relationships for survival, human beings may have developed an internal gauge of social value—a sociometer—that monitors the appraisals from the social environment (Leary et al. 1998), and we propose that the AI/IFG is an essential part of the sociometer, a function scaffolded on, and integrated with, its more original function in monitoring physiological resources. For example, the right IFG/AI is consistently active in relation to distress (e.g., during social exclusion), but less (proportional to marital quality) when during threat the hand of a subject is held by her husband, an important social resource (Coan et al. 2006). For another example, social status cues activate the right or bilateral IFG (Chiao et al. 2009; Marsh et al. 2009).

6.6.2 The Feeling of Effort

In the context of AI/IFG involvement in autonomic system function, the engagement of the right AI/IFG appears to reflect the control of arousal in the face of challenging task conditions (Eckert et al. 2009). However, complementary to its function to increase arousal with increasing demand, the AI/IFG also inhibits excessive exertion of effort. Increased thalamo-AI activation in the context of a fatigue-inducing handgrip exercise followed by task failure appeared to signal an increased homeostatic disturbance in the exercising muscle and may be of essential importance by mediating protective inhibition to maintain the integrity of the organism (Hilty et al. 2011). Similar findings were reported in other studies investigating sensations that alert the organism to urgent homeostatic imbalance such as air hunger, hunger for food, and pain (see Hilty et al. 2011).

Consistent with the perception of effort being related to the perception or monitoring of resources, Damasio (1999) considered mental effort to be a feeling, which refers to a conscious appraisal of one's own state (cf. Craig 2013). Brain areas involved in reactive control generate a feeling state of increased subjective effort, which increases with duration of reactive control. AI and right IFG activation have been related to the subjective perception of mental and physical effort and exertion (de Graaf et al. 2004; Jansma et al. 2007; Otto et al. 2014; Williamson et al. 1999, 2003; cf. Chap. 17). The IFG/AI areas that are active when people experience subjective effort are also implicated in compensatory effort allocation with time on task. Several studies suggested that increased attentional effort during performance over extended periods of time or after sleep deprivation is associated with increased activation of right-hemisphere ventral cortical areas including IFG/AI (reviewed in Tops et al. 2013; cf. Chap. 16).

More direct evidence for the involvement of the right IFG/AI in PRISM comes from a neuroimaging study of the ego-depletion effect (Friese et al. 2013). In this study, an initial act of self-control (suppressing emotions during a picture-viewing task) impaired subsequent performance in a second task requiring control (Stroop task: suppressing the meaning of color words while naming the color in which they are depicted). Participants who had recruited the right lateral prefrontal cortex while suppressing their emotions in the picture-viewing task committed more errors and showed less activity in the same area during a subsequent attempt at self-control in the Stroop task relative to participants in a control condition who had recruited this area not as strongly during the first task. An area in the right IFG was the only area that was particularly strongly involved during both the emotion suppression task and the Stroop task and showed the above-described ego-depletion pattern of strong recruitment in the emotion-suppression task and relatively reduced subsequent activation during the Stroop task. The medial frontal cortex, an area thought to be implicated in predictive control, which is relatively automatic and subjectively effortless, was also strongly involved during both the emotion-suppression task and the Stroop task, but did not show the ego-depletion pattern. These results are consistent with PRISM limiting effortful reactive control by the right IFG.

Finally, brain areas involved in reactive control appear involved in the inhibition of motivation, perhaps by increasing the subjective effort and aversiveness of reactive control. Moreover, the right IFG/AI may be implicated in PRISM through a role in the inhibition of incentive value and potential motivation (e.g., the perceived level of resources), increasing anhedonia. Support for this role of the reactive control areas has been found in studies of depression and anhedonia. Depression, which may involve low perceived social resources (status) and anhedonia due to PRISM, is associated with an increased sense of subjective effort (Morgan 1994). Source localization of a high-density event-related potential measure of resource mobilization showed an inverted-U shaped pattern of activation of the right IFG/AI with increased depressed mood, but low activation in individuals who showed the highest level of depressed mood (Tucker et al. 2003). Finally, anhedonia in depressed individuals has been associated with apparent increased inhibition by the right IFG of the processing of positive stimuli or experience (Light et al. 2011).

6.7 Discussion and Outlook

In the present chapter, we have described how protective inhibition, a classic Pavlovian principle, may be extended to understand self-regulatory and motivational functioning in social life. To this end, we have proposed the PRISM model, which holds that accumulation of potentially costly physiological activation increases a protective mechanism that increases resistance against this kind of activation by increasing subjective effortfulness and decreasing the perceived level of physiological and social coping resources. The PRISM model predicts and explains nonlinear dynamics over time in which high activation and mobilization of resources can turn into low activation, mobilization, and increased fatigue. Moreover, this dynamic process over time is integrated in a model that predicts mobilization of resources by required level of resources for successful performance, perceived level of resources, and controllability.

Protective inhibition in the classic Pavlovian sense may prevent costs from high-arousal responses by avoiding the processing of high-intensity stimulation. However, people are unlikely to avoid all arousal and mobilization of physiological resources, and thus mobilization may accumulate over time, eventually leading to PRISM. In this way, PRISM naturally opposes and regulates the need for stimulation. To temporarily decrease further stimulation and arousal responses and to facilitate recuperation, PRISM increases subjective perceptions of effort and aversiveness of tasks that initiate reactive (homeostatic) control. Moreover, PRISM decreases the level of perceived resources, thereby decreasing the potential motivation. This way PRISM counteracts motivation, specifically to implement reactive control, and increases the drive to withdraw.

Though inspired by classic Pavlovian work, the PRISM model represents a novel theoretical perspective at the interface of social and personality psychology and social-cognitive and affective neuroscience. As such, many aspects of the model await empirical testing. Nevertheless, we reviewed several lines of empirical research that are supportive of the PRISM model's predictions. The model explains why predispositions to high mobilization of resources (e.g., fear of negative social evaluation) relate to low mobilization in conditions that reflect the cumulative effects of high mobilization that increase PRISM. Because the PRISM model predicts dramatic changes in resource mobilization and even opposite associations with predictors over time, the model may help to resolve previous inconsistencies in the literature. Moreover, PRISM may bring patterns and effects to light that were previously obscured by an opposite effect at different points of PRISM dynamics that cancel each other out.

The various parameters of the PRISM resource model are not typically simultaneously measured or manipulated in a single experiment. This leaves the outcomes of most experiments underdetermined in terms of the PRISM resource model. In such cases, multiple interpretations are possible, and it may seem like there is always a possible interpretation in line with PRISM. This is the case for any model consisting of more than two parameters and a nonlinear relationship, as such a situation surpasses the complexity of most experiments. However, in many areas of inquiry, such complexity is necessary for developing meaningful approximations of reality. Hence, the underdetermination of many experiments that have been conducted so far for testing the PRISM model cannot be regarded a weakness of the model. Future experiments may measure or manipulate the various parameters of the PRISM model to obtain more conclusive evidence for or against the model, and increase our knowledge and understanding regarding the relevant values and ranges of the parameters.

Several details of the model need to be worked out. For instance, does PRISM inhibit affect as well as resource mobilization? Whether a reduction of affect that is found may depend on the level of affect in the non-PRISM control group or the condition, and whether moods are measured that are relevant to both PRISM and the experimental context. If PRISM decreases the level of perceived resources, then theories that affective states reflect levels of perceived resources (Sect. 6.6) suggest that PRISM inhibits (some) affect. However, measures of affective distress may relate positively to PRISM (e.g., Wardenaar et al. 2011) because it is the resource mobilization associated with distress that causes the protective inhibition and PRISM. State intensity may relate positively; chronicity or accumulation of intensity over time may relate negatively to mobilization of resources (reflecting PRISM). However, because state and trait (i.e., chronic) affect tend to be positively associated, their opposite correlations with resource mobilization may cancel each other out, hiding both relationships (MacKinnon et al. 2000). One way of resolving this problem is to measure both state and trait (or chronicity) variables and include them simultaneously in regression analyses as predictors of resource mobilization, such that the relationship of each predictor with resource mobilization is controlled for the opposite mediated relationship through the other predictor, and suppressed effects are uncovered (e.g., Tops et al. 2008).

The PRISM resource model thus draws attention to methodological issues such as inverted U-shaped relationships and suppressor variables, individual differences, and dynamic processes that evolve over time. The model also helps to identify variables or covariates that may be essential in stress coping research, such as levels of perceived (e.g., social) resources and potential motivation. Addressing these issues in future research may increase the consistency and interpretation of results of research on resource mobilization, chronic fatigue, and resilience.

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Part II

Interactions between Affect and Cognition in Self-Regulation

Affective Modulation of Cognitive Control: A Biobehavioral Perspective

7

Henk van Steenbergen

7.1 Introduction

A life well lived depends on a delicate balance between immediate and delayed rewards, between convenience and effort expenditure, and between letting go and hanging on. By keeping higher goals in mind, people may choose to resist an excess of leisure in favor of personal growth, for example, or permit themselves to give in to the pleasure of a well-earned vacation. That is, throughout life, people need to flexibly adapt their efforts to control their behavior.

The task of adapting one's efforts to varying life demands has been of longstanding interest to self-regulation researchers (e.g., Brehm and Self 1989; Carver and Sheier 1988; Duval and Wicklund 1972; Kuhl 1984). In more recent years, however, this topic has attracted increased attention among cognitive psychologists, who have become interested in the question how people adjust their levels of cognitive control to changes in task demands (Botvinick et al. 2001). Relatively to self-regulation research, cognitive control research has conducted more fine-grained analyses of active control processes in seemingly affectively neutral tasks that are somewhat artificial, but also subject to higher levels of experimental control. Despite these methodological differences, it is becoming increasingly apparent that self-regulation and cognitive control strongly overlap (e.g., Jostmann and Koole 2007; Robinson et al. 2010).

One area in which cognitive control research is particularly converging with self-regulation research has focused on the affective modulation of cognitive control (e.g., Dreisbach and Goschke 2004; van Steenbergen et al. 2009). Originally, most researchers thought of cognitive control as a "cold" cognitive process that operates more or less independently of affective processes. Recent studies, however, have shown that cognitive control is strongly modulated by affective factors, such as reward, humor, and mood (e.g., Dreisbach and Fischer 2012b; van Steenbergen et al. in press). Moreover, there appears to be significant overlap in brain areas involved in cognitive control and affective processes (Shackman et al. 2011). These new findings have great potential for informing not only cognitive control research but also self-regulation research, which has traditionally paid more attention to emotion (e.g., Baumeister et al. 1994; Koole 2009; Kuhl 2000). To further exploit this potential, the present chapter reviews recent research on the affective modulation of cognitive control.

In the following paragraphs, I set the stage with a brief discussion of modern research on cognitive control and control adaptation processes. Next, I turn to theories about affect and cognitive control and effort, and how these would predict affective modulation of control adaptation. This is followed by a review of recent empirical findings concerning the hedonic marking of cognitive

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control, and the effects of emotions, affect, stress, and stress-related psychopathology on cognitive control adaptation. I further review recent neuroimaging studies that hint at a possible neural mechanism that supports hedonic regulation. Finally, I summarize my main conclusions and consider implications of this work for understanding the biobehavioral foundations of self-regulation.

7.2 Cognitive Control and Adaptation

One central issue that experimental psychologists have been examining since the 1950s is how humans are able to focus their attention on relevant information and shield it against distraction from irrelevant information. This process, referred to as executive function or cognitive control, is thought to originate from prefrontal neural systems that orchestrates goal-driven behavior and self-control (Norman and Shallice 1986; see also Broadbent 1958; Posner and Snyder 1975; Shiffrin and Schneider 1977).

Cognitive control is typically investigated with laboratory tasks assessing response times, such as the classical Stroop task (Stroop 1992). The latter task requires participants to name the ink of color words, whereas the word itself should be ignored. When the name of a color (e.g., “blue,” “green,” or “red”) is printed in a color not denoted by the name (e.g., the word “green” printed in red ink instead of green ink), people are typically slower to name the colors and tend to make more errors compared to when the color of the ink matches the name of the color. This so-called Stroop effect shows that controlled processing usually cannot completely overcome the automatic tendency to read the word (Cattell 1886; Macleod 1991). Because the efficiency of focused attention in the Stroop task determines performance, this paradigm is a valuable tool to investigate the dynamics of cognitive control under the influence of modulating factors, such as affect and motivation. Similar measures can be obtained with other laboratory conflict tasks, such as the flanker task (Eriksen and Eriksen 1974) and the Simon task (Simon 1969).

One important function of cognitive control is to adapt the cognitive system to situational demands (Kahneman 1973). Because energy is limited, people typically invest effort only proportionally to the demands at hand (Ach 1935; Brehm 1999; Hillgruber 1912), and such adaptation has been observed in physiological measures of effort mobilization (Gendolla and Richter 2010). Notably, similar adaptation also occurs on a trial-to-trial level in conflict tasks that use a mixed presentation of incompatible and compatible stimuli (see Fig. 7.1a). Here, the conflict of the immediately preceding trial typically results in an adjustment in performance indicative of an increase in cognitive control (Egner 2007; Gratton et al. 1992). Specifically, as shown in Fig. 7.1b (left panel), the Stroop effect is smaller on trials that follow incompatible (conflict) trials than on trials that follow compatible (no-conflict) ones. This sequential congruency effect has often been dubbed “conflict adaptation,” and is thought to reflect an adaptation in cognitive control driven by the conflict in the previous trial (Botvinick et al. 2001; Egner 2007; Gratton et al. 1992; for alternative views see Hommel et al. 2004; Mayr et al. 2003; Schmidt 2013).

Conflict-monitoring theory (Botvinick et al. 2001) has proposed that adaptations in cognitive control originate from signals involving a conflict monitor localized in the medial parts of the prefrontal cortex (PFC), in particular the anterior cingulate cortex (ACC). The ACC is thought to signal the need for additional control to other more lateral regions in the PFC that implement subsequent top-down control (Botvinick et al. 2001; cf. Berlyne 1960). More recent work has shown that trials involving difficulty without conflict also trigger behavioral adjustments, as observed in tasks that use words that are difficult or easy to read (Dreisbach and Fischer 2011). It is thus likely that signals from the ACC indicating differences in task difficulty or disfluency are sufficient to drive adaptations in cognitive control. In this chapter, I therefore use the term “control adaptation” or “adaptive control” to refer to adaptations in cognitive control in response to changes in task demands.

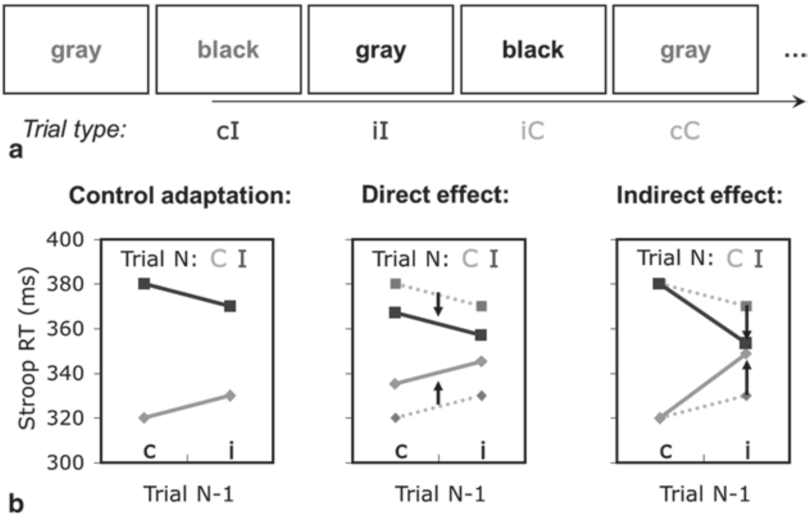

Fig. 7.1 **a** Example of a randomly selected sequence of Stroop trials being either compatible (*C*) or incompatible (*I*). Sequential-effect analyses compare current-trial compatibility effects (as indicated by uppercase letters *C* and *I*, trial *N*) on behavior as a function of the compatibility of the preceding trial (indicated by lowercase letters *c* and *I*, trial *N*-1). **b** *Left panel:* a typical example of control adaptation: The Stroop interference effect is smaller on trials that follow incompatible trials than on trials that follow compatible ones. *Middle panel:* A possible direct improvement of sustained cognitive control will reduce the interference effect; in other words, it results in a main effect on current compatibility. *Right panel:* A possible indirect improvement of cognitive control will increase conflict adaptation: the interference effect following a conflict trial is reduced in these cases

7.2.1 Theories About Affect and Cognitive Control

It has long been recognized that focused attention is not only needed in situations of cognitive demands and conflict but that it should also be mobilized when coming across dangerous situations where habitual actions are maladaptive (Baddeley 1972; Norman and Shallice 1986). Cognitive control adaptations might thus be driven by negative affective signals in general, of which conflict and demands are just a special case. Indeed, the idea that negative states modulate attention has a long tradition in psychology. For example, a link between negative affect and increased attentional focus has been suggested by theorists such as Easterbrook (1959), Derryberry and Tucker (1994), Schwarz (1990) and Fredrickson (2001), and it has been proposed that these changes reflect an effect of top-down control processes (Rowe et al. 2007; Vanlessen et al. 2013).

However, studies that have directly tested whether negative affective valence produces a sustained increase in attentional focus and cognitive control have provided mixed findings. Whereas the visual scope of attention has been found to be modulated by affective states when using the Navon task or detection tasks that involve neural measures of visual processing (Gasper and Clore 2002; Rossi and Pourtois 2012; Schmitz et al. 2009; Vanlessen et al. 2013), evidence for a similar affective tuning in conflict tasks is less consistent. Although some studies observed that, compared with positive affect, negative affect increases sustained cognitive control and thus reduces the main interference effect (e.g., the Stroop effect), other studies have not observed such direct effects (e.g., Chajut and Algom 2003; Bruyneel et al. 2013; Martin and Kerns 2011; Rowe et al. 2007; van Steenbergen et al. 2011). In addition, recent work has also suggested that affective tuning effects are more context specific than previously thought

(Huntsinger 2012). Moreover, some researchers have suggested that motivational intensity rather than affective valence drives attentional tuning (Kuhl 2000; Kuhl and Kazen 1999; Gable and Harmon-Jones 2008, 2010). Which affective dimensions determine attentional breath is an issue currently under discussion (cf. Friedman and Forster 2010, 2011; Harmon-Jones et al. 2011) and outside the scope of this chapter.

7.2.2 A New Approach: Testing Effects on Control Adaptation

In a more recent line of research, we have investigated the modulation of *dynamic adaptation* in cognitive control rather than the direct modulation of the interference effect itself. Changes in control adaptation may occur when affective states introduced in the task modulate emotional responses that were triggered by the task demands. Such indirect modulation might influence the strength of adaptive control as measured in trial-to-trial adjustments. As illustrated in Fig. 7.1b, such indirect effects on control adaptation can be dissociated behaviorally from direct effects on base levels of control. In other words, instead of a general reduction of the interference effect which would reflect an enhanced sustained or base level of interference control (Fig. 7.1b mid-panel), increased control adaptation is indexed by a reduced interference effect following a previous conflict trial only (Fig. 7.1b right panel).

The basic assumption of this line of research is that demanding situations trigger a negative, aversive state (cf. Botvinick 2007; Proulx et al. 2012). Ideas along these lines go back to the classic "law of least effort" (e.g., Gibson 1900; Hull 1943), which states that organisms tend to minimize the amount of effort they put into a task. Consequently, demands are typically evaluated as being costly and trigger avoidance behavior when possible (Botvinick 2007). One of the functions of this demand-driven negative affective state may be to guide future behavioral optimization, such as the improvement of control in order to avoid future occurrence of conflict (van Steenbergen et al. 2009). That is, demands might become hedonically marked (Lewin 1935; Morsella et al. 2011; Winkielman et al. 2003), and the aversive state associated with demands might help to subsequently mobilize cognitive effort.

Affect introduced during demanding tasks is expected to modulate demand-driven effort mobilization in an affect-congruent way (cf. Cabanac 1992). That is, positive affect might undo the negative state triggered by the demand, whereas negative affect might intensify it. Evidence for undoing effects comes from studies showing that positive affect counteracts cardiovascular aftereffects of negative affect (Fredrickson et al. 2000). Relatedly, mood states may carry diagnostic information (Schwarz and Clore 1983) which determine how task demands are evaluated. The amount of effort mobilized may depend on these appraisals (Gendolla 2000). Accordingly, negative affect increases the perceived task difficulty resulting in increased effort mobilization, albeit only as long as success is experienced to be possible and worthwhile (Gendolla 2000; cf. Brehm and Self 1989; Kahneman 1973; Kukla 1972). Control adaptation may thus go hand in hand with these changes in effort.

Figure 7.1b illustrates how affect might regulate the transient trial-to-trial adaptations typically observed in cognitive control tasks. If it is the aversive quality of a demand that drives the improvement of cognitive control observed following conflict, it should be possible to modulate such control operations using an affect induction. Accordingly, positive states may reduce conflict adaptation whereas negative states increase it (see Fig. 7.1b right panel, for an example of increased adaptation).

7.2.3 Hypothesized Neural Mechanism

At the neural level, affect might regulate cognitive control via subcortical areas modulating the PFC (Miller and Cohen 2001). The need for allocating additional cognitive control may be signaled by medial parts of the PFC, in particular the ACC. According to conflict-monitoring theory, conflict is detected in the ACC, which drives control adaptation by signaling the need for amplified goal-related processing to the lateral PFC (Botvinick et al. 2001). More recently, it has been shown that the ACC not only monitors information-processing conflict and demands but also responds to many events involving negative affect, such as monetary loss, pain, negative feedback, and social rejection (Botvinick 2007; Bush et al. 2000; Shackman et al. 2011). It is thus possible that affective modulation of control adaptation is supported via the neural integration of demand-related and affective-state signals in the ACC.

Preliminary evidence for the integrated coding of the conflict and affective signals in the ACC comes from studies measuring the so-called error-related negativity (ERN) in affective contexts. The ERN is a change in electrical brain potentials that occurs quickly after people have made a mistake. Localization studies indicate that the ERN likely originates from the ACC (Ridderinkhof et al. 2004) and might reflect the affective evaluation of performance errors (Hajcak 2012). Several studies have shown that negative affect is associated with amplified ERNs (e.g., Aarts and Pourtois 2010; Luu et al. 2000; Wiswede et al. 2009a) whereas positive affect is related to reduced ERNs (e.g., van Wouwe et al. 2011; Wiswede et al. 2009b). A similar modulation in the ACC during correct conflict trials might drive the modulation of adaptive control. That is, the ACC response to demands might be amplified in a negative affective context, which consequently increases control adjustments. Similar effects have been observed in a wide range of other palliative adaptations in response to changed task demands (Proulx et al. 2012).

The possibly opposing influences of demands and positive affect might reflect some compensatory effects at a neurotransmitter level. For example, Holroyd and colleagues (Holroyd et al. 2008; Holroyd and Coles 2002) have suggested that negative and positive events interact via dopamine modulation, which drives ACC activity. Conversely, there is evidence suggesting that the ACC sends feedback signals down to the midbrain, via the striatum—the input structure of the basal ganglia (BG)—to inhibit dopamine neurons (Frank 2005). Moreover, animal studies have shown that that both the striatum and the pallidum—the BG output structure—are involved in positive states. In particular, regions within the ventral striatum (VS) and ventral pallidum (VP) comprise so-called hedonic hotspots, which generate hedonic states in animals when stimulated, depending on opioid signaling (Haber and Knutson 2010; Kringelbach and Berridge 2009). We have hypothesized that affective influence on adaptive control is supported by neural interactions between these hedonic hotspots and the ACC (van Steenbergen et al. 2014; cf. Botvinick et al. 2009; Haber and Knutson 2010; Heimer et al. 1982).

7.3 Review of Empirical Findings

7.3.1 The Hedonic Marking of Cognitive Conflict

Although there is quite some evidence that processing fluency becomes hedonically marked (e.g., Morsella et al. 2011), researchers have only recently started to study whether conflict as elicited in cognitive control tasks also elicits negative affect. Using a variant of the affective priming task, Dreisbach and Fischer (2012a) have introduced congruent and incongruent Stroop color-word primes before an affective target. They found that incongruent Stroop color words facilitated the evaluation of negative targets. These data thus support the idea that conflict stimuli are automatically evaluated as negative events which then facilitate the evaluation of negative targets and slow down the evaluation of positive targets.

In a follow-up study, Fritz and Dreisbach (2013) have demonstrated that Stroop color-word primes also affect the spontaneous judgments of subsequent affective neutral stimuli. Here, it was observed that neutral target stimuli were more frequently judged as negative after conflict than after nonconflict primes. This study thus provides converging evidence for the idea that Stroop conflict is associated with negative evaluation.

Studies from other laboratories have focused on avoidance behavior possibly triggered by cognitive conflict. In line with data showing that participants avoid cognitive demands (Kool et al. 2010), it has been shown that participants systematically avoid choosing a task with a high proportion of conflict trials (Schouppe et al. 2013). A higher urge to quit following incongruent trials has also been reported (Lynn et al. 2012).

Schouppe and colleagues (Schouppe et al. 2012) have suggested that in standard conflict tasks, pressing a response button associated with the correct target could actually be qualified as an approach response. If conflict triggers avoidance actions, it is therefore possible that the typical slowdown observed on incongruent trials might reflect an incompatibility between the elicited avoidance tendency and the required approach response. If this is true, the compatibility effect would be reduced when participants use an avoidance response. This was indeed what their data showed, especially for Stroop trials inducing stimulus conflict.

Additional evidence for the affective marking of conflict comes from studies using psychophysiological measures of affect. For example, many studies have shown that conflict processing across different tasks is associated with elevated levels of arousal as measured with galvanic skin response (GSR) and pupil dilation (Brown et al. 1999; Laeng et al. 2011; Siegle et al. 2004, 2008; van Bochove et al. 2013; van Steenbergen and Band 2013; van Steenbergen et al. in press). Such findings suggest that elevated emotional arousal might be an important characteristic of conflict processing, in particular because trial-to-trial effects in arousal closely mirror similar behavioral patterns of control adaptation (van Steenbergen and Band 2013).

We have suggested that it is likely that only certain types of emotional arousal—such as those combined with a negative valence (cf. Thayer's (1989) conception of "tense arousal") drive improved control and adaptation effects (van Steenbergen et al. 2011; van Steenbergen and Band 2013). However, facial corrugator muscle activity, an established physiological marker of negative valence that responds to aversive stimulation (e.g., Larsen et al. 2003) and cognitive and physical effort (e.g., Boxtel and Jessurun 1993; Cacioppo et al. 1985; de Morree and Marcora 2010) has been shown to be insensitive to conflict, at least when measured in a Simon task (Schacht et al. 2010). Thus, further investigation is warranted.

Taken together, recent studies have shown to provide substantial evidence for the idea that conflict becomes hedonically marked. Effects of conflict were observed in measures of negative evaluation, avoidance behavior, and physiological measures of arousal. Future studies have to investigate whether physiological measures of affective valence are also sensitive to conflict.

7.3.2 Effects of Short-Term Affect on Adaptive Control

Although there is now accumulating evidence for the idea that conflict processing elicits aversive affect, this does not necessarily prove a causal role for affect in producing control adaptations. Demonstrating a causal role of conflict-driven aversion requires experimental manipulation; if negative valence drives conflict-driven control adaptations, such adaptation should be countered by a manipulation that undoes the affective consequence of conflict (van Steenbergen et al. 2009).

In a first attempt to demonstrate this effect, we (van Steenbergen et al. 2009) have introduced short-term positive affect immediately following conflict trials in a flanker task. We hypothesized that a positive state introduced immediately after the conflict trial would counteract the aversive quality of conflict and subsequent control adaptation. In the task we presented, participants were shown happy, sad, or neutral smiley faces that signaled an unexpected monetary gain, loss, or no gain/loss immediately following a response to the flanker trial. In line with predictions, the arbitrary feedback between trials affected subsequent control adaptations: Standard control adaptation effects were found in the loss and neutral conditions, whereas no adaptation was observed in the gain condition (van Steenbergen et al. 2009). Consistent with the notion that effortful situations are aversive (Botvinick 2007), this finding thus suggests that incompatible trials trigger a negative affective state that, unless neutralized by a positive event such as a monetary reward, increases adaptive control. A follow-up study using electroencephalography (EEG) replicated this modulation in behavioral adaptation (van Steenbergen et al. 2012a).

However, more recent studies from other laboratories have shown that it is highly unlikely that positive affect sui generis counteracts control adaptation. Note that in our work feedback was presented independently of the actual response made by the participants. In contrast, a study by Sturmer et al. (2011) that presented feedback contingently on performance in a Simon task observed that reward increased control adaptation. In another study by Braem et al. (2012), it was also found that performance-contingent reward increased control adaptation. Taken together, these studies suggest that, in contrast to the decreased control adaptation observed following random reward, performance-contingent reward actually increases control adaptation.

To account for the improved conflict-adaptation effect following performance-contingent reward, it has been suggested that reward might enhance cognitive control (Sturmer et al. 2011). It is also possible that reward signals reinforce task-specific representations and the response, which accounts for both increased conflict adaptation and increased conflict-driven task switch costs observed following reward (Braem et al. 2012). Differences in motivation rather than affect might also be important (Braem et al. 2012; van Steenbergen et al. 2012a). In a recent review of these conflicting findings, Dreisbach and Fischer (2012b) have speculated that the positive affective reaction produced by random gains is different from the affective reaction triggered by successful task performance. According to this account, successfully overcoming conflict might involve an intrinsic reinforcement signal (Satterthwaite et al. 2012) that is further enhanced by external performance contingent reward (Braem et al. 2012). On the other hand, noncontingent random reward might actually counteract this signal, as it might convey information that task performance is not a value by itself.

However, independent of these reward effects, high-arousing stimulation might also modulate control adaptations. This was demonstrated in a recent study by Padmala and colleagues (Padmala et al. 2011). These authors used arousing negative pictures, such as mutilated bodies, presented as arbitrary stimuli in between Stroop trials. The data showed that these negative pictures (in comparison to neutral pictures) prolonged reaction times and reduced control adaptation. Their data are in line with the suggestion that arousing stimuli may bias attention and expend or divert resources needed for control implementation (Pessoa 2009; cf. Schwarz 1990). Indeed, manipulation of task load (without emotional stimuli) has also been observed to reduce adaptation effects (Fischer et al. 2008; Soutschek et al. 2013). Notably, a very recent study by Braem and colleagues (Braem et al. 2013a) suggests that this effect might depend on trait punishment sensitivity. In this study, performance-contingent punishment was shown to increase control adaptation in low punishment-sensitive participants (as measured by the Behavioral Inhibition System scale), whereas high punishment-sensitive participants instead showed prolonged conflict-driven reaction times in the absence of increased adaptation. Thus, high-arousing stimuli that compete for shared resources may bias attention away from the main task which might result in reduced control adaptation.

To summarize, some data suggest that short-term positive affect can counteract control adaptation. However, motivation and arousal are also likely to play an important role in the adjustment of cognitive control. Future studies are needed to understand and dissociate the influence of these effects of affect, motivation, and arousal and their possible interactions.

7.3.3 Effects of Sustained Affect on Adaptive Control

We have recently also started to investigate how sustained affect—as opposed to short-term affect, i.e., emotions—induced prior to the conflict task modulates adaptive control. The mood behavior model (MBM) predicts that hedonic tone in sustained affective states such as mood modulates the appraisal of demand-related effort mobilization (Gendolla 2000). Along the same lines, we have hypothesized that adaptive cognitive control is mobilized proportional to the level of experienced task difficulty (van Steenbergen et al. 2010). Thus, control adaptations might be stronger when participants are in a negative mood in comparison to a positive mood.

To test this prediction, in one of our studies (van Steenbergen et al. 2010) we have used an affect-induction procedure in order to manipulate the participants' mood state. Critically, even though the MBM framework predicts affective valence (i.e., whether affect is positive or negative) effects only, this study investigated the impact of other affective factors as well. Since the work of Wilhelm Wundt (cf. Reisenzein 1992), emotion researchers have been using dimensional descriptions to account for the wide variety of affective states. As a result, several different theoretical frameworks have emerged that describe affective states with various dimensions and structures, including Russell's (1980) circumplex model, Watson and Tellegen's (1985) positive and negative affect distinction, Thayer's (1989) dissociation between tense and energetic arousal, and Larsen and Diener's (1992) description of eight combinations of pleasantness and activation. Recent psychometric studies have shown that all these models share a similar structure, which can be described with a Cartesian space that includes the dimensions valence and arousal (Yik et al. 1999). The valence or hedonic axis defines where affect is on a bipolar pleasant versus unpleasant dimension, whereas the arousal axis indicates the arousal or activation level on a low activation (sleep) versus high activation dimension.

Given these two fundamental dimensions, we investigated four groups of participants who underwent a standard mood-induction manipulation before performing a conflict-evoking flanker task. (cf. Jefferies et al. 2008). The four derived moods that were induced were anxiety (low pleasure, high arousal), sadness (low pleasure, low arousal), calmness (high pleasure, low arousal), and happiness (high pleasure, high arousal). In line with our prediction that negative effect would produce stronger conflict-driven adaptation effects, we observed reduced adaptive control for participants with low pleasure levels (anxious and sad participants) in comparison to participants with high pleasure levels (calm and happy participants). Notably, this effect was not accompanied or modulated by effects of arousal level; participants with high-activation moods (anxious and happy groups) did not show differences in adaptation effects in comparison with participants in low-activation moods (sad and calm groups; van Steenbergen et al. 2010).

Using a similar approach, Kuhbandner and Zehetleitner (2011) recently investigated the effect of pleasure and arousal on performance in a visual pop-out distractor task. Consistent with our findings, they observed reduced control adaptation for the positive in comparison to the negative affect groups. However, unlike our results, they also observed a main effect of arousal on sustained cognitive control as measured with the interference effect. High-aroused participants were more sensitive to distraction than low-aroused participants. Using computational modeling, Kuhbandner and Zehetleitner (2011) further demonstrated that these effects on control adaptation versus interference reflect independent effects on control adaptation versus base level of control.

We have also studied the effect of a more implicit manipulation of bodily states, probably associated with affective valence (Cacioppo et al. 1993; but see also Harmon-Jones and Allen 1998). Here, we tested whether approach and avoidance body feedback as induced with an arm flexion versus extension also impacted control adaptation (Hengstler et al. in press). In line with an affective valence account, approach was indeed associated with less control adaptation in comparison to the avoidance condition. In addition, independently of the effects on adaptation, the avoidance state also increased sustained control as indicated by a reduced interference effect (Koch et al. 2008; Koch et al. 2009). These findings thus suggest that motor feedback aspects of affect might play an important role in the modulation of adaptive control.

To summarize, across different manipulations of sustained affective states and across different tasks, it has been observed that the valence dimension of affect determines control adaptations: More negative affect was found to be associated with more control adaptation, whereas more positive affect was associated with less control adaptation. Motor feedback aspects of affect might play an important role in this modulation.

7.3.4 Effects of Depression and Stress on Adaptive Control

We have also started investigating the effects of depressive symptoms on control adaptation. Here, we considered that—analogous to negative mood effects in healthy samples—dysphoria in remitted depressed individuals may similarly improve demand-driven behavioral adaptation. Enhanced demand-driven effort recruitment in depression has indeed been demonstrated in cardiovascular measures (Brinkmann and Gendolla 2007).

To test the effects of depression on control adaptation, we have analyzed the effects of a pharmacological manipulation (acute tryptophan depletion, ATD) in remitted depressed participants on control adaptation as measured in a Simon task. ATD is known to lower central serotonin levels, which increases depressive symptoms in vulnerable populations. Our results confirmed predictions: ATD-induced depressive symptoms were associated with more control adaptation (van Steenbergen et al. 2012b).

It is important to note, however, that the effects of transiently induced depressive symptoms reported here may differ from the chronic effects observed in depressed patients. As other studies have shown, depression has been associated with reduced control adaptation (Clawson et al. 2013; Meiran et al. 2011; Pizzagalli 2011). It is possible that differences in task-difficulty appraisal account for these conflicting findings. As mentioned earlier, MBM theory (Gendolla 2000) proposes that the association between mood and effort mobilization is linear only up to the point that success is possible and worthwhile for the participant. However, when demands become perceived as too high to actively cope with, negative mood may actually trigger demand-driven disengagement (cf. Brehm and Self 1989; Kahneman 1973; Kukla 1972). Evidence for this effect has been reported in mood-induction studies and can also be shown in dysphoric participants when they perform tasks with extremely high fixed demands (Brinkmann and Gendolla 2008). Thus, it is possible that depressive patients show reduced control adaptation because they experience conflict as too difficult to adequately cope with.

More evidence for reduced control adaptation comes from stress research, which often exposes people to extreme demands that are difficult to cope with. For example, reduced control adaptation has been observed when participants are exposed to the Trier Social Stress Task in comparison to a control group (Plessow et al. 2011). Decreased control adaptation has also been observed when participants receive negative feedback concerning their task performance, an effect that is particularly strong in (subclinically) depressed participants (Holmes and Pizzagalli 2007).

Collectively, these observations suggest an inverted-U relationship between negative affect and control adaptation (cf. Brehm and Self 1989). It is an important aim for future studies to understand the generalizability of these findings and to disentangle the effects of increased negative affect and putative reduced availability of resources (e.g., due to rumination) in depression (cf. Meiran et al. 2011) as well as in other mood and anxiety disorders (cf. Larson et al. 2013). MBM theory assumes that the interaction between both factors determines the actual appraisal of the demand, which in turn modulates effort mobilization. Future studies might test whether this also holds true for control adaptations.

7.3.5 Neural Mechanisms

As described earlier in this chapter, indirect effects of affect on cognitive control may involve the PFC, in particular its medial parts including the ACC. To test this hypothesis, in one study we (van Steenbergen et al. 2012a) recorded EEG while participants responded to the flanker task with smileys presented during the intertrial interval (cf. van Steenbergen et al. 2009). The EEG allowed us to analyze neural oscillations in the theta band, which are likely to originate from the ACC and the surrounding medial frontal wall (Cohen et al. 2008). In line with conflict-monitoring theory (Botvinick et al. 2001) and previous findings, frontocentral theta power was increased by flanker conflict. More importantly, positive feedback following conflict inhibited this neural oscillation. Based on these findings, it might be argued that theta oscillation provides an index of ACC activity signaling the need for more cognitive control, and that the inhibition of this signal by reward prevented the subsequent control adaptation as observed in behavior.

Given that ACC modulation might originate from subcortical areas related to the processing of positive affect, such as the BG, fronto-striatal interactions were investigated in another study using functional magnetic resonance imaging (fMRI). In this study, funny versus neutral cartoons were used to manipulate participants' hedonic state before they performed a flanker task (van Steenbergen et al. in press). In line with predictions, humor was shown to decrease control adaptation. In addition, it increased neural activity in regions usually associated with hedonic states, particularly in the VS and VP, so-called hedonic hotspots that are responsible for pleasure causation in animals (Kringelbach and Berridge 2009). We observed that activity in these areas, in turn, inhibited the neural response to conflict in a rostral ACC (rACC) region. Activation in this region also proved predictive of adaptive control improvement in the neutral context. Thus, it is likely that the rACC is involved in the affective appraisal of task demands and/or online control improvements, driving performance adaptations as observed in the subsequent trial. Inhibition of this rACC response by positive affect might have prevented this control adaptation.

In the same study, we also showed that activity in the dorsal ACC (dACC) was co-modulated with behavioral adaptation, suggesting that it is involved in monitoring the conflict at hand. Given the aversive quality of cognitive demands, it is likely that activity from the dACC acts as a general aversive (Botvinick 2007) or error signal (Alexander and Brown 2011; Dreisbach and Fischer 2012a; Proulx et al. 2012) that inhibits hedonic processing in the VS (Leknes and Tracey 2008).

Functional connectivity analyses further confirmed the interactions between conflict and hedonic areas. Results showed that neural signals in the VS were negatively coupled (anticorrelated) with dACC, whereas the VP was negatively coupled with rACC. Given these findings, it is most likely that the VP modulates rACC activation, which in turn drives conflict-driven control. The resulting adaptation might subsequently be registered in the dACC, which then sends feedback signals back to the VS. Affective state is likely to modulate these interactions via the BG (van Steenbergen et al. in press). Figure 7.2 illustrates these interactions.

Taken together, our neuroimaging findings are in line with predictions from the conflict-monitoring theory suggesting that the ACC plays an important role in the online evaluation of demands, which may subsequently drive extra cognitive control. Indirect affective modulation of cognitive control probably involves the modulation of rACC and dACC activity via reward-related processing in the VS and the VP (van Steenbergen et al. in press). The exact temporal dynamics and neurochemical basis of this neural circuitry have not been investigated yet.

7.4 Future Directions

7.4.1 Different Affects, Different Effects

Although many studies reviewed in this chapter found evidence for emotion and mood effects on adaptive control, some studies have shown that it is not likely that positive affect sui generis reduces adaptation effects, in particular not when short-term affect is induced. For example, de-

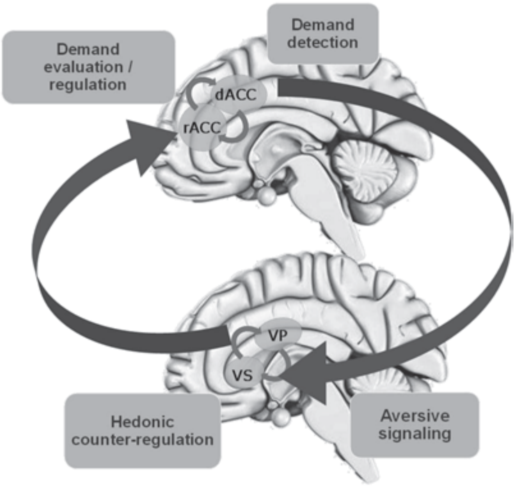

Fig. 7.2 Interactions between basal ganglia and ACC that are likely to support the affective modulation of control adaptation. *Labels* indicate the proposed function of the respective areas. *rACC* rostral anterior cingulate cortex, *dACC* dorsal anterior cingulate cortex, *VS* ventral striatum, *VP* ventral pallidum. (Reprinted by permission from Oxford University Press: Cerebral Cortex, van Steenbergen et al. (in press), copyright (2014))

pending on the way the reward manipulation was implemented, decreased (van Steenbergen et al. 2009; van Steenbergen et al. 2012a) versus increased (Braem et al. 2012; Sturmer et al. 2011) control adaptation was observed (see also Braem et al. 2013b).

One critical issue for future research is to investigate which underlying dimensions or aspects of reward drive increases versus decreases in adaptive control. For example, research by Berridge and colleagues (e.g., Berridge and Robinson 2003) has shown that reward involves different components, including learning, affect (liking), and motivation (wanting). As has recently been argued by Chiew and Braver (2011), it is likely that those components have different effects on cognitive control. We have proposed that affective liking might be associated with reductions in adaptive control, whereas motivational states (wanting) increases adaptive control (van Steenbergen et al. 2012a; cf. Gable and Harmon-Jones 2011).

Considering the diverging findings from studies on negative mood, depression, and stress, the influence of negative affect also needs further study. Building on the assumed nonlinearity between task demands and effort mobilization (Brehm and Self 1989; Kahneman 1973; Kukla 1972), we have postulated that the relationship between negative affect and control adaptation is inverted U-shaped (van Steenbergen et al. 2012b). Studies investigating control adaptation may investigate this possibility by manipulating multiple levels of conflict/task difficulty (cf. Forster et al. 2011) and affective valence.

7.4.2 Neurochemistry

Although BG–ACC interactions are likely to drive affective modulation of control adaptation, the neurotransmitter systems supporting this modulation are currently not known. Although many neurotransmitters have been proposed to modulate cognitive processing by adjusting neural signal-to-noise ratios, it is likely that dopamine and opioids are among the central ones involved in the affective and motivational modulation of cognitive control (Aarts et al. 2012; Chiew and Braver 2011).

It is possible that the BG–ACC interactions identified by our research, in particular those between dACC and VS, critically depend on dopamine. Dopaminergic signaling might support control adaptations (cf. Duthoo et al. 2013; van Bochove et al. 2013), especially their motivational aspects (Barbano and Cador 2007; Berridge 2007; Kringelbach and Berridge 2009; Leknes and Tracey 2008). On the other hand, recent evidence suggests that the hedonic dimensions (liking) of affect are under control of opioid transmission (Barbano and Cador 2007; Berridge 2007; Kringelbach and Berridge 2009; Leknes and Tracey 2008). Because opiates can reduce or eliminate the negative emotional state induced by painful stimuli, they may also mediate the modulating role affect has on evaluating and monitoring behavioral demands (Shackman et al. 2011). Interestingly, opioid receptors have been found to be most densely distributed in the ACC, particularly in its rostral parts (Luu et al. 2000; Zubieta et al. 2003). Opioids may therefore support the informational function affect has in producing indirect effects on cognitive control, possibly via interactions between VP and the rACC. One essential topic for future research is to investigate the shared neural mechanisms of demand and pain processing (Shackman et al. 2011) and to study whether opioid signaling also mediates the hedonic impact on control adaptation.

7.4.3 Other Types of Adaptive Control

A final issue for future research to be mentioned here concerns the question how affective modulation of control adaptation is related to other measures of adaptation in experimental paradigms. For example, according to conflict-monitoring theory, adaptation to demanding events has much in common with another type of adaptation, usually referred to as post-error adaptation (Botvinick et al. 2001): Reactions after an error are usually slower than after correct trials. Because post-error slowing may reflect cautious processing in response to the error, it has been taken as an index of cognitive control. Given that both errors and demands are generally thought to be registered in the brain as aversive events, affective modulation may involve a similar mechanism, probably involving the ACC (Botvinick 2007).

Indeed, several studies have shown that negative affect amplifies the neural processing of errors, although this increased neural activation does not always modulate post-error slowing (e.g., Hajcak et al. 2004; Luu et al. 2000; Lindstrom et al. 2013). However, whether effects on post-error slowing reflect an adaptive increase of cognitive control is subject to debate. It is also possible that post-error slowing reflects attentional capture, which hinders subsequent performance (Notebaert et al. 2009). Post-error slowing has also been associated with steeper increases in negative affect and reduced task-focused coping in response to stressors in daily life, suggesting that it might be an index of maladaptive strategies (Compton et al. 2011).

Adaptations of control have also been observed in task-switching tasks. Here, conflict has been shown to impair the efficiency to subsequently switch to other tasks (Goschke 2000). Moreover, adaptation effects have been observed to reverse after task switches. This suggests that interference control also tends to reduce following conflict introduced by another task (e.g., Notebaert and Verguts 2008). Thus, conflict-driven adaptations seem to improve performance of the (local) task at hand, which is maladaptive when a switch to another task is necessary. Reward (motivation) has already been shown to increase conflict-driven task switch costs (Braem et al. 2012) and future studies should investigate whether positive affect reduces it. Such a finding would be in line with other studies linking positive affect to cognitive flexibility (Dreisbach and Goschke 2004).

Finally, it has been argued that sequential congruency effects reflect not only control adaptation but also other processes (see, for reviews, Egner 2007; Schmidt 2013). For example, stimulus/response repetitions and contingency learning likely contribute to the sequential adaptations observed (Hommel et al. 2004; Mayr et al. 2003; Schmidt and De Houwer 2011), although it is challenging to experimentally control for these effects without introducing new confounding factors (Duthoo and Notebaert 2012; Schmidt and De Houwer 2011). Nonetheless, it is not unlikely that behavioral adaptations reflect not only conflict-driven control processes but also feature binding and contingency learning (Botvinick et al. 2001; Hommel et al. 2004; Schmidt and De Houwer 2011), and/or a combination of control and learning (Verguts and Notebaert 2009). Future studies should investigate whether the influence of affect and motivation as reviewed here are affecting control adaptation specifically, or whether (a combination of) other processes are also modulated (cf. Trübutschek and Egner 2012).

Conclusions

As many studies reviewed in this chapter have shown, positive affect helps to reduce control adaptations to cognitive demands, likely by reducing the aversive state induced by these demands. Negative affect, on the other hand intensifies such adaptation—at least as long as success is possible and worthwhile. This affective modulation of control was found to be driven by neural processing in subcortical "hedonic hotspots" which attenuated demand-related processing in the ACC and behavioral adaptation.

Viewed from a broader perspective, the findings I have reviewed here demonstrate the importance of the temporal dynamics that underlie self-regulation processes; they show that cognitive control can quickly increase in response to stimuli that conflict with current goals. The ability to quickly allocate more cognitive control in challenging situations might prove critical in many situations requiring self-regulation. Particularly, quick increases in self-control might be adaptive when the stimulus that conflict with one's primary goal is only available for a short period of time. Those situations occur rather often in daily life, for example, when one passes a McDonald's while driving on a highway or when a waitress offers a delicious but unhealthy snack during a cocktail party. Transient increases in cognitive control in such situations might be sufficient to behave according with long-term goals (e.g., staying healthy). In other situations, quick increases in self-control might be sufficient to drive behavioral strategies such as moving unhealthy food out of sight or reach, making the need for intensive sustained self-control superfluous. Such flexibility in the short-term implementation and adjustment of goals has been seen as characteristic of good self-management and self-regulation skills (Baumeister et al. 1994).

The evidence for a role of affect in and on the dynamic adjustments in cognitive control, as reviewed in this chapter, emphasize the important role that affect plays in the mobilization of effort and self-control processes. Whereas positive affect might help to prevent a too strong impact of cognitive demands on self-control (Garland et al. 2010), a little bit of negative affect on the other hand might help us to stay focused when dealing with a difficult situation. In other words, positive and negative affect might help to regulate the balance between task perseveration and flexibility (Dreisbach and Goschke 2004; cf. Carver and Scheier 1990; Carver 2003; Kuhl and Kazen 1999). In this respect, both positive and negative affective states can have adaptive value for self-control when experienced in the right context (Gruber et al. 2011).

By showing how neural interactions drive adjustments in cognitive control, we have started to develop a more mechanistic understanding of self-control processes and the role that affect plays in it modulation. In particular, we have suggested that mutual interactions between hedonic hotspots in the BG on the one hand, and dorsal and rostral parts of the ACC on the other hand, drive the hedonic regulation of adjustments in cognitive control (van Steenbergen et al. in press). Examining these mechanisms further may provide new insights in the biobehavioral basis of a wide range of other phenomena where affect plays a critical role in adaptive behavior and self-regulation (cf. Proulx et al. 2012).

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Error Monitoring Under Negative Affect: A Window into Maladaptive Self-Regulation Processes

8

Kristien Aarts and Gilles Pourtois

8.1 Introduction

When making errors, we quickly detect the mismatch between our performed action and action goal, and we regulate our behavior accordingly. However, such quick error detection does not only reflect a cognitive process in the sense that it would stimulate learning exclusively but the detection of an error is also accompanied by emotional effects. When committing an error, we might for example experience arousal, sadness, anger, or anxiety. These affective processes can be either up- or downregulated depending on situational factors or personality traits. Hence, the study of error detection, and more generally action monitoring, offers a unique opportunity to explore self-regulation processes and their alterations in specific psychopathological conditions such as anxiety and depression.

8.1.1 What is Entailed by Self-Regulation?

In the literature, self-regulation has often been defined in conjunction with other constructs like self-control, impulse control, cognitive control, executive functions, or goal-directed behavior (see, for example, Bandura 1991; Muraven and Baumeister 2000). In light of these frameworks, self-regulation can be conceived as the process of regulating automatic responses, thoughts or feelings, in order to behave in accordance with internal and/or external goals. Accordingly, self-regulation can be seen as a continuous process enabling organisms to reach homeostasis by comparing the current state to the expected one. Self-regulation is therefore best visible when a deviation occurs between the current and expected state, and a remedial action or process is required in order to rapidly restore or correct this mismatch.

8.1.2 Error Commission and the Urge to Regulate the Self

Errors are prototypical instances of cases requiring self-regulation because they signal a discrepancy between the actual and the expected action. Indeed, they are often considered to be goal obstructive and hence require a change in the behavior.

However, for a long time, errors have been neglected in cognitive psychology. Rabbitt

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(1966) was one of the few researchers who investigated errors. Other cognitive psychologist researchers probably interpreted errors as rare and noisy events (i.e., attentional lapses or breakdowns in cognitive control, see O'Connell et al. 2009) that had to be excluded from the analyses.

More recently, this view has been challenged to some extent and researchers have begun to explore the causes and consequences of errors in laboratory conditions bearing in mind that these specific events might convey an important meaning for the organism and be processed by specific brain networks (Debener et al. 2005; Gehring et al. 1990). In this framework, errors are therefore important events that can be used to study brain processes involved in self-regulation. However, it is relatively challenging to explore error monitoring in laboratory conditions because errors are also rare and to be avoided events. Increasing task difficulty or decreasing stimulus visibility to increase the number of errors are non-preferred strategies, because in these conditions where uncertainty increases, the efficiency of error-detection processes is reduced (Charles et al. 2013; Notebaert et al. 2009).

To overcome this problem, specific experimental methods can be used to unlock a high number of errors within a short period of time, without blurring their goal obstructive meaning. Among them, the speeded go/no-go task stands out as a valuable procedure (Vocat et al. 2008). This task requires participants to respond to the "go stimulus," which is presented frequently but to withhold responding when encountering a specific "no-go stimulus," which is presented less frequently. Moreover, to promote the occurrence of many false alarms (FAs, corresponding to overt responses with the no-go stimulus), a response deadline (calibrated and updated for each subject separately) can be introduced in order to incite participants to adopt a fast response mode and eventually increase error commission (Aarts and Pourtois 2010). Hence, using this task, errors are relatively frequent and mainly correspond to a breakdown in inhibitory control (Miyake et al. 2000).

8.1.3 Self-Regulation During Error Monitoring and Negative Affect

As briefly outlined above, errors are not simply noisy events promoting learning (Holroyd and Coles 2002) but they also trigger affective reactions (Hajcak and Foti 2008; Pourtois et al. 2010), as well as attentional orienting effects (Notebaert et al. 2009; Ridderinkhof et al. 2009). Interestingly, converging evidence also shows that early error-monitoring brain processes are overactive in individuals characterized by high levels of negative affect or internalizing disorders (Olvet and Hajcak 2008; Vaidyanathan et al. 2012). These overactive processes during the monitoring of response errors likely reflect maladaptive self-regulation during action monitoring. In the next section, we first review the neurophysiology (electroencephalography - EEG) methods of error-monitoring brain processes, before emphasizing how negative affect influences them, with different effects when contrasting (subclinical) anxiety to clinical depression. Finally, we integrate these findings in a framework enabling us to derive hypotheses and predictions regarding the nature of maladaptive self-regulation processes in anxiety and depression during action monitoring.

8.2 The Neurophysiology of Error Monitoring

In 1990, two independent groups (Falkenstein et al. 1990; Gehring et al. 1990) described an event-related potential (ERP) component associated with error commission, the error-related negativity or error negativity (ERN/Ne). While this deflection has ever since drawn the attention of many researchers in the field, the neurophysiology of error commission is not limited to this early ERP deflection. Usually, the conscious detection of errors is accompanied by the generation of the error positivity (Pe), which is a large positive ERP component following the ERN/Ne (Falkenstein et al. 2000; Nieuwenhuis et al. 2001). Moreover, an ERN/Ne-like component

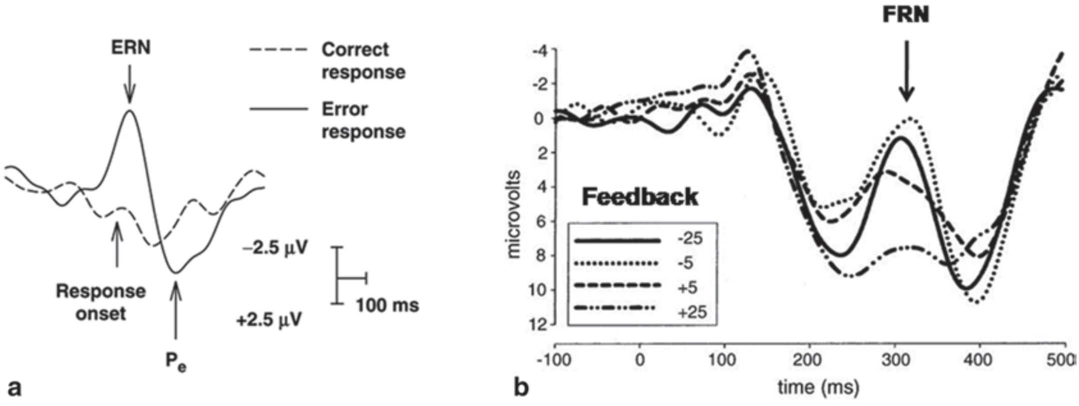

Fig. 8.1 **a** Illustration of the ERN and Pe components elicited following response errors (Amodio et al. 2006). This figure is reproduced with permission from Oxford University Press. **b** Illustration of the FRN component elicited following the presentation of external feedback (Hajcak et al. 2006). Larger FRNs were observed for monetary losses compared to gains. This figure is reproduced with permission from Elsevier

has also been reported in situations where action monitoring is based on the processing of external evaluative feedback, as opposed to internal motor representations, and was labeled the feedback-related negativity (FRN; Luu et al. 2003; Miltner et al. 1997). Hereafter we elaborate on the functional meaning of these different ERP components reflecting non-overlapping processes during early stages of action monitoring.

8.2.1 The Error-Related Negativity

The ERN/Ne is an early negative ERP component (see Fig. 8.1a), time-locked to the onset of a response error. The ERN/Ne is thought to reflect the activity of a dopaminergic-dependent system involved in action monitoring and comprising dedicated frontostriatal loops, including the rostral cingulate zone (Frank et al. 2005; Holroyd and Coles 2002). The ERN/Ne is elicited between 0 and 100 ms after the onset of an incorrect response committed during an interference task (e.g., go/no-go, Stroop, flanker, or Simon task) over fronto-central leads. Usually, a comparable negative, but smaller component than the ERN/Ne is also generated following correct responses at the same early latency; the correct-related negativity (CRN; Vidal et al. 2000). The CRN and ERN/Ne components are assumed to reflect the activity of a generic action monitoring system, whose amplitude allows to discriminate between correct and incorrect actions (Roger et al. 2010). The fact that the ERN/Ne reaches a maximum amplitude at fronto-central electrodes is consistent with the assumption that its intra-cerebral generators are located in the rostral cingulate zone or dorsal anterior cingulate cortex (dACC; Debener et al. 2005; Dehaene et al. 1994; Herrmann et al. 2004).

Several competing theories have been put forward in the literature to account for these remarkable electrophysiological properties. Initially, this ERP component was interpreted as reflecting a “cognitive” mismatch signal between the intended and actual motor action (Falkenstein et al. 1990; Gehring et al. 1993). Alternatively, Holroyd and Coles (2002) posited in their influential model that the ERN/Ne is a reward-prediction error signal. Using the reinforcement-learning framework, these authors stated that the ERN/Ne is generated when the current action is worse than the expected one. This negative prediction error is reflected by a phasic decrease of dopamine in deep midbrain regions, which releases the dACC via specific frontostriatal loops, and in turn yields the ERN/Ne component. By comparison, Botvinick et al. (2001) underscored that the ERN/Ne is not specifically elicited following response errors, but rather signals a conflict among competing responses. Finally, some authors (Luu et al. 2000; Olvet and Hajcak 2008) have advocated that the ERN/Ne corresponds to an affective evaluative signal related to the differential emotional significance of response errors. Consistent with this view, these authors have reported changes in the amplitude of the ERN/Ne as a function of the negative affective state or trait of the participants.

8.2.2 The Error-Positivity

This ERN/Ne component is usually followed by a large positive component, the error positivity (Pe; see Fig. 8.1a). The Pe is a broad deflection resembling the P3 component, peaking over the vertex 150–300 ms after response error onset, with neural generators involving more rostral anterior cingulate cortex (ACC) as well as posterior cingulate and insular cortex regions, compared to the ERN/Ne component (Dhar et al. 2011; Herrmann et al. 2004; O'Connell et al. 2007). Although the Pe has been less investigated than the ERN/Ne component, some authors have linked this positive wave component to the conscious registration of errors, likely by means of the activation of specific interoceptive processes (Dhar et al. 2011; Nieuwenhuis et al. 2001). Alternatively, it could also reflect an affective appraisal of errors (Falkenstein et al. 2000; van Veen and Carter 2002), a P300-like attention orienting response (Ridderinkhof et al. 2009), or an accumulation of evidence process timely informing about error commission (Steinhauser and Yeung 2010).

8.2.3 The Feedback-Related Negativity

Whereas the ERN/Ne and Pe components reflect error detection based on internal monitoring processes, the FRN (see Fig. 8.1b) likely reflects negative feedback detection. The FRN shares many electrophysiological properties with the response-related ERN/Ne component: It is a negative component peaking at fronto-central electrodes roughly 250–300 ms post-negative feedback onset and that is likely generated within the same dACC regions as the ERN/Ne (Gehring and Willoughby 2002; Miltner et al. 1997). According to Holroyd and Coles (2002), the same dopaminergic-dependent reinforcement learning brain system underlies the FRN and ERN/Ne. Usually, the FRN is larger for negative compared to positive feedback and it is also larger for unexpected compared to predictable outcomes (Holroyd et al. 2003). These findings point to the involvement of the FRN in the processing of the valence or reward value of the feedback.

8.3 Altered Error Monitoring in Negative Affect

Because errors are not only rare or emotionally significant events but also have a rather negative connotation and enhanced arousal value (Hajcak and Foti 2008; Pourtois et al. 2010), error-detection processes may be different in specific affective psychopathological conditions. Converging neurophysiological evidence has shown that internalizing disorders and negative affect are indeed differently related to early error- detection processes, in particular at the level of the ERN/Ne component, which is typically enhanced in these individuals (Olvet and Hajcak 2008). Before we review this evidence, we break down the construct of negative affect, and make the distinction between anxiety and depression as these two internalizing disorders seem to exert different effects on early-monitoring brain processes and in turn self-regulation.

8.3.1 Negative Affect: Dissociating Anxiety from Depression

Negative affect is one of the two dimensions that has consistently been observed as an important factor of the affective structure (Watson and Tellegen 1985). In contrast to the other affective dimension (i.e., positive affect), negative affect has been characterized by subjective distress. This negative affect characteristic has been shown to play a role in internalizing disorders (Brown 2007; Clark and Watson 1991), which is a class of disorders that is best characterized by a tendency to internalize psychological distress (Krueger 1999). Several studies reported that individuals with high levels of negative affect were experiencing more anxiety and depressive symptoms (Jylha and Isometsa 2006). However, despite the fact that anxiety and depression belong to the same class of internalizing disorders that is primarily characterized by negative affect, these two psychopathology conditions are not fully overlapping (Clark and Watson 1991), as outlined here below.

8.3.1.1 Anxiety

Phenomenology Anxiety is an adaptive warning reaction that prepares the body to react to potentially dangerous situations. Anxious reactions consist of changes at emotional, cognitive, physiologic, and behavioral levels. Anxious individuals experience, for example, high levels of negative affect (Brown 2007). They are hypervigilant (Eysenck 1992), showing a specific attention bias toward threat (Mathews and MacLeod 1994), and they show a tendency to worry or ruminate (Muris et al. 2005). Physiologically, hyperarousal is observed (Brown 2007); at the behavioral level, anxious individuals are characterized by avoidance and neuroticism (Gray 1982). Usually, these state-dependent reactions serve the function to protect us from harm (Lang et al. 2000). However, when individuals are characterized by a sustained increased sensitivity to stressors (i.e., high trait anxiety) or when anxious reactions become chronic, anxiety can become maladaptive, eventually resulting in a disorder which strongly interferes with daily life (Rosen and Schulkin 1998).

Neurobiology Because a common characteristic among anxiety disorders is excessive distress (Clark and Watson 1991), neurobiological effects of anxiety have been established based on animal models of fear (LeDoux 1996; Phelps and LeDoux 2005). What these different models share in common is the predominant role of the amygdala in the pathogenesis and maintenance of the disease (Etkin and Wager 2007; Shin and Liberzon 2010). Also the insular cortex, a region involved in proprioception and interoception (Craig 2002), is found to be hyperactive in a wide range of anxiety disorders (Etkin and Wager 2007; Shin and Liberzon 2010). However, in accordance with the variability in the phenomenology across anxiety disorders, this increased amygdala and insula activity are also variable depending on the type of anxiety disorders (Etkin and Wager 2007). Interestingly, also the ACC, this large medial frontal cortex area that is typically involved during error monitoring, has consistently been found to be dysfunctional across several anxiety disorders (Bishop 2009; Etkin and Wager 2007; Shin and Liberzon 2010).

8.3.1.2 Depression

Phenomenology Although anxiety and depression may be seen as belonging to a shared continuum (with anxiety disorders evolving to depression) and strongly covary (Mineka et al. 1998), major depressive disorders (MDDs) have a different phenomenology. MDD is a syndrome that is characterized by persistent negative mood, and also by anhedonia or a decrease in the ability to experience positive affect (Kring and Bachorowski 1999). Moreover, research has also confirmed that these emotional disturbances are backed up by deficits regarding information processing in general. More specifically, depression is associated with cognitive biases toward negative information (De Raedt et al. 2010), mainly related to memory but less to attentional processes that are more selectively influenced by levels of anxiety (Mineka et al. 2003). Some authors have suggested that these cognitive impairments are actually related to executive functioning, and more specifically to a failure to disengage from negative stimuli (Koster et al. 2005), which can therefore form the base of rumination (Gotlib and Joormann

2010) (i.e., the tendency or style to think repetitively about the causes and consequences of negative or adverse life events; Nolen-Hoeksema et al. 2008). These cognitive and emotional disturbances are usually accompanied by somatic disturbances and, are diagnostic of depression (American Psychiatric Association—DSM-IV, 2000).

Neurobiology Depression cannot be related to a circumscribed dysfunctional brain area, but effects of depression on brain activity are best explained by a network account (De Raedt and Koster 2010). Regions that are found to be most affected by depression are the frontal cortex, the hippocampus, the striatum, the subgenual ACC (or ventromedial prefrontal cortex), limbic and paralimbic areas like the amygdala, thalamus, hippocampus, basal ganglia, and anterior temporal lobes. Some of these regions (i.e., frontal cortex, the hippocampus, the striatum, and limbic areas such as the subgenual cingulate cortex) were found to be smaller in depressed patients compared to healthy controls (Anand and Shekhar 2003). The functional activation in some of these regions, together with other regions, was also found to be influenced by depression. Depression-related decreased activations were observed in "cognitive" control regions, such as the dorso-lateral prefrontal cortex (dlPFC) and ACC (Davidson et al. 2002; Mayberg 1997), while increased activations were evidenced in other limbic and paralimbic regions (i.e., hippocampus, amygdala, thalamus, basal ganglia, and anterior temporal lobes; Anand and Shekhar 2003). Mayberg (1997) put forward the idea that a dysregulation between limbic and cortical areas might play a key role in depression. According to Mayberg (1997), the reciprocal links between these areas are assumed to be regulated by yet another region, namely the subgenual ACC which is found to be overactive in depressed individuals. Accordingly, various therapies targeting selectively this portion of the ACC for the treatment of depression have been proposed in the literature (Mayberg 2009; Mayberg et al. 1997).

8.3.2 Shared Abnormal Error-Monitoring Processes in Anxiety and Depression or Dissociable Effects

Both anxiety and depression are thought to be characterized by an increased sensitivity towards errors and negative feedback (Eshel and Roiser 2010; Holmes and Pizzagalli 2008; Pizzagalli et al. 2006). This enhanced reactivity to errors in individuals with internalizing disorders has also been confirmed by previous ERP studies showing numerically larger ERN/Ne and/or CRN amplitudes in these individuals (Hajcak et al. 2003; Vaidyanathan et al. 2012). Based on this evidence, some authors have put forward the notion that the ERN/Ne might be considered as a reliable endophenotype for internalizing disorders (Olvet and Hajcak 2008). In the next section, we review the evidence supporting this idea.

8.3.2.1 Anxiety: Overactive ERN/Ne

Accumulating neurophysiological evidence suggests that anxiety disorders are associated with altered early error-monitoring brain processes, and more specifically an enhanced ERN/Ne component, including obsessive-compulsive disorder (OCD; Endrass et al. 2010) or generalized anxiety disorders (Weinberg et al. 2010). However, a numerically larger ERN/Ne is usually not only observed in individuals with clinical levels of anxiety or clear cut anxiety disorders but also in healthy participants showing high levels of subclinical trait anxiety (Aarts and Pourtois 2010; Hajcak et al. 2003). Typically, an overactive CRN is also evidenced in these individuals suggesting that the effect of negative affect on action monitoring is generic, and not restricted to the processing of errors (ERN/Ne component, but see Aarts and Pourtois 2010). Moreover, this effect of anxiety is component specific, affecting the amplitude of the ERN/Ne and CRN components selectively, without influencing the subsequent Pe component. This selectivity is important since it pinpoints an alteration of the early processing of errors (as well as correct responses in the case of the CRN) in anxiety, occurring during a processing stage where the reward prediction value or valence of the action is probably readily processed in the rostral cingulate zone (Holroyd and Coles 2002).

Interestingly, other ERP studies also showed that, besides these early overactive effects seen in anxious or depressed individuals, the ERN/Ne amplitude stands out as a reliable predictor of stress regulation (which is an important component of anxiety) in daily life. Compton et al. (2013), for example, found that a larger difference between CRN and ERN/Ne (or better error-correct differentiation) during a Stroop task predicted less cortisol increase (and thus a better stress regulation) during this task in healthy participants. By contrast, the Pe was not related to this psychophysiological stress measure. Moreover, Inzlicht and Gutsell (2007) found that ERN/Ne amplitudes were smaller during a standard interference task when participants were instructed to suppress negative emotions beforehand, which is a maladaptive self-regulation strategy. Also, participants with effective error detection (larger ERN/Ne-CRN amplitude difference) tend to show less self-reported negative affect and more task-focused coping behaviors in response to daily stressors reported over a two week period (Compton et al. 2008b). These findings suggest thus that the ERN/Ne might be a good predictor of regulation to stress in daily life. However, no study to date has tested whether such an association between the size of the ERN/Ne and regulation to stress may be compromised in participants with elevated levels of negative affect.

With respect to the neural processing of external evaluative cues (i.e., feedback and the FRN component) and modulatory effects of anxiety, the existing literature is rather scarce. Anxiety seems to decrease the FRN component (Aarts and Pourtois 2012; Gu et al. 2010), as opposed to the consistent amplitude increase found for the ERN/Ne.

8.3.2.2 Depression: Blunted Pe?

Some ERP studies reported larger ERN/Ne amplitudes in MDD patients compared to healthy controls (Aarts et al. 2013b; Chiu and Deldin 2007; Holmes and Pizzagalli 2008), while other studies reported similar (Compton et al. 2008a; Schrijvers et al. 2008, 2009) or even smaller ERN/Ne amplitudes in MDD patients (Ruchsow et al. 2004, 2006). Effects of depression on the CRN component are not always consistent either: Olvet et al. (2010) and Schrijvers et al. (2009) reported larger CRN amplitudes in depressed patients, but Holmes and Pizzagalli (2008) found comparable CRN amplitudes between depressed and control individuals.

Likewise, discrepant findings have also been reported regarding the Pe component in depression. While Chiu and Deldin (2007), Compton et al. (2008a), and Holmes and Pizzagalli (2008) observed similar Pe amplitudes for controls and MDD patients, Aarts et al. (2013b) and Schrijvers et al. (2008, 2009) reported smaller Pe amplitudes in depressed individuals than healthy control individuals. Combined together, these studies point therefore at a different modulatory effect of depression than anxiety on the early detection and regulation of errors. One of the key differences between depression and anxiety might thus concern the Pe component, which remains unaffected by anxiety but has been found in some studies to be decreased in depression. Given that the Pe component has been linked to error awareness, or the specific processing of the affective significance of errors, the Pe component in depressed individuals might actually reflect an abnormal attention orienting toward the emotional significance of errors. Accordingly, the picture seems to emerge that while anxiety would interfere with the rapid extraction of the valence or reward-prediction error value of errors (overactive ERN), depression would instead influence a later stage of processing (smaller Pe). As reviewed below (see Sect. 8.4), recent evidence suggests that the characteristic maladaptive ruminative thinking associated with depression might selectively smear the processing of the emotional significance of response errors indexed by the Pe.

With respect to the processing feedback and its possible impairment in depression, only few ERP studies have been conducted. This is relatively puzzling because depression has repeatedly been shown to be associated with abnormal reactions toward stimuli signaling reward and punishment (Eshel and Roiser 2010). Among the few existing ERP studies, Tucker et al. (2003) reported a small differentiation at the level of the FRN component between positive and negative feedback in individuals who scored either low or high on a depression scale, whereas individuals who scored in the middle were characterized by a larger FRN, suggesting a nonlinear relationship between the severity of depression and amplitude variations at the level of this specific action monitoring component. Foti and Hajcak (2009) also reported smaller FRN amplitudes in depressed compared to control participants. By contrast, Santesso et al. (2008) investigated feedback processing in remitted depressed individuals and showed a larger differentiation between positive and negative feedback, compared to controls. However, Ruchsow et al. (2004) did not report any difference at the level of the FRN between positive and negative feedback processing in depressed patients.

8.3.3 Interim Conclusions

To sum up, we have reviewed neurophysiological evidence suggesting that possible alterations in early error monitoring may concern dissociable processes in anxiety and depression. Usually, high anxious individuals show an increased ERN/Ne component during the early monitoring of errors, while the subsequent Pe component is unchanged. No such pattern is seen in depression (Vaidyanathan et al. 2012). Recent evidence suggests that depression could lead to a reduced Pe component compared to healthy controls (Schrijvers et al. 2008; Aarts et al. 2013b). Hence, while anxiety and depression can be viewed as sharing many commonalities within the broader construct of negative affect, non-overlapping effects during early stages of error monitoring appear to arise for them, suggesting that different self-regulation problems might characterize these two internalizing disorders.

8.4 Error Monitoring in Anxiety vs. Depression: Toward a Unified Neurobiological Framework

8.4.1 Deficient Early Extraction of the Emotional Value of Errors in Anxiety

Although anxiety has been linked to an increased ERN/Ne (but not Pe) component during error monitoring (Aarts and Pourtois 2010; Hajcak et al. 2003), the functional meaning of this neural processing remains fuzzy. The reason therefore is that in all ERP studies reviewed above, high anxious individuals do not differ from low anxious participants regarding accuracy or speed. What does this enhanced ERN/Ne component in high anxious participants thus truly reflect if it is not related to a measurable change in behavior? To account for this discrepancy, Luu et al. (2000) initially suggested that the ERN/Ne component may reflect the enhanced emotional significance of an error. Accordingly, an increased ERN/Ne in anxiety would reflect the differential processing of the emotional valence of errors. These events might match with their current affective state and hence be temporarily "gated" by specific action monitoring systems. Although this idea appears plausible, very few studies have corroborated it so far. Therefore, we recently devised a new experimental paradigm enabling us to test this idea (Aarts et al. 2012, see Fig. 8.2).

In line with the logic underlying evaluative priming effects, we found that participants categorized a negative word faster as negative when the preceding action was incorrect than when the preceding action was correct. A mirror symmetric effect was observed for the categorization of positive words (see Aarts et al. 2012). These results thus showed that actions performed during a go/no-go task are evaluated "online" along a genuine valence (negative–positive) dimension. Noteworthy, this early "online" affective tagging of the action was modulated by trait anxiety: The more anxious participants were, the smaller the action–word evaluative priming effect became. In other words, this correlation suggests that high anxious individuals were less able at relat-

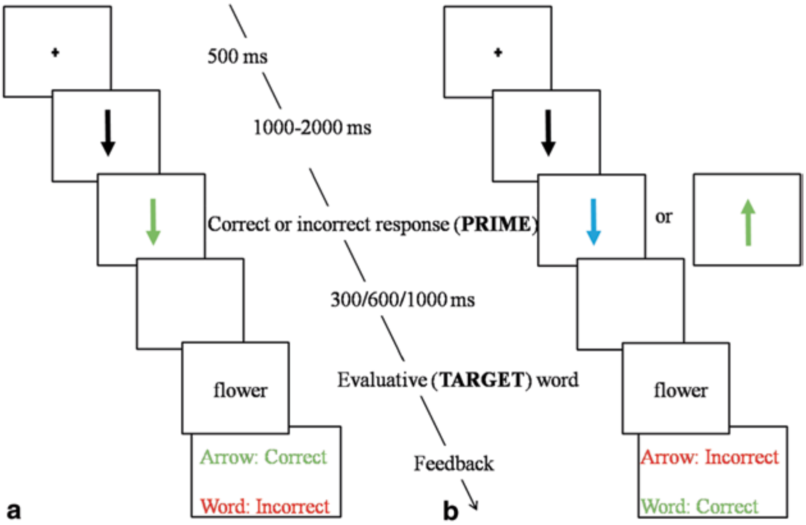

Fig. 8.2 Illustration of the evaluative priming paradigm used to infer the affective value ascribed "online" by participants to correct vs. incorrect actions (see Aarts et al. 2012). Participants had first to respond to **a** go stimulus (i.e., when the colored arrow became green and kept its initial orientation relative to the cue) or **b** to withhold responding to no-go stimulus. Errors were unlocked by means of a stringent time pressure, and 300–1000 ms after each response, either a positive or a negative word was presented. Participants were asked to discriminate the valence (either positive or negative) of this word. This figure is reproduced with permission from Elsevier

ing their erroneous and correct actions to affect (either positive or negative). More generally, these results lent support to the assumption that the online emotional processing of actions is impaired in anxiety (Aarts et al. 2012), revealing a problem in a component of self-regulation in this specific internalizing disorder.

Moreover, in a follow-up study (Aarts 2013a), we sought to assess whether the ERN/Ne and CRN components might be related to this evaluative priming effect. We reasoned that if the ERN/Ne and CRN components reflect the activity of a generic performance monitoring system (Vidal et al. 2000), with shared neuro-anatomical substrates within the rostral cingulate zone (Roger et al. 2010), then the amplitude difference between these two components might encode the differential processing of the emotional valence of incorrect and correct actions. In other words, if correct actions are linked to reward and more positive affect, this effect might be captured by a smaller CRN component. By contrast, if errors are associated with more negative affect, then this effect might be related to a larger ERN/Ne component. The ERP results obtained in this follow-up study (Aarts et al. 2013a) confirmed this prediction: Across participants, the larger the evaluative priming effect (i.e., the more individuals discriminated correct from incorrect actions along an emotional valence dimension), the larger the ERN/Ne–CRN difference corroborating a link between this early ERP component and the early differential processing of the emotional valence of correct (more positive) and incorrect (more negative) actions. Further, because accumulating evidence reviewed above suggests that the ERN/Ne and CRN components are larger in anxious individuals, we surmise that this might be associated with a reduced online emotional tagging of incorrect and correct actions. However, future ERP studies are needed to confirm this conjecture.

The assertion that anxiety disrupts the "online" emotional tagging of actions is also evidenced by studies investigating evaluative feedback processing, and more specifically the FRN component (Frank et al. 2005). These prior ERP studies consistently found that high anxious individuals differentiated negative feedback less from positive feedback (as indicated by a smaller FRN difference between positive and negative feedback compared to non-anxious individuals; Aarts and Pourtois 2012; Gu et al. 2010). In short, trait anxiety might blur the process enabling extracting the emotional valence of an external evaluative feedback (being either positive or negative), when this process relies on concurrent generative and predictive processes happening already at the level of the action performed just prior to the presentation of this external evaluative cue.

8.4.2 Depression is Associated with Excessive Self-Referential Processing During Early Error Monitoring

Although depression is usually seen as a disorder that substantially overlaps with anxiety (Clark and Watson 1991; Mineka et al. 1998; Watson et al. 1995), it seems that errors are processed differently in these two internalizing disorders. While anxiety appears to alter the ERN/Ne component, selectively, depression has been less systematically associated with an overactive ERN, while recent ERP studies point at a numerically reduced Pe component in these patients (see Aarts et al. 2013b for a recent overview).

Interestingly, when examining which factor specifically predicted this electrophysiological effect (Pe component) during error monitoring in major depression, we found in a recent study (Aarts et al. 2013b) that the trait-related ruminative thinking style was in fact providing the best predictor, besides the variability accounted for by trait anxiety or depression severity per se. This outcome appears especially valuable given that rumination might be related to executive functions deficits (Watkins and Brown 2002), including the monitoring of errors. For example, Koster et al. (2011) reviewed evidence that high ruminators show difficulties in disengaging their attention away from negative information. Since errors are usually lumped together with negative affect (Aarts et al. 2012) at the level of the ERN/Ne (Aarts et al. 2013a) on the rostral cingulate zone (Aarts and Pourtois 2010), an excessive ruminative thinking style, defined as a maladaptive self-regulation strategy (Nolen-Hoeksema et al. 2008), could therefore interfere with this specific process. Moreover, it might also alter the subsequent Pe component which is meant to enable these motivationally significant events to break through into awareness and influence attention control systems. As our ERP results suggest, major depression primarily influences this latter process (reduced Pe component) suggesting that this internalizing disorder, by means of its rumination component, might hamper the conscious processing of the emotional significance of errors (Nieuwenhuis et al. 2001; Ridderinkhof et al. 2009). Hence, these neurophysiological results highlight a modulatory effect exerted by depression onto early error-monitoring brain functions. This effect might account for the abnormal self-regulation typically observed in these patients in daily life situations, where the rapid, continuous, and conscious detection of response errors fosters not only learning but also adaptive behavior more generally (see also van Steenbergen et al. 2010; van Steenbergen et al. 2012 for more information on how affect might regulate conflict-driven adaptation specifically).

8.4.3 Conclusions and Future Perspectives

In this chapter, we have reviewed recent neurophysiological evidence and behavioral results showing that anxiety interferes with the early marking of errors as more negative events (at the level of the ERN/Ne). While nonanxious individuals readily differentiate errors from correct actions along a specific valence dimension (and not merely arousal dimension as suggested previously, see Hajcak and Foti 2008), high anxious individuals appear to experience a specific problem to ascribe an affective valence to their actions (either correct or incorrect). By contrast, depression appears to impair early error-monitoring brain functions, but at a later latency following response error onset compared to anxiety and its modulation of the ERN, namely when these events need to be consciously registered (Pe component). In this latter case, an exces-

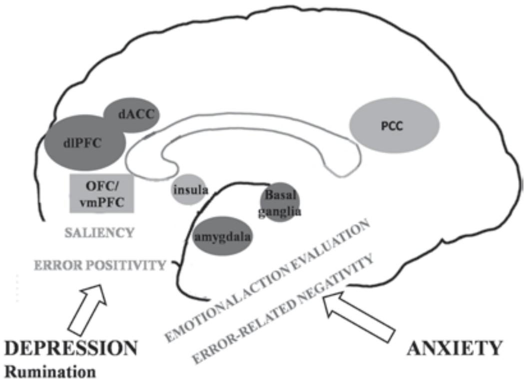

Fig. 8.3 Neuro-anatomical model emphasizing non-overlapping routes through which anxiety ERN/Ne and depression/rumination (Pe) might dynamically influence and shape early stages of error monitoring and hence core self-regulation processes

sive ruminative thinking style stands out as the core self-regulation impairment accounting for this neurophysiological change. In other words, rumination likely hijacks attention or executive function resources needed otherwise to process "consciously" the salience of these deviant events rapidly following their occurrences (Seeley et al. 2007).

Because the ERN/Ne and Pe map onto non-overlapping neural networks in the human brain (see Fig. 8.3), we propose that these two internalizing disorders likely modulate self-regulation during error monitoring via non-overlapping routes. While anxiety mainly affects early dopaminergic-dependent frontostriatal loops during action monitoring (ERN component), comprising the rostral cingulate zone as an important integration hub (Holroyd and Coles 2002), depression would alter error-monitoring processes by means of specific modulations in non-overlapping anterior cingulate (perhaps located more rostrally or ventrally, see Aarts et al. 2013b) or posterior cingulate and insular (Craig 2002; Dhar et al. 2011) regions (Pe component). In the latter case, the deficit or modulation associated with depression would be explained by the activation of a ruminative thinking style blocking the conscious access to the emotional significance of these events. Although these ERP studies inform about possible non-overlapping impairments during the early detection of response errors in anxiety and depression (and hence a core component of self-regulation more generally), future studies are needed to confirm that these two internalizing disorders are indeed associated with dissociable effects and self-regulation abnormalities during performance monitoring.

An interesting avenue for future research would be to try shielding action-monitoring processes from the effect exerted by rumination in depression. For example, we would predict that blocking rumination experimentally (by means of a verbal working memory load component for example) might be related to a partial restoration of the Pe component in depressed patients. Likewise, it would be especially interesting to measure on different occasions over a prolonged time period (by means of a longitudinal study for example; see Compton et al. 2008a) whether the abnormal affective tagging of actions seen in high anxious individuals at the level of the ERN/Ne component (see Aarts et al. 2012) could evolve (either "positively" or "negatively") and then relate these neurophysiological and behavioral changes to either a deterioration or amelioration in the phenomenology and/or symptomatology of this internalizing disorder (e.g., distress, worry, or hypervigilance). Such evidence would strengthen the assumption that these ERP markers (ERN/Ne and Pe) are not epiphenomena, but rather could be used directly in order to better characterize the scope of changes in self-regulation processes occurring during error monitoring in anxiety or depression.

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Pupillometry and Memory: External Signals of Metacognitive Control

9

Megan H. Papesh and Stephen D. Goldinger

9.1 Introduction

The human memory system is often characterized as two broad memory subsystems: The declarative system, which helps us remember daily occurrences and specific events, and the semantic system, which permits the general knowledge of meanings and concepts (e.g., Tulving 1972). Although the putative distinction between these systems (and other potential subsystems) is often debated, they share at least one commonality: Neural processes—the allocation of attention and other neurocognitive resources—are required during both encoding and retrieval. For decades, researchers have used on-line measures of neural function to inform theoretical accounts of human recognition memory. Functional magnetic resonance imaging (fMRI), event-related potentials (ERPs), and single-cell recordings from hippocampal and parahippocampal areas have all been used with much success and much expense. Recently, researchers have "rediscovered" *pupillometry,* a less invasive, but nevertheless sensitive, measure of neural activity obtainable via the most standard eye-tracking equipment. In this chapter, we review the history of pupillometry (which dates back to the 1700s), as well as recent advances in technology that are currently allowing fine-grained inferences about the neurophysiology underlying declarative, or episodic, long-term memory. Finally, as befits a volume focused on mechanisms of self-regulation, we address evidence that pupillary responses are tightly connected to feelings of *meta-memory*: The pupils are known to not only dilate during retrieval from long-term memory but also dilate when people encode items that will lead to successful retrieval in the future. This only occurs during intentional learning, and seems to reflect the ongoing assessment of cognitive performance.

9.2 Brief Historical Background

Pupillometry, the psychological study of pupillary reflexes, is currently experiencing a resurgence of scientific interest, after having been all but abandoned after the 1970s. Despite the recent influx of interest, the field actually has a long and somewhat romantic history. For example, *Atropa Belladonna,* the hallucinogenic (and toxic) plant, often called "deadly nightshade," gets its scientific name for its historical use as a dilating agent. Although originally used for clinical purposes, it was eventually added to women's eye drops as a cosmetic treatment (bella donna means "beautiful woman" in Italian; Forbes 1977; Wilks 1883; Wootton 1910). When applied to the eyes, belladonna causes enlarged pupils, which was

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meant to mimic the signs of arousal or sexual interest.[1] This is the origin of the phrase "eyes dark with desire," as pupil dilation can signal sexual arousal (Aboyoun and Dabbs 1998; Bernick et al. 1971; Hamel 1974; Hess 1965; Tombs and Silverman 2004). Perhaps less romantically, pupil size has been used for centuries to examine visual and cognitive processing, with Charles Darwin (1872) relating pupillary reflexes to fear and other emotions in animals. In fact, Loewenfeld (1958) noted that interest in "paradoxical pupil dilation" (i.e., pupillary reflexes which occur in the absence of environmental changes) began in the mid-1700s (Fontana 1765). Although preceded by a handful of earlier attempts to study pupil size (e.g., Berrien and Huntington 1943; Mentz 1895; Roubinovitch 1900), Hess and colleagues, who initiated a series of systematic studies in the 1960s, are often credited with sparking decades of interest in the relationship between pupil size and mental events, such as emotions or thoughts (Goldwater 1972; Hess 1965; Hess and Polt 1964; Loewenfeld 1993).

9.3 Physiology and Neurophysiology of Pupillary Reflexes

The pupils are circular apertures that allow light into the eyes, and they are controlled by two muscles within the iris, the radial dilator pupillae and the circular sphincter pupillae. These muscles are differentially affected by activation in the sympathetic and parasympathetic systems, within the autonomic nervous system (Steinhauer et al. 2004). The sympathetic system, which controls the dilator muscles, is mediated by the posterior hypothalamic nuclei; when stimulated, it produces enlarged pupils. The parasympathetic system is linked to the sphincter muscles and is mediated by the Edinger–Westphal complex of the oculomotor nucleus; when inhibited, the sphincter muscles relax and the pupils dilate. Throughout the day, these systems work in opposition of one another to produce an average resting pupil diameter of approximately 3 mm (Wyatt 1995). When ambient lighting is low, the pupils will typically dilate, increasing to an average diameter of 7 mm (plus or minus a standard deviation of 0.9 mm; MacLachlan and Howland 2002), or more than 120 % their resting size. Cognitively evoked dilation reflexes, however, are typically much more modest, in the range of 0.5 mm (Beatty and Lucero-Wagoner 2000), which is difficult to appreciate with the naked eye.

Pupillary reflexes are closely related to activity within the locus coeruleus (LC), part of the noradrenergic system. The LC emits inhibitory signals along the parasympathetic pathways known to yield pupillary dilation during psychologically relevant events (Wilhelm et al. 1999). The LC is the sole source of the neurotransmitter NE throughout the forebrain, and, because it sends its densest signals to brain areas involved in selective attention (Foote and Morrison 1987), the LC has been implicated as mediating attentional processing throughout the entire brain (Corbetta et al. 2008; Coull et al. 1999; Eldar et al. 2013; Gilzenrat et al. 2010; Sara 2009). In combined single-cell intracranial recording and pupillometry studies with monkeys, researchers have documented a tight correspondence between pupillary reflexes and activity in cells within the LC-NE system (Rajkowski et al. 1993; Rajkowski et al. 2004). As shown in Fig. 9.1, during a signal-detection task in which a monkey was required to fixate on a spot of light, dynamic dilation and constriction closely tracked the activity of simultaneously recorded LC neurons. Observable in the figure are periods of tonic (or baseline) firing, characterized by continuous firing rates of 1–3 Hz, interspersed with periods of phasic firing rates, characterized by short bursts of 8–10 Hz (Aston-Jones et al. 1991, 1994, 1997). These phasic bursts correlate well (approximately $r = 0.60$) with pupil diameter, suggesting that enlarged diameters reflect greater levels of LC activity (Rajkowski et al. 1993, 1994). This sort of relationship, reflecting well-correlated LC activity and pupillary reflexes, has been documented in other animal species as well (Gilzenrat et al. 2003, 2010; Koss 1986).

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[1] In fact, a recent ocular-health trend inspired by Lady Gaga, the use of "circle lenses," is designed to do the same thing, but without drugs. Because of the physical risks (such as blindness!), the FDA never approved their use in the USA.

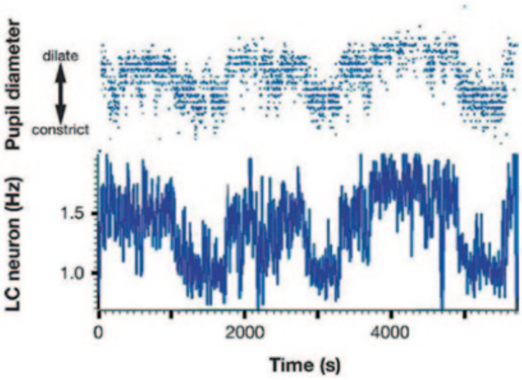

Fig. 9.1 The *top curve* represents dynamic pupil dilation and constriction as a monkey fixated its gaze on a spot of light during a signal-detection task. The *bottom curve* depicts phase-locked firing rates of an LC neuron recorded simultaneously with the pupillary responses. (From Aston-Jones and Cohen 2005. Copyright, Annual Reviews, 2005. Reproduced by permission)

The human LC-NE system is anatomically deep in the brain and is not typically germane to clinical assessments of epilepsy. As such, it has not been tested with single-unit recordings. Nevertheless, researchers have documented differences in tonic and phasic pupil size using indirect means and inferences (Dureman and Scholander 1962; Gilzenrat et al. 2003). For example, the tonic–phasic relationship depicted in Fig. 9.1 during a visual signal-detection task with monkeys was conceptually replicated in human volunteers who completed an auditory signal-detection task. Beatty (1982) required participants to monitor a stream of tonal bursts for a target tone. Although tonic (baseline) pupil size was unaffected by the amount of time people spent on the task, phasic pupil size decreased with task duration, but still reliably peaked following target detection. Additional evidence for a relationship between pupil size and the LC in humans comes from pharmacological manipulations of NE. When sympathomimetic drugs are administered, central NE increases, along with baseline (i.e., tonic) pupil size; increased tonic size has the side effect of also reducing the variability in pupil waveforms and reflexes to ambient lighting (Hou et al. 2005; Phillips et al. 2000a, b). The opposite effects are observed when sympatholytic drugs are administered, as they decrease both central NE levels and baseline pupil sizes (Hou et al. 2005; Phillips et al. 2000a, b). Even in dark-adapted conditions, which inhibit the parasympathetic system, the pupils still respond to the onset of a cognitively demanding process (Steinhauer and Hakerem 1992). Combined, the evidence strongly suggests that pupil size provides a reliable, easily observable, index of LC activity in various human attention tasks (e.g., Einhauser et al. 2008; Gabay et al. 2011; Gilzenrat et al. 2010; for reviews, see Heaver 2012; Laeng et al. 2012).

Neural processes related to the allocation of attention pervade, and are arguably necessary for, almost all cognitive tasks. Given the role of NE in modulating arousal, we might ask whether pupillary reflexes fall solely in the domain of attention, or whether pupillometry be applied to other, more specialized, areas of cognition. The answer lies in the neurophysiology of the pupillary reflex. Because the autonomic pathways known to mediate cognitively evoked pupil changes hold reciprocal connections with the central nervous system (CNS), it has been suggested that those pathways can modulate, or be modulated by, CNS structures related to myriad cognitive processes (Gianaros et al. 2004; Steinhauer et al. 2004). Investigations into the neural mechanisms of successful learning and memory in animals have revealed close correspondences between successful performance and the involvement of the NE system (Croiset et al. 2000). For example, LC neurons in rats show learning-dependent increases in activation during slow-wave sleep, suggesting that the LC plays an important role in memory consolidation (Eschenko and Sara 2008). Such findings are paralleled by recent findings from human experiments, wherein increased autonomic responses (e.g., skin conductance) are positively correlated with memory strength for emotional words (Buchanan et al. 2006). Additionally, the LC receives input from the vagus nerve, a parasympathetic pathway that is often stimulated as a treatment for medically intractable epilepsy (Groves and Brown 2005). When patients undergoing vagal nerve stimulation learn a list of words prior to treatment, their retention of those words is enhanced, suggesting that this pathway modulates memory formation and consolidation (Clark et al. 1999). Additional evidence for a role of the LC-NE system in human memory has been documented in a combined pupillometry–fMRI study (Sterpenich et al. 2006). When participants retrieved memories of neutral faces embedded within emotional contexts (e.g., a photo of a snake), LC activity was linearly related to pupil size, suggesting that successful retrieval depends, at least in part, on reinstating the arousal levels that were present during encoding. The LC-NE system, therefore, seems to be involved in attention and other high-level cognitive functions.

9.4 Pupillometry and Cognition

Early scientific investigations into the relationship between pupil size and ongoing mental processes (at the time called *pupillography*, owing to the painstaking, by-hand, nature of the measurements) focused almost exclusively on the role of emotions and arousal. In one of the first such studies, Hess and Polt (1960) studied pupillary changes as men and women viewed photographs of a partially nude male, partially nude female, a landscape, a mother and child, and a baby. They observed that male participants' pupils dilated most to the partially nude female, while women's pupils dilated most to the picture of the mother and child. From this, they inferred that pupil size reflected participants' individual interest in the depicted topics (although others argued that sample size and poor stimulus control precluded firm conclusions; see Janisse 1977). Despite criticisms, Hess and colleagues later replicated this finding, showing that homosexual men had larger pupillary reflexes to photographs of male, relative to female, nudes, while heterosexual men showed the opposite pattern (Hess et al. 1965). Many experiments have shown reliable linear relationships between levels of sexual arousal and pupil dilation (e.g., Aboyoun and Dabbs 1998; Hess 1965; Lawless and Wake 1969; Peavler and McLaughlin 1967), although many also included uncontrolled stimulus characteristics, such as luminance or visual features (Janisse 1977), which are well known to produce tonic pupillary reflexes.

Hess's legacy is not limited to investigations into sexual preference, however: Hess and Polt (1964) conducted one of the first studies into mental arithmetic and pupillometry. With five participants and four multiplication problems of increasing difficulty, they observed approximately monotonically increasing pupil sizes in proportion to difficulty (see Fig. 9.2). Despite the small sample size, this finding appears robust, and has replicated several times (Bradshaw 1968a; Klingner et al. 2011; Marshall 2002; Payne et al. 1968). If you have a friend or a colleague who does not mind you gazing into their eyes for an uncomfortable moment or two, give it a try: Ask them to maintain fixation on you, and answer two math problems. Start with "What is 2+4?" and then proceed to "What is 32−19?" You may not see any phasic dilation to the first question, but the second question will usually produce a reliable dilation response. (A word of caution is required on the interpretation of this exercise: People may be uncomfortable or embarrassed when attempting to answer the more difficult question, so the phasic reflex may reflect emotional arousal, rather than the cognitive effort associated with mental arithmetic. That does not make the demonstration any less fun, however.) This finding has even been applied to study individual differences in mathematical abilities. Ahern and Beatty (1979, 1981) observed larger pupil dilations in less intelligent college students, relative to their more intelligent peers, as they solved the same mental arithmetic problems, suggesting that pupil size is sensitive to between-individual differences in cognitive abilities.

Although early pupillography investigations were criticized on the grounds that now-standard experimental controls were not implemented (see Võ et al. 2008), subsequent work incorporated more rigorous methods, designed to eliminate the unwanted influence of tonic reflexes. Because pupils dilate reflexively to changes in luminance, color, or the spatial frequency composition of visual input, care must be taken to equate, as much as possible, stimulus characteristics in experimental designs that utilize pupillometry (Porter

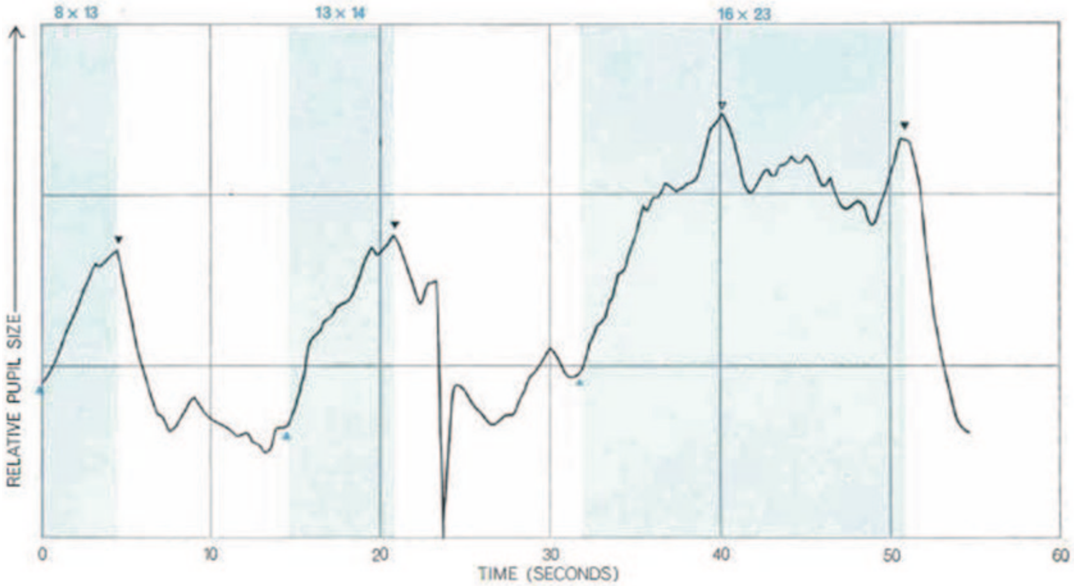

Fig. 9.2 Changes in pupil size as a participant answers three mental arithmetic problems (shown at the *top* of the graph). *Blue triangles* represent when the problem is posed, and *inverted black triangles* mark when the participant provided an answer. The *open inverted triangle* marking the third problem appears to reflect the participant reaching a solution before verifying and reporting it. (From Hess 1965. Copyright: Scientific American, Inc. Reproduced with permission)

et al. 2007). Porter and Troscianko (2003) identified several methodological approaches that minimize unwanted pupillary reflexes, including the use of a relatively low-stimulus contrast, avoiding colored stimuli, and using relatively long-stimulus exposure durations. Goldinger and Papesh (2012) recently added to this list of constraints by suggesting the use of relatively long (e.g., 1000 ms or more) inter-trial intervals and baseline-correction procedures. Both suggestions guard against *carryover effects,* as when the difficulty of trial *n* influences the pupillary waveform of trial $n+1$. By using tightly controlled materials and methods, researchers have been able to provide more reliable inferences about the nature of pupillometry and high-level cognition. Kahneman and colleagues are probably best known for initiating interest in what is now called the *task-evoked pupillary reflex (TEPR)*. TEPRs occur independently of tonic changes in pupil diameter, and they arise approximately 400 ms after the onset of a stimulus (Partala and Surakka 2003), peaking within 1–2 s. Kahneman and Beatty (1966; Kahneman et al. 1967) used time-locked TEPRs to examine the mental processing load as participants held a series of digits in working memory for subsequent recall. As shown in Fig. 9.3, with each additional digit added to working memory, pupil diameter increased. As participants recalled the digits, they observed monotonically decreasing pupil sizes with each outputted item. These classic experiments have been repeated, and the findings replicated, using modern eye-tracking technology (Klingner et al. 2011).

Because TEPRs are sensitive to within- and between-task variations in cognitive demand (or “cognitive effort,” “mental workload,” etc.), and they reflect individual differences in cognitive abilities, Kahneman (1973) used them as the primary index of processing load in his *capacity theory* of attention. Although pupillometry declined in use for some time after the 1970s, recent technological and methodological advances have motivated pupillometric investigations of many cognitive phenomena, including Stroop interference (Laeng et al. 2011), working memory (Heitz.et al. 2008), word naming (Papesh

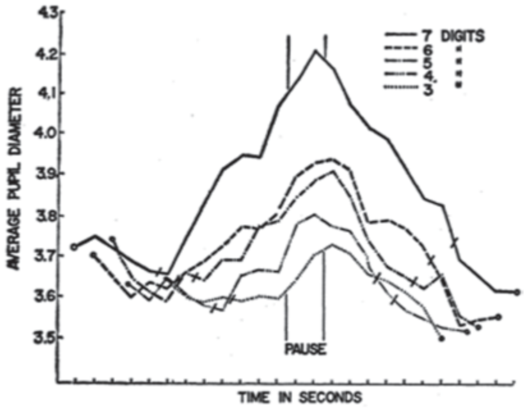

Fig. 9.3 Average pupil diameter as participants encode, briefly store, and then repeat strings of digits varying from three to seven numbers. *Slash marks* appear on the waveform just before the presentation of the first digit and just after the last digit is recalled. The *x*-axis is marked off in 1-s intervals by *tick marks*. (From Kahneman and Beatty 1966. Copyright: American Association for the Advancement of Science. Reproduced with permission)

and Goldinger 2012), visual search (Porter et al. 2007), face perception (Goldinger et al. 2009), sentence comprehension (Just and Carpenter 1993), speech perception (Zekveld et al. 2011), intelligence (Van der Meer et al. 2010), attentional vigilance (Steinhauer et al. 2004), and lexical decision (Kuchinke et al. 2007). To date, most studies utilizing TEPRs have examined capacity-limited processes in immediate or short-term memory tasks. Of interest for the present chapter, however, are long-term recognition memory processes, for which capacity cannot be determined.

9.5 Pupillometry and Long-term Memory

In the study of memory, pupillometry can be likened to ERP waveforms (Beatty 1982); just as ERPs reflect electroencephalographic activity, TEPRs reflect CNS activity. Comparing neurophysiological measures across study and test has been used to differentiate the neural activity associated with subsequently remembered versus forgotten information in both fMRI (e.g., Ranganath et al. 2004) and ERP investigations (e.g., Cansino and Trejo-Morales 2008; Duarte et al. 2004; Guo et al. 2006). This *subsequent-memory paradigm* allows researchers to record brain activity during memory encoding, and use it to predict subsequent retrieval success or failure. While ERP and fMRI measures are often time-consuming and expensive, pupillometry provides researchers with an efficient means to implement the subsequent-memory paradigm in various memory tasks, complementing their classic behavioral measures (e.g., accuracy and response time).

In the first documented investigation into long-term memory processes and pupil size, Beatty and Kahneman (1966) asked participants to recall seven-digit sequences from short- or long-term memory. Short-term memory sequences were random seven-digit strings read by the experimenter, and the long-term sequence was the participant's phone number. They observed that retrieving from long-term memory was associated with enlarged pupils, relative to retrieving the (subjectively more difficult) string from short-term memory. Subsequent work by Gardner et al. (1974a) confirmed this finding. Participants in their experiment were made pre-experimentally familiar with a series of nonsense consonant–vowel–consonant (CVC) syllables during a learning phase. Later, when they were exposed to familiar and unfamiliar CVCs, Gardner et al. (1974a) observed enlarged pupils to the familiar CVCs and relatively constricted pupils to the unfamiliar strings. In a subsequent replication attempt with auditory words, Gardner et al. (1974b) failed to observe this difference, possibly owing to the fact that they used all high-frequency (i.e., relatively common) words. When the stimuli consisted of randomly generated consonants, however, they once again observed a difference between the old and new stimulus items. Such results led Gardner et al. (1978) to suggest that, rather than reflecting mental effort, pupil size is more closely related to encoding and retrieval from memory. Despite the suggestiveness of these findings, interest in pupillometry, as it pertains to long-term memory, disappeared until surprisingly recently.

Although a handful of studies in the 1990s reported the use of pupillometry, it was not until 2008 that pupillometry began to reappear in the long-term memory literature (although see Maw and Pomplun 2004). Võ et al. (2008) investigated memory for emotionally valenced words and observed better memory for emotional, relative to neutral, items. Although they did not observe any pupillary differences at encoding as a function of subsequent memory, they found a reliable *pupil old/new effect* at retrieval, such that hits (correct "old" judgments) yielded larger pupil diameters than correct rejections (correct "new" judgments). The magnitude of this effect was affected by the emotional content of the retrieved words: Emotional words slightly diminished the pupil old/new effect, suggesting that pupil size is sensitive to not just memory processes but also the modulation of those processes by other factors. The authors interpreted their findings as reflecting the increased effort necessary to recollect the key details of the encoded events. Items that were not recollected, therefore, were not accompanied by the telltale sign of enlarged pupils.

Kafkas and Montaldi (2011) drew a similar conclusion from a study of long-term memory for pictures of objects, using a modified remember/know (RK) task to better precisely infer the influence of recollection on pupil size. Typically, the RK paradigm is used to differentiate occasions of detailed recollection from trials with only ahistorical feelings of familiarity (reflecting two putatively distinct contributions to recognition memory), by asking participants to evaluate their subjective sense of meta-memory with each "old" decision. When participants are able to recollect contextual details from encoding (e.g., what item came before or after the target item), they give a "remember" response, but when they can appreciate an item as old without concomitant recollective experiences, they give a "know" response. Kafkas and Montaldi (2011) had participants first complete an incidental encoding phase, during which time they passively viewed pictures, with no specific instructions to purposefully remember. Later, they completed a modified RK test: To examine both the strength and type of memories, Kafkas and Montaldi gave participants three familiarity responses (F1, F2, and F3), with each higher number representing a "stronger" feeling of familiarity, and one recollection response (R), which was to be used only in the event that the participant was able to retrieve contextual detail(s) from encoding. Participants were not asked to *try* to recollect details; they were only to use the R response when recollection occurred spontaneously. Although they did not find that pupil size differentiated recollection from familiarity during retrieval, examination of pupil size during incidental encoding revealed pupillary differences as a function of memory strength; as subsequent memory strength increased, pupil diameters *decreased*.

This pattern, smaller pupil diameters to stimuli that are subsequently remembered with a high degree of confidence, has not consistently been observed, and may reflect differences in the type of encoding or retrieval processes that are encouraged. Otero et al. (2011) examined long-term memory using pupillometry in the RK paradigm, with intentional encoding procedures for both visual and acoustic material. Although they did not report effects of subsequent memory on encoding data, they observed reliable memory effects on pupil size at retrieval. Specifically, when participants reported that they "remembered" items, their pupils were larger, relative to when they reported "knowing" that items were old (both "old" responses, however, elicited larger pupils than correct rejection of new items). Although this could be interpreted as reflecting differences in the processes of recollection and familiarity, their second experiment suggested that the effect was primarily driven by memory strength. Specifically, they used a "levels of processing" manipulation to ensure that different items were studied with relatively deep or shallow orientations, as deeper levels of processing are known to facilitate subsequent retrieval. For example, if participants focus on shallow features during encoding (e.g., syllable counting), their subsequent memory is less accurate, relative to focusing on deeper features (e.g., pleasantness ratings). Otero et al. (2011) observed reliable differences in pupil size between deep and shallow items at retrieval, such that words encoded with deeper processing were associated with larger pupils. In interpreting their results, the authors appealed to gradations

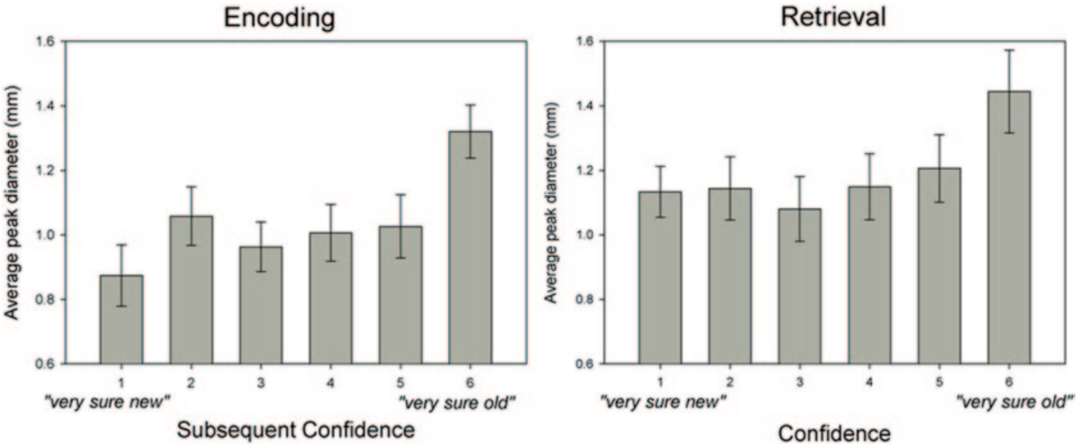

Fig. 9.4 Average baseline-corrected peak pupil diameters during encoding and retrieval of spoken words, groups by the confidence expressed in the old/new retrieval decision. (Adapted from Papesh et al. 2012)

of *memory strength,* rather than assuming the existence of separate neural and cognitive mechanisms for recollection and familiarity.

Papesh et al. (2012) came to a similar conclusion, using a memory test without RK responses. Participants intentionally memorized words and nonwords, spoken by two speakers. Later, they provided confidence-based memory decisions to old and new words, using a scale ranging from 1—*very sure new* to 6—*very sure old*. During the test, old words were spoken in their original (studied) voice, the other encoding voice, or a new voice. Like previous researchers, we observed a reliable pupil old/new effect, such that pupil size was larger for recognized items, relative to forgotten or correctly rejected items. Unlike Kafkas and Montaldi (2011), however, we observed a positive relationship between pupil size at encoding and subsequent memory strength, suggesting that greater cognitive effort at encoding predicted subsequent retrieval success (see Fig. 9.4). Although this pattern apparently contradicts that observed by Kafkas and Montaldi (2011), the findings are not necessarily irreconcilable, owing to differences in stimulus materials and task demands. Whereas Papesh et al. (2012) used auditory stimuli and intentional encoding, Kafkas and Montaldi used visual material and incidental encoding. Incidental encoding procedures, in particular, could potentially eliminate TEPRs, as participants do not actively engage in committing items to memory, and incidental encoding is known to recruit different neural processes than intentional encoding (Kapur et al. 1996). It has also been established that auditory stimuli elicit larger pupillary reflexes than visual stimuli in many tasks (see Fig. 9.5; Klingner et al. 2011), owing to either the dual-code nature of visual stimuli or the increased perceptual demand required to interpret auditory signals. Regardless of the underlying cause of auditory–visual differences in the magnitudes of TEPRs, it remains a potential explanation for the discrepancies across studies.

A novel finding by Papesh et al. (2012) was that pupil size during recognition was also sensitive to the cue match between the study and test voices; when the voices at study and test matched, pupil diameters were larger, relative to when the test voices were familiar or new. We interpreted this finding with reference to Whittlesea's (1997) SCAPE framework for recognition decisions (see also Papesh and Goldinger 2011). According to Whittlesea and Leboe (2000) and Whittlesea and Williams (1998, 2001), recognition decisions are the end product of a two-stage process. In the first stage, *production* of mental states, the perceiver elaborates upon perceptual inputs and "fills in" any missing information by bringing to mind associated labels or concepts (Neisser 1967). During the second stage, *evaluation,* the perceiver automatically evaluates the

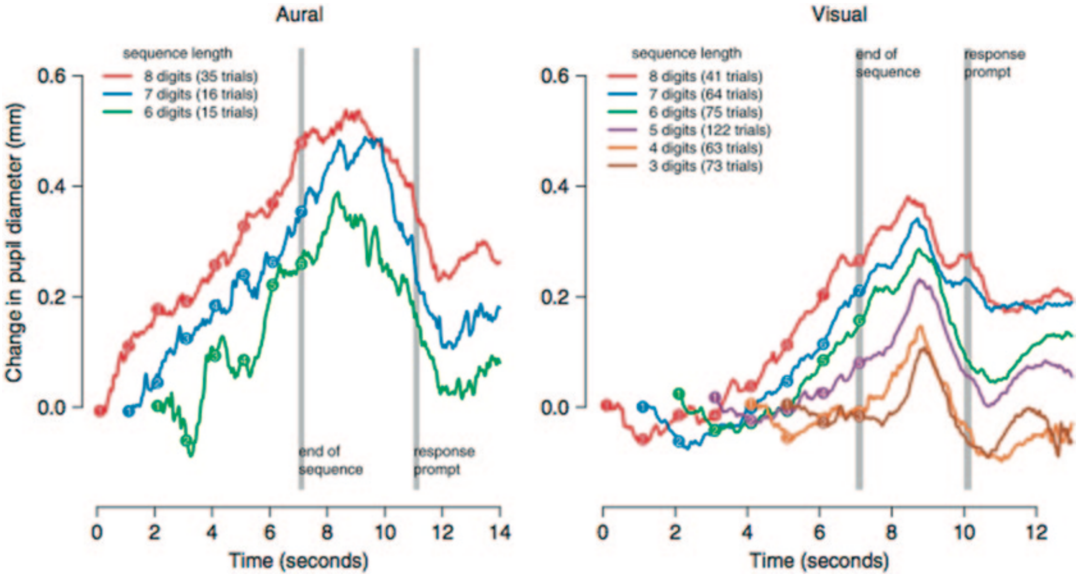

Fig. 9.5 Task-evoked pupil dilation during auditory (*left*) and visual (*right*) digit-span memory tasks, with separate lines for different sequence lengths. *Circles* on the waveforms represent the time at which each digit was spoken or displayed on screen. *Vertical lines* represent the end of the digit sequence and the start of the recall prompt. (From Klingner et al. 2011. Copyright, John Wiley and Sons. Reproduced with permission)

success of the production process. This is not a direct evaluation of the *stimulus,* but rather an evaluation of the relative harmony of mind (e.g., a heuristic decision about the fluency with which the production process was completed). Papesh et al. (2012) suggested that their cue-match pupillary data reflected this two-stage process, such that participants were bringing to mind encoded memories, and drawing upon production processes at retrieval that matched those during encoding. In fact, we observed reliable correlations between pupil size at study and test for almost all levels of confidence, suggesting that pupil size is not only sensitive to the existence of memories but also the retrieval and decision processes engaged prior to behavioral responses. This is also consistent with the combined pupillometry–fMRI data from Sterpenich et al. (2006), who found that arousal levels at retrieval were reinstatements of those experienced at encoding.

Subsequent work by Kafkas and Montaldi (2012) replicated the pupil old/new effect: Again using the modified RK paradigm, they observed enlarged pupils when information was recollected, relative to when participants reported experiencing only gradations of familiarity. This pupil old/new effect was not contingent on accurate *reporting* of memory, but also exists when participants are instructed to feign amnesia or provide all “new” responses to both old and new items (Heaver and Hutton 2011). This suggests that these reflexes are not under cognitive control, and that pupil size faithfully reports memory, even when the perceiver does not. Interestingly, however, the *experience* of memory seems to be necessary to elicit an old/new effect in pupil size. Although Heaver and Hutton (2011) observed a (slightly attenuated) pupil old/new effect in the absence of correct “old” responses, it can nevertheless be argued that participants were at least having the experience of memory. Laeng et al. (2007) examined pupil size changes in amnesia patients as they encoded and attempted to retrieve semantic information. Although the patients could not explicitly recall many of the studied facts, their pupil sizes were sensitive to the novelty of new facts; they observed the opposite of the pupil old/new effect—old information yielded relatively small pupil diameters, compared to new information.

One potential criticism of the aforementioned studies is that motor responses are confounded with pupillary reflexes (except in the case of

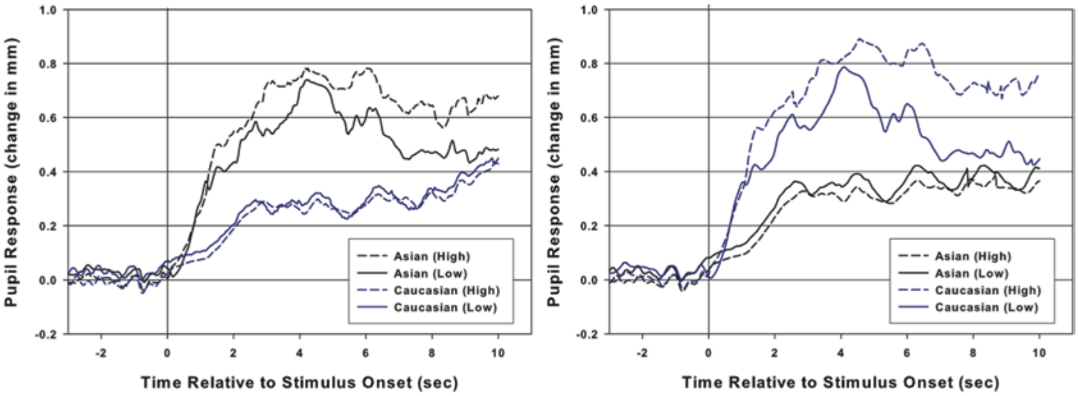

Fig. 9.6 Average pupil diameter during encoding of same- and other-race faces for White (*left panel*) and Asian (*right panel*) participants, with separate lines classifying groups by their subsequent memory performance (high- versus low-recognition ability). (Adapted from Goldinger et al. 2009)

subsequent memory data), as preparing a motor response can account for almost 70 % of observed dilation in some studies (Hupé et al. 2009). To eliminate motoric effects while investigating the role of memory strength in the pupillary reflex, van Rijn et al. (2012) had participants learn paired associates in blocks of four or seven pairs, with some items repeated in order to provide increases in memory strength for certain pairs. During retrieval, target items were presented 6 s before the response prompt, allowing the researchers to measure the effect of memory retrieval, independent of motor execution. Consistent with an interpretation of memory-based TEPRs as reflecting retrieval *effort,* they observed decreasing pupil sizes with increasing repetition frequency, suggesting that stronger memories were easier to retrieve. Despite being opposite in direction of the typical pupil old/new effect, this result is entirely consistent with the SCAPE (Whittlesea 1997) account of memory decisions. Repetition frequency is well known to enhance perceptual fluency, and as perceptual fluency increases, the cognitive effort usurped in processing decreases, yielding less dilated pupils. If participants in this study were engaging in the production and evaluation stages as outlined in SCAPE, then their retrieval pupil sizes should nicely correspond to their encoding sizes. Without pupil data from encoding, however, this interpretation remains untested.

Despite the speculative nature of our SCAPE-based interpretation of van Rijn et al.'s (2012) data, it is conceptually supported by findings from the face recognition literature. Goldinger et al. (2009) used pupillometry to examine the *own-race bias* in face recognition (i.e., the finding that members of a majority race are typically deficient at differentiating among members of a minority race). Participants intentionally studied own- and other-race faces, followed by a basic old/new recognition test. Based on their test performance, participants were classified as either low or high scorers, and their pupil sizes during encoding were examined as a function of that classification. As shown in Fig. 9.6, participants' pupils dilated most when they studied other-race faces, even though those faces were generally recognized less accurately than own-race faces. This finding is consistent with van Rijn et al. (2013), in that the less demanding, and more likely to be recognized, items elicited lower TEPRs. Additionally, however, low-scoring participants' pupillary responses to other-race faces were not as large as their high-scoring counterparts (in Fig. 9.6, compare the higher pairs of solid and dashed lines). In fact, lower-scoring participants selectively withdrew effort over time. This finding suggests that the pupillary reflex during memory studies is more complicated than simply representing recollection, familiarity, memory strength, or novelty. Rather, the interpretation of TEPRs during encoding and retrieval from long-term memory will be dictated by the empirical demands of the task and the retrieval success or failure of the perceivers. As pupillometric investigations of long-term memory processes are still relatively scarce, it remains an open area of investigation, capable of revealing a great deal about the function of human memory.

9.6 Summary and Conclusions

Just as ERP and fMRI (and, recently, single-unit recording from human patients) provide insight into the underlying neurocognitive architecture of human declarative memory, pupillometry provides great promise for making similar inroads, but with more efficient and readily available technology. Already, there exist debates over the interpretation of pupil data from standard recognition memory paradigms, with great progress being made toward understanding the pupillary manifestation of memory strength and specificity. Whereas some researchers suggest that TEPRs during memory retrieval reflect the function of a demanding recollection process (e.g., Kafkas and Montaldi 2012), others suggest that these patterns are more closely related to the strength of the memory signal, and not necessarily one specific process or another (Otero et al. 2011), paralleling well-known debates in the field of recognition memory (e.g., Wixted 2007; Yonelinas 2002). Progress in science is made through such fruitful debates, and pupillometry promises to inform that debate.

Regardless of the eventual interpretation regarding TEPRs and long-term memory, they clearly reflect its processes. Strong neurophysiological connections between pupil size and memory, and the empirical evidence reviewed here, suggest that these barely perceptible pupillary reflexes belie a flurry of neurocognitive activity. We opened this chapter with a discussion of the romantic history of pupillometry, focused on the famous connections between pupillary reflexes and amorous desire. Janisse (1977, p. 1) described the pupil as “the only visible part of the brain,” and likened it to a “permanently implanted electrode.” For scientists with interest in attention, memory, and other high-level cognitive processes, these are romantic words indeed, with their own promise of future excitement.

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From Distraction to Mindfulness: Psychological and Neural Mechanisms of Attention Strategies in Self-Regulation

10

Lotte F. van Dillen and Esther K. Papies

10.1 Introduction

> The basic law of the mind:
> *As you see—so you feel*
> *As you feel—so you think*
> *As you think—so you will*
> *As you will—so you act*
> K. Sri Dhammananda

As this quote suggests, stimuli that we perceive in our environment often have seemingly uncontrollable effects on our desires and behavior. This is especially true for affective and motivationally relevant stimuli, like a rich piece of chocolate cake, a pack of cigarettes, or the angry face of our spouse. However, as we will discuss in this chapter, insights from psychology and neuroscience, as well as from Buddhist teachings, show that these processes are not as difficult to prevent or overcome as they may seem, if we know how to regulate the focus and the quality of our attention.

The central aim of the current chapter, therefore, is to investigate attention strategies that may facilitate self-regulation. In this context, the term self-regulation refers to the ability to control one's affective responses and/or behavior in line with one's goals, and self-control refers to the more specific case of resisting an attractive short-term reward in order to ensure attainment of a longer-term goal. In the current analysis, we use the term affect in the broadest sense, encompassing all mental states that can have a positive or negative valence, and that can motivate approach or avoidance behavior. Affective responses play a central role in adaptive behavior, as they direct people's attention to possible threats and incentives in their environment (Bradley 2009). The unfolding of a behavioral response thus starts with the attentional capture of affective information (Gross and Thompson 2007).

The present analysis will focus on the attention strategies of distraction and mindfulness. By distraction, we mean shifting attention from the original object of attention onto a different focal object. Our current use of distraction does not involve *unintentional* attentional capture by a certain stimulus, and it does not involve mind wandering. Rather, distraction depends on the availability of a compelling substitute to occupy one's attention, in order to prevent attention being focused on unwanted content (Gerin et al. 2006). Mindfulness, on the other hand, implies regulating the focus as well as the quality of one's attention. This can imply paying attention to the focal object, but at the same time observing one's own reactions to the object and seeing them as mental events, instead of getting immersed in them as usual.

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In the following, we first discuss the basic concepts of attention. We will then continue by reviewing both behavioral and neuropsychological research on why affective responses are difficult to control, and suggest that this can at least partly be explained by the attentional priority of affective information. Next, we describe how affective responses may be regulated through the capture of attention by distracting information, and we will show that loading one's working memory resources with a distracter task can be an effective self-regulation strategy. Then, we will discuss theoretical underpinnings and empirical evidence on the application of mindfulness, which can change the quality as well as the regulation of attention. We will close this chapter by discussing the overlap, differences, and relations between various attention strategies, as well as implications for their application**.**

10.2 The Attentional Priority of Affective Information

Attention reflects the enhanced processing of some aspects of the environment while ignoring others (Johnston and Dark 1986). As such, attention is used to select the information that is most relevant for an individual's current goals from the constant stream of information that an individual is exposed to. Attention is commonly thought to be controlled by two mechanisms: bottom-up processes that are driven by salient information properties (i.e., stimulus-driven), and top-down processes in accord with people's ongoing plans and behaviors (i.e., goal-driven; Corbetta et al. 2008; Egeth and Yantis 1997; Pessoa and Ungerleider 2004).

Bottom-up attention filters select information on the basis of salient aspects that are likely to be important for adaptive behavior (Egeth and Yantis 1997), such as threat or reward, or other features with a strong biological relevance (Bradley et al. 2009). The nervous system responds to these particular aspects in a powerful and automatic manner, such that they are prioritized in further processing (Knudsen 2007). Top-down attentional control, on the other hand, is directed by the plans and actions people engage in, and may be crucial for flexible, goal-directed behavior (Corbetta et al. 2008). Top-down attentional control has the capacity to modulate or overwrite bottom-up attention filters and prioritizes information most relevant for the current task goal (Knudsen 2007; Pessoa and Ungerleider 2004). Accordingly, top-down attentional control may lie at the heart of effective self-regulation.

The human brain is designed in a way that affective information easily captures attention via bottom-up processes (Anderson and Phelps 2001; Berridge 2009; Bradley 2009). Research has demonstrated how processing of both threat and reward can occur quickly and unintentionally, and triggers responses across a broad array of sensory modalities (Berridge 2009; Bradley 2009; Nolen-Hoeksema et al. 1993). Self-regulation theorists have referred to this affective primacy as the core contributor to self-control failure (Mann and Ward 2004; Metcalfe and Mischel 1999). The "hot/cool model of willpower" (Metcalfe and Mischel 1999), for example, suggests that motivational "hot" cues about a desired object activate arousal, driving individuals to the immediate goal response, and that to override this tendency, informational "cool" cognitive cues about the stimulus are needed to direct attention to maladaptive aspects of the situation. As oftentimes, such "cool" reminders are not present, go unnoticed, or lack urgency, "hot" cues gain primary control over our behavior. For example, when exposed to an attractive piece of chocolate cake at one's favorite coffee house, this may trigger simulations of its creamy texture, the rich chocolate flavor, and the expectation of reward from eating it (Papies 2013) which may capture attention and inhibit thoughts about its calorie content and one's long-term health goals (Papies et al. 2008). Accordingly, self-control can be considered as a "battle" that arises due to conflicting representations that compete with each other to influence behavior, with the affective response, due to its attentional primacy, commonly having a notable advantage (Hofmann and Van Dillen 2012).

Affective information not only draws attention more easily through bottom-up processes, once it gains access to our working memory system, but it also facilitates attention via top-down processes to other affective information (Kavanagh et al., 2005), which may result in a vicious cycle of thinking that can prolong and intensify people's affective states (Kavanagh et al. 2005; Papies et al. 2008; Siemer 2005). For example, individuals, who tend to engage in negative ruminative thinking after an initial negative event, display exacerbated depressive symptoms over time, and are at a higher risk of developing new depressive episodes (Nolen-Hoeksema and Morrow 1993). Similarly, preferential attention for desirable targets enhances the motivation of attaining these targets (Gable and Harmon-Jones 2011), which in turn, has been found to relate to the intensity of cravings (Berridge 2009; Kavanagh et al. 2005), and, ultimately, self-control failures such as relapse (e.g., Field and Eastwood 2005; Franken 2003).

10.3 Distraction as a Tool for Self-Regulation

One explanation for the detrimental effects of affective processing on goal-directed human behavior is the idea that affective responses draw upon limited working memory resources (Kavanagh et al. 2005). More specifically, affect may increase the allocation of attention to affect-congruent information, at the cost of task-related information (Joormann and Siemer 2004). Thus, affect may "hijack" cognitive processing systems commonly engaged in top-down control. Paradoxically, the idea that affect occupies limited mental resources has also been the starting point for research on an effective self-regulation strategy, namely distraction.

Whenever people direct their attention away from a focal event, they engage in distraction. In a series of experiments, popularly known as "the marshmallow test," Mischel and colleagues demonstrated the phenomenon of using distraction for self-regulation in preschool children (Metcalfe and Mischel 1999; Mischel et al. 1989). In this paradigm, a young child can choose a desired treat immediately, such as a marshmallow, but can decide to wait until the experimenter returns in order to get two of the desired treats. Typically, in such experiments, attention to motivational stimuli drives children to choose the immediate reward (i.e., the affective primacy effect). However, children who were encouraged to think about pleasant, distracting thoughts (i.e., "if you want, while you're waiting, you can think about Mommy pushing you on a swing") were more capable of foregoing the immediate reward than children who had not been given this opportunity (Mischel et al. 1989).

Research has demonstrated the effectiveness of distraction by a wide range of activities, such as visualizing neutral scenes (Joormann and Siemer 2004; Rusting and Nolen-Hoeksema 1998), sorting cards (Morrow and Nolen-Hoeksema 1990), responding to colored lights (Christenfeld 1997), playing a game of Tetris (Holmes et al. 2009; Van Dillen et al. 2012), and filling out bogus questionnaires (Glynn et al. 2002). Apparently then, the effects of distraction are not restricted to a specific task type, but rely on more general aspects of attentional processing. Indeed, as we suggest in the present analysis, distraction may reduce bottom-up attention to affective information through the use of limited working memory resources for task-related top-down attentional control processes.

10.3.1 A Working Memory Account of Distraction

The basic assumption of our working memory account (Van Dillen and Koole 2007) is that task-related and affective information compete over working memory resources because working memory capacity is limited. When working memory demands of other activities are low, processing of affective information will by default receive priority due to bottom-up attentional selection, and may accordingly impact people's mental states and behavior. However, when a focal task requires more top-down control, for example, because of its high complexity, more working memory resources are needed to perform the task effectively, such that fewer resources will be available for affective processing (Knudsen 2007). Bottom-up attention to affective stimuli, and the subsequent processing thereof, thus may depend on the availability of working memory resources—even if these stimuli have previously been assumed to automatically capture attention regardless of the current state or mindset of the organism (Pratto and John 1991).

In an initial set of studies testing these hypotheses (Van Dillen and Koole 2009), people categorized the gender of angry and happy facial expressions, while they concurrently performed a more or less demanding focal task, such as solving simple or more complex math equations or rehearsing a one- versus eight-digit number. In this context, the emotional expression of the faces is irrelevant for performance on the gender-naming task. Accordingly, longer response latencies to angry than to happy faces index greater bottom-up attentional interference of negative information (reflecting a negativity bias, Pratto and John 1991). Participants indeed displayed such a negativity bias, but only when working memory load was low. When working memory load was high, participants responded as fast to angry as to happy faces. Moreover, picture negativity did not interfere with performance on the focal digit span task. In an extension of this work, we found that the N2 component and the late positive potential (LPP) complex of the event-related brain potential, an index of motivated attention that commonly displays greater amplitudes to negative as opposed to positive cues, and that emerges at around 250 ms following stimulus presentation, no longer differentiated between angry faces and happy faces under high load conditions and was generally attenuated (Van Dillen and Derks 2012).

In another recent extension of our working memory account to the domain of appetitive motivation (Van Dillen et al. 2013), we demonstrated that loading working memory by means of a digit span manipulation not only reduces the negativity bias but also the attentional bias to attractive compared to neutral stimuli. Specifically, only under conditions of no or low working memory load did participants display an attentional bias to motivationally relevant stimuli, such as attractive food and attractive faces of opposite-sex others. When participants were under high working memory load while processing these stimuli, the attentional bias disappeared. Together, these findings suggest that occupying working memory with a demanding task can reduce bottom-up attentional selection of both aversive and appetitive stimuli. This may have important implications for self-regulation, as we discuss shortly.

10.3.2 Distraction and Affective Responses

In the previous section, we discussed findings that demonstrated that bottom-up attention to affective information requires the use of limited working memory resources, which may underlie the effectiveness of distraction as a self-regulation strategy. If taxing working memory reduces prioritized attention to affective information, this may subsequently impact people's affective responses to this information and their evaluations of this information. Indeed, quite a number of findings now suggest this is the case.

In the first systematic exploration of these mechanisms, Erber and Tesser (1992) examined the effect of the amount of effort that participants invested in a distracter task. Here, participants viewed an emotionally arousing film clip after which they solved math equations for 10 min and then reported their moods. Participants displayed less negative moods in response to the film clip when they were told that effort at the distracter task was instrumental for performance rather than unrelated to performance, or when they solved complex rather than simple math equations. Erber and Tesser (1992) explained their findings in terms of a limited capacity model, arguing that: "…it may be that a task which requires the bulk of people's cognitive resources 'absorbs' moods by preventing further preoccupation with mood-related thoughts" (p. 342).

If affective responses require limited working memory resources, the intensity of the response may not only depend on the presence of a distracter task but also on the degree to which a task incorporates working memory resources. Provided that working memory capacity is a limited, but continuous variable, the involvement of working memory resources by a distracter task should have a gradual impact on people's negative feelings, such that a highly demanding task reduces the intensity of people's negative feelings to a greater degree than a moderately demanding task, whereas a moderately demanding task will still be more effective than a mildly demanding task.

In a set of three experiments (Van Dillen and Koole 2007), we systematically varied working memory load of a distracter task and examined its effect on self-reported negative affect. Participants viewed a series of neutral, mildly negative, or strongly negative pictures, followed by a more or less demanding task (or no task) and a feeling scale. Across the three experiments, variations in working memory load were indeed found to moderate the impact of viewing negative pictures on negative feelings (Van Dillen and Koole 2007). Participants reported less negative feelings after viewing negative pictures when they performed a complex task rather than no task, or a simple task. The moderating effect of performing a task on negative feelings was stronger when the task was unpredictable, than when it was predictable, and was stronger for intensely negative stimuli (which engage more working memory capacity; Siemer 2005) than mildly negative stimuli. In line with a working memory account, these experiments thus demonstrated how the intensity of participants' negative feelings was the result of a dynamic use of working memory resources by both task-related and affective processes.

In a neuroimaging experiment (Van Dillen et al. 2009), with a similar design as the just described series of studies on distraction (Van Dillen and Koole 2007), it was tested more directly whether working memory load modulated affective responses, or, perhaps, simply reduced the accessibility of affective information for conscious reflection. Working memory load again resulted in attenuated self-reported negative feelings. More importantly, working memory load was found to downregulate activity in brain systems engaged in affective processing. Performing a complex task compared to a simple task reduced responses to negative pictures in the bilateral amygdalae, and the right insula. Inversely, performing a complex rather than a simple task resulted in increased activity in regions implicated in cognitive processing, such as the right dorsolateral frontal cortex and superior parietal cortex. The decrease in activity in emotional brain regions was related to the increase in activity in working memory regions of the brain, suggesting that increases in task load actually "tuned down" the emotional brain.

Similar effects have been reported of working memory load on brain responses to painful stimuli (Bantick et al. 2002; Frankenstein et al. 2001). For example, pain intensity scores to thermal stimuli, as well as activity in areas of the pain matrix (i.e., thalamus, insula, the anterior cingulate cortex, ACC), are reduced significantly by high working memory load (Bantick et al. 2002). Novel evidence using spinal high-resolution neuroimaging suggests that the attenuating influence of high compared to low working memory load on pain may reach beyond the brain and moderate responses to incoming pain signals at the earliest stage of central pain processing (Sprenger et al. 2012). In a recent neuroimaging study involving the influence of working memory load on appetitive responses to high-calorie food pictures (Van Dillen and Van Steenbergen 2013), moreover, selective responses to attractive high-calorie foods in so-called hedonic brain regions such as the ventral striatum and the medial prefrontal cortex (Berridge 2009) turned out to be significantly reduced under high compared to low working memory load.

The neuropsychological evidence just described thus provides further evidence that working memory load reduces affective experiences by disrupting actual processing of affective information, and not, for example, by interfering only with the conscious reflection and elaboration on this information.

10.3.3 Distraction and the Regulation of Behavior

Although the regulation of attention and affective responses can be an important goal in itself, self-regulation is often targeted at the control of actual behavior. An important question thus is to what extent distraction can be a helpful tool to regulate (unwanted) behavior. In what follows, we describe research findings that suggest that taxing working memory resources can reduce the impact of affective and motivational cues on (social) judgments and on behavior.

In one study, Bushman et al. (2005) investigated the role of angry rumination in triggered displaced aggression, which is the displacement of anger (and the associated aggressive behavior) in response to an initial provocation to an unrelated mildly annoying event. Previous research has demonstrated that the intensity of angry feelings mediates the relationship between an initial provocation and displaced aggression (Pedersen et al. 2000). Bushman and colleagues, however, showed that any process that distracts processing resources away from an anger provocation effectively decreased triggered displaced aggression. In a similar vein, Van Dillen et al. (2012) showed that the impact of disgust on moral judgments depends on the availability of mental capacity. It has been widely demonstrated that feelings of disgust lead to harsher judgments of moral convictions (Wheatley & Haidt 2005). Van Dillen and colleagues showed that when participants played a game of Tetris (distraction condition) rather than reflecting on their feelings in response to a disgust film clip (rumination condition), they reported less disgust, and, accordingly, made milder judgments about the moral conviction.

Importantly, performing a demanding distracter task may not only affect unwanted affective influences in the interpersonal domain but also in the control of appetitive impulses. In a recent study (Van Dillen et al. 2013, Study 3), participants were exposed to tempting food cues in a categorization task, while they were simultaneously performing a highly demanding distracter task or not. Afterwards, they could choose an attractive unhealthy snack or a healthy snack as a reward from the experimenter. Participants who had been exposed to food temptations while performing the highly demanding distracter task were less likely to select an attractive but unhealthy snack over a less tasty but healthy snack, compared to control participants. This effect was especially pronounced among participants who were generally highly responsive to tasty food cues (i.e., who scored high on the Power of Food Scale, Lowe et al. 2009). These findings again show that high working memory load can prevent elaborations of pleasure and reward in response to attractive food stimuli, so that their impact on the subsequent motivation to actually indulge in them is reduced. Further corroborating this process, being exposed to attractive food pictures while holding a high, compared to a low working memory load, also curbed the development of cravings in response to such food cues. Again, an important mediator of the affect–behavior link seems to be how much working memory resources are available for further elaboration on an affective stimulus.

10.3.4 Distraction's Possible Limitations

As we have seen, distraction can be a powerful self-regulation strategy, as it disrupts the attentional selection and subsequent processing of affective information, and its influence on behavior (Van Dillen et al. 2013). Yet, distraction is unlikely to be the ultimate solution to all of people's self-regulation problems. Indeed, when a strong desire has already been aroused, maintaining a high cognitive load sometimes makes it more difficult to resist temptation (e.g., chocolate cake) and pursue a long-term goal (e.g., dieting; Ward and Mann 2000)—possibly because cognitive load interferes with (top-down) self-control efforts, rather than with the (bottom-up) affective responses that lead to temptation. Working memory load may thus have opposing effects on self-regulation depending on the timing of the distracter task.

Little is known, moreover, about the long-term effects of distraction, with some research suggesting memory costs for the to-be regulated material, due to reduced reprocessing in working memory (Kron et al. 2010; Sheppes and Meiran 2008). Whereas this may have beneficial consequences in some instances (e.g., working memory load during the consolidation of emotional memories can reduce traumatic memory intrusions, Holmes et al. 2009), such memory costs may also preclude learning, and the integration of affective information in a broader context. As the source of affective responses thus remains unchanged, responses to more stable problematic situations may rebound once people cease to distract themselves (but see Bonanno et al. 1995). It is therefore important to consider other forms of attention regulation that allow people to deal in more comprehensive ways with their affective responses.

10.4 Beyond Distraction: Mindfulness

One alternative strategy of regulating attention that has gained increased popularity recently is mindfulness. This approach is based on insights and practices that Buddhist practitioners have developed over thousands of years during meditation and systematic study of the human mind. These insights are increasingly recognized and integrated in Western science, and studied in psychology, neuroscience, and the emerging domain of contemplative science.

The Western term mindfulness is most often used to refer to an open and nonjudgmental form of awareness that is centered on present-moment experiences, including one's thoughts, emotions, and sensations[1] (Kabat-Zinn 2003). A useful operational definition has been offered by Bishop and colleagues (2004). This specifies two components of mindfulness, namely attention regulation, with increased top-down control of attention, and the quality of one's attention, which we refer to as the perspective of *mindful attention*. While both of these components are typically practiced in mindfulness training (such as mindfulness-based stress reduction, Kabat-Zinn 1994), they may have separable effects on attentional processes. We now discuss each of these components and their application to self-regulation.

10.4.1 Training Attention Regulation Through Meditation

Attention regulation refers to top-down control of one's attention such as to maintain it on a chosen object, despite distractions. This can be trained by meditation practice, which is a crucial part of mindfulness training. Here, the practitioner typically focuses attention continuously on a chosen stimulus, such as the breath or a visual object, and returns attention to the focal object once it has inadvertently shifted away. With regular practice, attention becomes increasingly stable, which improves attention and executive control (Lutz et al. 2008). Mindfulness interventions with a focus on attention regulation have shown effects on variety of cognitive tasks that rely on working memory and executive control, reflecting increased control over attention (e.g., Jha et al. 2007; Mrazek et al. 2013; Slagter et al. 2007).

These cognitive benefits of the attention-training component of mindfulness are associated with functional and structural changes in several cortical regions supporting attentional processes. Sustaining attention during meditation has been shown to rely on attention networks involving, among others, the dorsolateral prefrontal cortex (DLPFC) for focused attention, and the anterior insula and dorsal ACC for detecting that one's mind has wandered from the chosen target (Hasenkamp et al. 2012). Using these attention networks for meditation becomes increasingly efficient with experience, such that less activation is required to maintain focused attention (Brefczynski-Lewis et al. 2007). This is also reflected in increased functional connectivity within attentional networks in experienced meditators (Hasenkamp and Barsalou 2012). Extensive meditation practice has been shown to

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[1] For a discussion of the use of the term in Buddhhism, see Lutz, Dunne, & Davidson, 2007.

be associated with increased cortical thickness in regions associated with attention, interoception, and sensory processing, including the prefrontal cortex (PFC) and right anterior insula (Lazar et al. 2005). These effects reflect the focus of meditation practice, namely to keep focusing attention on one's breath and sensory experiences for an extended period of time (Lazar et al. 2005).

Thus, the attention training in mindfulness approaches makes it increasingly easy to disengage from distracting thoughts or stimuli and return to one's chosen object of attention. More generally, training attention regulation benefits self-regulation, because effective attentional deployment by increased top-down control over attention allows one to disengage from affective or tempting stimuli, helps to identify and shift attention to other cues, supports cognitive change strategies such as reappraisal or even distraction, and facilitates emotion regulation in other ways (Van Dillen et al. 2012; Wadlinger and Isaacowitz 2011). Indeed, various studies have shown that attention training in the context of mindfulness training benefits emotion regulation and facilitates dealing with stress, illness, anxiety, and other affective challenges (see Wadlinger and Isaacowitz 2011, for a review). Even a 15-min focused attention exercise has been shown to reduce affective responses to strongly valenced stimuli (Arch and Craske 2006). Supporting these psychological effects, neuroimaging findings suggest that mindfulness training increases gray matter density in regions involved in emotion regulation, such as the hippocampus, the posterior cingulate cortex (PCC), and the temporo-parietal junction (TPJ; Hölzel et al. 2011).

In mindfulness practice, people usually train attention regulation to be able to keep attention focused on the present moment, rather than engage in mind wandering or getting immersed in affective states. People typically spend a large amount of time daydreaming or mind wandering, but this mind wandering often makes us unhappy (Killingsworth and Gilbert 2010) and is associated with biological markers of stress (Epel et al. 2013; but see Baird et al. 2012, for how mind wandering can help problem solving). Mindfulness practice has been shown to reduce such mind wandering, including the excessive rumination about past events associated with depression (e.g., Mrazek et al. 2013; Teasdale et al. 2000). Thus, focusing attention on one's present-moment experiences appears to be an effective way to regulate one's overall affective state and well-being (see Brown et al. 2007).

The work on mindfulness discussed so far has suggested that attention training can facilitate self-regulation because it increases top-down control over attention. Research on mindfulness, however, suggests that focusing attention is particularly effective if it is accompanied by adopting a certain perspective on one's experiences, which we call mindful attention. Thus, we now describe the mindful attention perspective on one's experiences in more detail and discuss its implications for self-regulation.

10.4.2 Mindful Attention

Mindful attention refers to the metacognitive awareness that one's experiences are in essence mental events, and transient in nature (Papies et al. 2012). Mindful attention utilizes the uniquely human faculty of being able to observe one's own mental processes, and see their inherent character as mental events (Lutz et al. 2008; Papies et al. 2012; Teasdale 1999). In the mindfulness literature, this metacognitive awareness is also referred to as "decentering," and in self-report measures, this aspect of mindfulness is captured in subscales assessing the nonidentification or nonreactivity to one's experiences (e.g., Baer et al. 2006; Lau et al. 2006). While much empirical work has examined the effects of the attention-training component of mindfulness, the metacognitive awareness component of mindfulness has received little research attention. Therefore, and in order to examine the effects of mindful attention systematically, we recently developed a brief laboratory training procedure (Papies et al. 2012) in which participants learn to apply this perspective to their own experiences. This training allows us to examine the effects of mindful attention in controlled experiments.

In this mindful attention training, participants view a series of stimuli that potentially induce affective or motivational responses, such as pictures of positive and negative scenes, pictures of highly tempting and neutral food objects, or pictures of attractive and less attractive opposite-sex others. While viewing these pictures, participants are instructed to simply observe their reactions to them, and to consider the transitory nature of these reactions as passing mental events, which arise and disappear. Thus, participants are asked to simply observe all of their responses, without avoiding or suppressing them, and to view them as passing mental events.

We assume that typically, when participants view objects and scenes in such pictures, they spontaneously simulate how they would interact with them and what the resulting experiences would be (Barsalou 2009; Papies and Barsalou 2014). When seeing pictures of attractive food items, for example, participants simulate eating and enjoying the food, which is reflected in them representing such food in terms of its taste, texture, and hedonic qualities (Papies 2013), as well as in activations in primary gustatory and reward areas in the brain (Simmons et al. 2005). As discussed above, to the degree that enough cognitive resources are available, these simulations can unfold into full-blown experiences of craving and desire (see Van Dillen et al. 2013), and increase the motivation to obtain the presented stimuli. However, when applying mindful attention, participants actively consider these thoughts and reward expectations, they learn to see how these mental events are triggered by the pictures they are viewing, and they can observe them arise and disappear. As a result of applying this perspective, participants should be less likely to get immersed in vivid simulations of pleasure and reward, and the motivation toward the presented stimuli might be reduced.

The results of a number of experiments indeed confirm these hypotheses. Applying mindful attention to pictures of attractive food eliminated approach impulses toward these stimuli in a reaction-time-based approach-avoidance task (Papies et al. 2012), and reduced choices for attractive, high-calorie food over neutral, healthy food in both a laboratory and a field setting (Papies et al. 2014). In addition, cravings for food were reduced among mindful attention compared to control participants (Papies et al. 2014). Similarly, applying mindful attention to pictures of opposite-sex other reduced the temptation of these stimuli for participants who had a strong motivation for casual sex (i.e., an unrestricted socio-sexual orientation, Simpson and Gangestad 1991). A recent neuroimaging study on this topic showed that mindful attention reduces experienced cravings among cigarette smokers, as well as craving-related neural activity in response to cigarette pictures, particularly in a region of the ACC (the subgenual ACC). Moreover, changes in the connectivity between brain areas implicated in the experience of craving, such as the sgACC and the ventral striatum, suggested that mindful attention may decouple craving neurocircuitry, without active downregulation by PFC regions (Westbrook et al. 2013). Accordingly, these findings suggest that mindful attention may reduce bottom-up attention directly, without the engagement of top-down control networks.

The above studies demonstrate that mindful attention can decrease the motivation for otherwise highly tempting stimuli. As one learns to see one's thoughts of pleasure and reward in response to attractive stimuli as mere mental events, these thoughts become less compelling, and they are less likely to lead to motivated behavior toward these stimuli. Mindful attention reveals that the reward from a stimulus comes merely from one's own thoughts about it, making the stimulus *itself* less attractive, without requiring active downregulation of its reward value.

Some similar findings have been reported from applications of mindfulness for dealing with negative affect. In particular, seeing one's depressed or even suicidal thoughts as mere mental events is crucial for the effectiveness of mindfulness-based approaches to reduce relapse in depression (see Williams 2008). In a recent neuroimaging study, moreover, patients with generalized anxiety disorder (GAD) who followed a mindfulness training showed changes in connectivity between amygdala and PFC regions (i.e., increased positive coupling) which correlated with the strength of symptom improvements (Hölzel et al. 2011). These changes are interpreted as an increased "decentering," which allows one to observe one's own experiences as mere mental events, as it is trained in mindful attention. However, more research is needed to systematically examine the application of the mindful attention perspective in this domain.

Together, these studies show that regulating the quality of one's attention to change one's relationship with one's own thoughts and experiences can be an effective strategy to enhance self-regulation and well-being. This applies to reducing the affective and motivational impact of both positive and negative information. Importantly, this does not imply that reactions to affective information are simply attenuated. During painful stimulation, mindful attention has, for example, been observed to result in activations in the ACC, thalamus, and insula—regions associated with primary pain processing, whereas activity in evaluative regions, such as the amygdala and hippocampus, did decrease (Grant et al. 2011). Possibly, mindfulness increases sensitivity to primary affective reactions, which should facilitate adequate self-regulation as one can deal with these reactions before they gain momentum through additional rumination and elaboration (Teper et al. 2013).

10.4.3 Changing the Focus or the Quality of Attention

The attention strategies outlined here, that address the focus, the regulation, and the quality of one's attention, differ in important ways. As discussed above, changing the focus of attention may contribute to self-regulation in the face of strong affective or motivational stimuli to the degree that it prevents the development of full-blown affective responses and cravings. This suggests that strong affective responses rely on the availability of cognitive resources, and that engaging these in a competing task can therefore promote self-regulation. However, applying distraction is not always possible, and in addition, may be less effective in acute self-control situations (i.e., Ward and Mann 2000). Moreover, the attenuating impact of working memory load on actual sensory experiences may result in compensatory behavior once people indulge in a temptation, for example, by consuming more salty or sugary foods to make up for weakened taste experiences (Van der Wal and Van Dillen 2013). In addition to distraction, changing the focus of attention can also be achieved by training attention regulation, for example, through meditation. However, the ability to do this spontaneously and effectively may develop only with substantial practice (Wadlinger and Isaacowitz 2011).

In contrast, the perspective of mindful attention reduces the intensity of full-blown motivational responses by revealing their nature as passing mental states. Indeed, mindful attention seems to be at its most effective when individuals aremost susceptible to the reward of the presented stimuli, for example, because they are hungry, or because they have a strong interest in casual sex (Papies et al. 2014). Possibly, when one's desires are most vivid and intense, they are more easily observed, and more easily seen as mere mental events, which arise and eventually dissipate. Therefore, mindful attention might be most effective when temptation is strong. Briefly applying mindful attention to observe one's experiences as mere mental events may thus also facilitate the application of distraction or other forms of regulating attention, as it may reduce the immersion in one's initial affective responses (see Papies et al. 2014). However, when affect is too strong, distraction may be the best way to create the opportunity for the application of more effortful techniques. Future research should examine systematically the optimal conditions for the use of each strategy.

Both the attention training techniques of mindfulness and the systematic application of mindful attention to facilitate self-control outside the laboratory may require substantial practice. Once learned, these strategies may have pronounced long-term effects (Wadlinger and Isaacowitz 2011). However, the effort and time required to learn and enact them make them less effective for individuals who are not highly motivated to address their self-control problems. Thus, changing the focus and the quality of attention may both have advantages and disadvantages, suggesting that there is no one-size-fits-all solution for all self-regulation challenges.

Clearly, there may be other attention strategies that enhance self-regulation, and that share features with one or both of the approaches we described. For example, research suggests that taking a global (rather than a local) perspective on emotional information reduces attentional capture of this information (Gable and Harmon-Jones 2012). As with mindful attention, this strategy allows people to view things in a different perspective, while at the same time, attention is paid to other nonemotional information, which is also central to distraction and attention regulation training through meditation.

Another example of such an integrative approach is eye movement desensitization and reprocessing (EMDR) therapy (Lee and Cuijpers 2013). Here, participants are guided to retrieve a painful or otherwise intrusive memory, and while reliving their emotional peak experience, they are instructed to maintain their attention on alternating visual or auditory stimuli. With repeated treatment, the intensity of these memories is commonly strongly reduced. Accordingly, EMDR has proven an effective therapy for treating affective disorders ranging from emotional trauma to addiction (Lee and Cuijpers 2013). The effectiveness of this intervention may depend critically on the combination of both attention to one's affective reactions and distraction, which simultaneously allows the disruption of traumatic recollection in working memory and increased psychological distance from the trauma (Gunter and Bodner 2008). Thus, whereas the application of a specific strategy should be tailored to the context and to the individual's need, distraction, mindful attention, and other attention strategies such as EMDR may prove highly effective self-regulation tools in a variety of domains.

Conclusion

Integrating insights from psychology and neuroscience, in this chapter, we investigated attention strategies that may facilitate self-regulation, namely distraction, training attention regulation (through mindfulness meditation), and mindful attention. We presented evidence that these strategies affect both the focus and the quality of attention, and as a result, the impact of affective information on thoughts, feelings, and behavior. Whereas seemingly opposing in nature, we have found that both distraction and mindfulness can undermine intrusive thinking patterns in response to affective information that normally result in more impulsive behavior.

We have seen, moreover, that the effectiveness of these strategies is reflected not only in behavioral measures of self-regulation success but in neurophysiological indices as well, and how combining these behavioral and neuroscience measures can help to understand underlying mechanisms of attention strategies. For example, neuroscience studies of both distraction and mindfulness point to the involvement of prefrontal control regions along with brain regions engaged in processing of threat and reward, suggesting that these self-regulation strategies may affect (at least in part) the same neural network. These strategies may, however, engage this network in different ways, as distraction seems to involve the increased engagement of prefrontal brain regions for task-related processing, whereas training attention regulation may affect the connectivity between control and affective brain regions. Preliminary evidence, moreover, points to the possibility that specifically mindful attention affects the reactivity of affective and primary sensory regions, even in the absence of top-down prefrontal control. Examining these attention strategies further, especially their neuropsychological signatures and their long-term effects, may provide new insights in what makes them effective for particular self-regulation situations.

At any moment in time, humans can only keep a few things in their minds. Ironically, this fundamental limitation of human information processing may also have some beneficial consequences. Because processing both affective and non-affective information requires the use of limited attention resources, people can control affective processes via the allocation of attention. By either intentionally directing attention away from affective information or by mindfully observing one's own reactions to it, the impact of this information on subsequent thought and behavior can be regulated to facilitate long-term goal pursuit and well-being.

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Part III

The Central Nervous System and Self-Regulation

11

From the Reward Circuit to the Valuation System: How the Brain Motivates Behavior

Mathias Pessiglione and Maël Lebreton

11.1 Introduction

> That which is unmoved is the practical good, and that which produces movement and is moved is the faculty of desire […], while that which is moved is the animal; and the instrument by which desire produces movement is then something bodily. Hence, it must be investigated among the functions common to body and soul.
> Aristotle, De Anima 433b13 (4th century BC).

Why do we do what we do? Some of our actions are pure habits—sequences of movements that unfold over time, triggered either by the previous movement or by a familiar stimulus. By opposition, some actions are properly motivated: In that case, movements are directed toward a goal, i.e. an anticipated situation that has a positive value. The concept of value has become central in modern accounts of behavioral regulation. Values determine both the direction of behavior (the selected goal) and its intensity (the amount of expended energy). In this chapter, we first sketch a short history of how the value concept has emerged, next we describe the properties of the brain valuation device, then we illustrate how values can be influenced by, or exert an influence on, other brain systems, and finally we close by pointing some unresolved issues that deserve further investigation.

11.2 Two Short Scientific Stories

Values are used as key determinants of behavior in at least two scientific fields: animal learning and economic choice theories.

11.2.1 Animal Learning

> Give me a child and I'll shape him into anything
> B. F. Skinner

The history of scientific animal conditioning can be started with Edward Thorndike (Thorndike 1911). In a famous study, Thorndike was examining how a cat would learn to pull a string so as to open the cage door and eat the fish placed outside. He discovered that cats do not learn from watching a demonstration made by the experimenter or another cat: they learn by trial and error. At some point, they get angry, pull out their claws, scratch the cage and accidently pull the ring, so the door opens and they get the fish. It does not follow that they understood the trick: the same behavior will be repeated in the next trial. However, they will get out faster and faster, until the action of pulling the rope becomes automatic. Based on this

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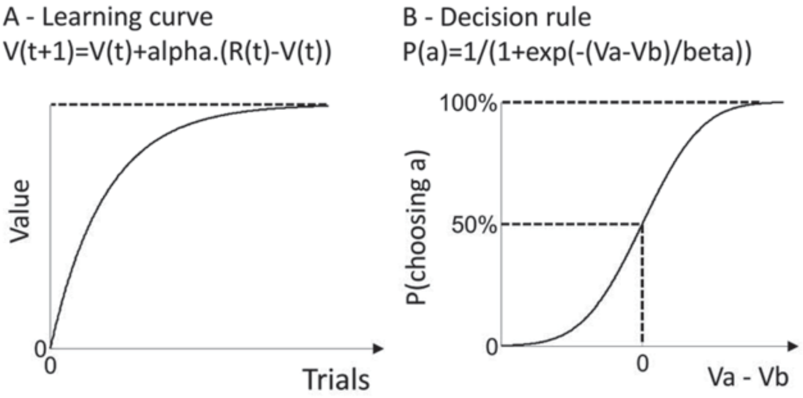

Fig. 11.1 Learning and decision psychometric functions. **a** A central law of animal learning theory. Typical learning curves are negatively accelerated and converge to a plateau. This dynamics can be captured by the Rescorla and Wagner rule, which states that from trial *t* to trial *t*+1, the reward value of a contextual cue is updated in proportion to the reward prediction error (actual reward minus expected value). Parameter alpha (termed "learning rate") captures the weight of prediction error on value update. **b** A central law of economic choice theory. Typical choice functions have a sigmoid shape with respect to decision value. In the case of a binary choice between options **a** and **b**, this shape can be captured with a softmax rule, which states that the probability of choosing option **a** is a logistic function of the difference between option values. Parameter beta (termed choice "temperature") captures the stochasticity of decisions (which is the opposite of the propensity to choose the option with highest value)

observation, Thorndike formulated the law of effect: "Responses that produce a satisfying effect in a particular situation become more likely to occur again in that situation."

This formulation was the basis for the development of associative learning (or reinforcement learning) theory. The idea is that primary rewards (like food) reinforce the link between a stimulus and a response, such that the response is more likely to be triggered at the next occurrence of the stimulus. This type of learning has been later called operant or instrumental, because the response is necessary for obtaining the reward, by opposition to classical or Pavlovian learning, in which the response is an ineffective appetitive reflex (such as salivation). Pioneers of instrumental conditioning (with Watson and Skinner as most famous names) identified key factors of associative learning, for instance contiguity—the reward must closely follow in time the stimulus–response events, or contingency—the stimulus–response events must increase the probability of getting the reward. For our purposes, the most interesting principle is certainly that of Rescorla and Wagner (Rescorla and Wagner 1972), which states that learning speed is proportional to reward prediction error (actual minus expected reward). This prediction error signals the discrepancy between observations and expectations, and therefore the need for updating contingencies. It has a sign: associations are strengthened when the outcome is better than expected, weakened in the opposite case (see illustration in Fig. 11.1a).

It was only two decades later that neuroscientists identified a plausible biological substrate—phasic dopamine release, for reward prediction errors. Midbrain dopaminergic nuclei were already known to induce self-stimulation behavior in rodents (Olds and Milner 1954). These animals were implanted with electrodes in the ventral tegmental area, which delivered electrical stimulation each time they would press a lever. Rats rapidly learned and repeated frenetically this operant behavior, as if the direct stimulation of dopamine neurons was bypassing the role of natural rewards. Another hint that dopamine was signaling reward came from the discovery that most recreational drugs associated with high hedonic states boost dopamine release (Imperato et al. 1986; Leone et al. 1991; Wise et al. 1995). This is when dopamine became the "pleasure molecule" for the media, and a central part of the brain reward system for neuroscientists. Despite this evidence, Wolfram Schultz and his colleagues, recording single-cell activities in monkeys, intended to link the activity of dopamine neurons to motor parameters, such as the amplitude or speed of movements. This was because degeneration of dopamine neurons was known to induce Parkinson's disease, a condition primarily characterized by motor deficits: akinesia (paucity of movement), limb rigidity, and resting tremor. Yet the dopaminergic activity did not reflect motor parameters; what Shultz discovered is that dopamine neurons fire when the monkey obtains a reward, specifically if it was unexpected (Ljungberg et al. 1992; Mirenowicz and Schultz 1994; Schultz et al. 1993).

In the behaviorist era, mental or cognitive processes were banished from the explication of behavior. Reward was an objective property of what would reinforce the behavior, and symmetrically punishment is what would discourage behavior (or reinforce behavior avoidance). In theory of animal learning, reward prediction errors were impacting on the strength of stimulus–response associations. However, as the theory developed with more sophisticated machine learning algorithms, designed to have robots finding their way in complex environments, intervening variables made their appearance. In particular, the role of reward prediction, later termed expected value, became explicit. What was learned in this new generation of algorithms (Sutton and Barto 1998), such as the actor–critic model, is the expected value attached to a given situation or a given action.

In parallel, a community of scientists had developed an interest for the effects of incentives on behavior intensity (measured by speed or force) and not just action selection (Berridge 2004). It is important to distinguish the effects of incentives, which precede and motivate the action, from the effects of rewards, which follow and reinforce the action. Scientists investigating motivation also forged intervening concepts to avoid the combinatorial explosion that soon occurs when one intends to draw a list of all possible stimulus–response associations. Incentive value is one of these concepts; it can be understood as the feature of a goal that will activate the behavior toward this goal (Dickinson and Balleine 1994). Importantly, it was demonstrated that animals could work a lot for goals that are not objective rewards. For instance, rats can climb a barrier a 100 times in order to get a few drops of saccharin (Sheffield and Roby 1950), which cannot be digested into glucose and therefore cannot serve as energy supply for the organism. Thus, the expected values that drive our behavior had been acknowledged as subjective, with the hedonic component coming front stage (Bindra 1978; Bolles 1972; Cabanac 1992; Toates 1986).

11.2.2 Economic Choice

> Let us weigh the gain and the loss in wagering that God is…. If you gain, you gain all; if you lose, you lose nothing. Wager, then, without hesitation that He is.
>
> Blaise Pascal, Thoughts (1669)

The concept of expected value separately emerged in the community of philosophers and economists who intended to formalize how humans make choices. Blaise Pascal, more than three centuries ago, was perhaps the first to formulate the maximization principle that may underlie choices. When facing options, we start by drawing the consequences of taking each alternative, then for each consequence we estimate the probability of occurrence and the amount of pleasure that we would get from it. The option to be chosen is the one that maximizes the product of probability and pleasure, summed over all envisaged consequences. For instance, in the famous Pascal's wager (Pascal 1669), we have no information about whether God exists (probability is 50 %). If God does not exist, then our actions have no consequence on our happiness after we die. If God does exist, then acting as a believer will earn us infinite pleasure (in heaven), whereas acting as a nonbeliever will inflict us infinite pain (in hell). Therefore, we must believe in God.

The maximization principle is still in vigor nowadays (see illustration in Fig. 11.1b), even in contemporary choice theories intending to account for the fact that real human agents are not as rational as the fantasized homo economicus. However, these theories put no constraint on the preferences that agents should have. They are free to prefer hell to heaven, but their choices should be consistent with a stable function of preferences (Samuelson 1938; Savage 1954; Von Neumann and Morgenstern 1944). In other terms, to be considered as rational, choices must satisfy a number of axioms. As an example, choices should be transitive: if you prefer A to B and B to C, then you should prefer A to C. Unfortunately, even these basic principles are frequently violated by human agents. A common way to adapt economic models is to introduce distortions of the two key dimensions defined by Pascal: probability and pleasure (or in more modern terms, utility). Bernouilli introduced the curvature of the utility function: A same objective difference will induce less increase in subjective utility when it comes to high amounts of money (Bernoulli 1738). Kahnemann and Tversky suggested the prospect theory, according to which subjective estimates create an asymmetry between gains and losses (both in the initial slope and in the curvature of the utility function), and a sigmoid distortion of objective probability (inflating small probabilities and shrinking high probabilities). This type of distortion can explain some interesting manifestation of choice behavior, such as risk aversion and loss aversion (Kahneman and Tversky 1979).

However, even with these amendments, economic decision theory still misses a number of spectacular deviations from rational behavior. One pervasive case is contextual dependency, meaning that different preferences can be expressed for a same choice set placed in different contexts. In a famous experiment (Ariely et al. 2003), Dan Ariely asked participants whether they would buy a bottle of wine for a dollar figure equal to the last two digits of their social security number, which was of course totally arbitrary. Then, they asked participants how much they would be willing to pay for this bottle of wine. Answers to this second question revealed that subjects with higher social security number give higher price estimates. This is an example of anchoring effect, where a logically independent element of the context can distort the assignment of subjective value. Less than two decades ago, a subset of experimental economists became interested in understanding how the brain makes decision, kicking off the field of "neuro-economics." The hope was to discover biological constraints that could be incorporated into economic models so as to improve choice prediction (Camerer et al. 2004; Fehr and Rangel 2011; Glimcher 2009; Rangel et al. 2008). In other words, one could reasonably assume that the brain under natural selection has evolved choice heuristics that are generally adapted to natural environment but locally maladaptive in artificial situations of the modern economic world. Another hope was to find a way to decode values directly from neural signals, instead of asking the subject, so as to access true preferences. Collaboration with neuroscientists was made easier by the use of a common concept, value, to explain behavior, and by the availability of neuroimaging scanners that allowed investigating brain activity in humans.

11.2.3 The Brain Valuation System

Fifteen years later, many studies have tried to identify neural signals encoding reward or value. A neural network, successively known as the brain reward circuit and the brain valuation system (BVS), has been delineated (Bartra et al. 2013; Haber and Knutson 2009; Kable and Glimcher 2009; Peters and Büchel 2010b; Rangel et al. 2008). The main components are the orbitofrontal cortex (particularly the ventromedial prefrontal cortex, VMPFC) and the ventral striatum (VS), which together constitute the limbic fronto-striatal circuit. Other key components are the posterior cingulate cortex (PCC) and limbic structures such as amygdala and hippocampus (see illustration in Fig. 11.2a). Furthermore, interesting properties of the valuation signal have been identified, which we briefly review in the next paragraphs.

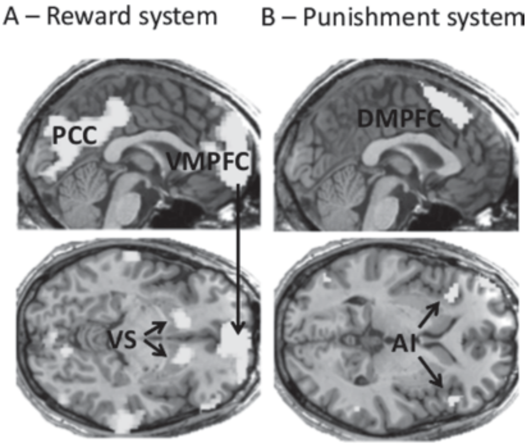

Fig. 11.2 Two opponent brain systems for reward and punishment. *White blobs* show typical activation maps obtained in a single subject following "correct" (*left*) and "incorrect" (*right*) feedback on a cultural quiz (ongoing study). Significant blobs are superimposed on the individual anatomical scan. The same regions show linear correlation with levels of reward (positive value) and punishment (negative value), respectively. *PCC* posterior cingulate cortex, *VMPFC* ventromedial prefrontal cortex, *VS* ventral striatum, *DMPFC* dorsomedial prefrontal cortex, *AI* anterior insula

11.2.4 Parametric Coding

The first studies to identify reward-related activities used paradigms derived from animal conditioning. The orbitofrontal cortex proved responsive to reward occurrence when recording both single-cell activity in monkeys (Hikosaka and Watanabe 2000; Thorpe et al. 1983; Tremblay and Schultz 1999) and hemodynamic signal in humans (Berns et al. 2001; O'Doherty et al. 2001). Functional magnetic resonance imaging (fMRI) studies using associative learning paradigms further demonstrated that the VMPFC and VS were reflecting expected reward at the time of cue and reward prediction error at the time of outcome (Gottfried et al. 2003; Pagnoni et al. 2002). Moreover, prediction error signals were modulated by dopaminergic drugs, in a manner that predicted the effects on learning performance (Pessiglione et al. 2006). Drugs that boost dopamine release amplify learning from positive outcomes, whereas drugs that block dopamine transmission amplify learning from negative outcomes (Bódi et al. 2009; Frank et al. 2004; Palminteri et al. 2009). As the VMPFC and VS are prominent targets of dopaminergic axons, their response to reward prediction and prediction error might reflect dopaminergic input.

However, another generation of paradigms was designed to investigate valuation in non-learning contexts, by implementing simple likeability ratings or economic binary choices. Again, the response of VMPFC and VS to option presentation was found to be linearly correlated with values (Blair et al. 2006; Kennerley et al. 2011; Padoa-Schioppa and Assad 2006; Plassmann et al. 2007). This parametric encoding of value was therefore not related to the necessity of tracking arbitrary contingencies between cues and outcomes, as was the case in associative learning paradigms. Moreover, values were subjective: In a same subject, it would vary with internal state such as satiety (Gottfried et al. 2003; Small et al. 2001). Also, different subjects could make different choices, and have different likeability ratings for the same object. Neural value signals varied across individuals with subjective preference, and not with the objective properties of the displayed options (Lebreton et al. 2009; McClure et al. 2004b).

11.2.5 General Device

One key assumption of standard economic theory is that all option values can be assigned on a same scale. This would allow for arbitrating between options that seem incommensurable, for instance, doing your homework versus going to a movie. Having a "common neural currency," that is, a neural signal representing the value of any possible option, would simplify choice problems to a great extent (Montague and Berns 2002). A lot of evidence has been accumulated for the VMPFC being such a general valuation device (Levy and Glimcher 2012). Some studies have directly compared different categories of objects from different modalities (faces, food, money, houses, paintings, trinkets, cars, tastes, odors, music, etc.) and found that their value was reflected in the same BVS, particularly the VMPFC (Chib et al. 2009; Kim et al. 2011; Lebreton et al. 2009; Levy et al. 2011; Salimpoor et al. 2013). It remains possible however that within this system, different subregions process different subcategories. It has been suggested for instance that more anterior parts of the VMPFC were dedicated to valuating more abstract objects (such as money vs. food) than more posterior parts (Sescousse et al. 2013). It was also suggested that both category-independent and category-specific valuation systems are implemented in the VMPFC (McNamee et al. 2013).

11.2.6 Automatic Processing

Another important issue is whether valuation processes are triggered by the necessity of making a choice, or if they automatically apply to any object that comes to attention. Early studies investigating Pavlovian processes suggested that stimuli triggering appetitive reflex are automatically valuated. Further studies have then examined whether this property could be generalized to any item that comes to mind, by scanning subjects while they were passively viewing the items (Levy et al. 2011), or rating an independent dimension of the items such as the age (Lebreton et al. 2009) or making judgments about a central stimulus with the item in the background (Harvey et al. 2010; Tusche et al. 2010). Subjective values of the proposed items were then obtained by asking subjects to make ratings or choices after the scanning session. In all cases, these values could be partially decoded from the activity of the BVS. These results suggest that the BVS is always on, assigning values to all sorts of representation that come under attentional focus. This automatic valuation might not be neutral for the other ongoing cognitive processes and might impose some bias on seemingly independent task performance.

A related question is whether a representation must be conscious in order to be processed by the BVS. This question has been addressed using subliminal presentation of visual cues that could have different values, such as coin images or abstract symbols associated with rewarding outcomes. Behavioral results showed that the value of subconscious stimuli could affect performance in tasks such as force production, perceptual discrimination, or gambling decision (Aarts et al. 2008; Bijleveld et al. 2010; Pessiglione et al. 2007, 2008; Seitz et al. 2009). These behavioral effects were underpinned by neural activity in the ventral striato-pallidum complex, which could differentiate the values of subconscious cues (Pessiglione et al. 2007, 2008). Contrary to the case of automatic processing, where visual items are consciously perceived but irrelevant to the ongoing task, subconscious processing seem thus to involve the subcortical part of the BVS.

11.3 Interaction with Other Brain Systems

In order to influence the behavior, the BVS must interact with circuits responsible for controlling action execution. In this section, we review some investigations on how the BVS interacts not only with motor or executive circuits but also with other circuits that may participate in the valuation process.

11.3.1 Motor and Executive Systems

A simple case is the process of incentive motivation, through which higher expected reward is translated into more vigorous behavior. Different measures of the energy expended in the behavior have been employed, such as response time and grip force. A widely used paradigm is the monetary incentive delay task, in which subjects can win various incentives if their response time falls below a preset limit. fMRI data have repeatedly showed that activity in the VS was proportional to incentive level (Knutson et al. 2001; Knutson et al. 2003). Similar results were obtained using the incentive force task, in which payoff is proportional both to the incentive and to the force exerted on a power grip. Not only did VS activity increase with incentive level but also it was predictive of motor performance (Pessiglione et al. 2007; Schmidt et al. 2009). The principle was further generalized to cognitive effort (as illustrated

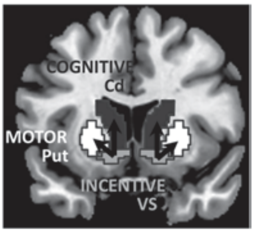

Fig. 11.3 Schematic illustration of a neural account for incentive motivation. Regions of interest correspond to the striatal parts activated by monetary incentives (*light gray*), motor effort (*white*), and cognitive effort (*dark gray*). Depending on task demand (*motor or cognitive*), the ventral striatum (*VS*) switches effective connectivity between putamen (*Put*) and caudate (*Cd*) nucleus. Thus, the ventral striatum appears as a key motivation region, whose activity reflects incentive level and predicts task performance, and capable to drive both motor and cognitive striato-frontal circuits. (Adapted from Schmidt et al. 2012)

in Fig. 11.3): Depending on task demand, the VS switched connectivity between the putamen and caudate, so as to boost activity in the motor versus cognitive fronto-striatal circuits, respectively (Schmidt et al. 2012). Other authors have suggested that the motivation control of executive systems by valuation systems occur at the cortical level, between medial and lateral prefrontal regions (Kouneiher et al. 2009).

Many studies have also examined how expected values could influence brain regions underpinning motor execution in choice paradigms. In monkeys, single-unit activities were found to integrate movement and value coding in several brain regions, such as the basal ganglia, premotor or parietal cortex (Hikosaka et al. 1989; Lauwereyns et al. 2002; Pasquereau et al. 2007; Platt and Glimcher 1999; Samejima et al. 2005). For instance, a neuron with selectivity for a preferred movement direction can fire in proportion to the associated expected reward. These activities could participate in a mechanism of competition where each neuron would vote for its preferred action. For fMRI in humans, movements must be more grossly different in order to yield separate neural representations. This can be obtained for instance with hand versus eye movement, or with left versus right hand movement. Several studies have reported interaction between value and motor codes in regions such as the anterior cingulate cortex and orbitofrontal cortex (Palminteri et al. 2009; Wunderlich et al. 2009). However, the question of whether simple binary choices are made in the stimulus space or in the action space is still intensely debated, with authors claiming that the values encoded in the orbitofrontal cortex relate to stimuli (Padoa-Schioppa 2011; Rangel and Hare 2010) and others arguing that they relate to actions (FitzGerald et al. 2012; Gershman et al. 2009).

11.3.2 Episodic Memory System

So far, we have encompassed paradigms where values were assigned to objects represented in perceptual systems, the visual occipitotemporal pathway in most cases. However, typical long-term goals are situations that we never observed in the past and that we have to imagine. The past decade has provided compelling demonstrations that imagining future situations involve the same brain regions (in the medial temporal lobe) as retrieving memories from the past. Indeed, patients with damage to the medial temporal lobe, and particularly to the hippocampus, suffer not only from memory loss but also from a difficulty in simulating future situations (Hassabis et al. 2007; Schacter et al. 2007). The hippocampus might therefore be critical for the ability to valuate imagined situations, by providing a simulation with enough details to make it attractive. This idea was corroborated by a recent study that involved subjects choosing between novel food items made of a combination of familiar elements (Barron et al. 2013). fMRI results showed that the construction and valuation of these novel rewards implicated both the hippocampus and medial prefrontal cortex. Thus, while observed objects are represented in perceptual systems, and imagined objects in memory systems, the values of these objects are in both cases encoded in the BVS.

The ability to imagine future outcomes with sufficient details seems crucial for common cases of inter-temporal choices, in which we must decide between an immediate reward that we can perceive with our senses and a delayed reward that requires mental simulation (Boyer 2008; Rick and Loewenstein 2008). Traditional paradigms in behavioral economics have investigated inter-temporal conflicts using binary choices between smaller-sooner and bigger-later monetary payoffs (Kable and Glimcher 2007 McClure et al. 2004a). A consistent finding is that the dorsolateral prefrontal cortex, a region classically involved in cognitive control, is recruited when subjects resist impulsive behavior (i.e., choosing the immediate rewards). A new generation of inter-temporal tasks has integrated “episodic tags” that suggest using the money for a given purpose, for instance, vacations in Paris. These paradigms have revealed that episodic tags make subjects less impulsive, an effect underpinned by functional connectivity between the VMPFC and hippocampus (Benoit et al. 2011; Peters and Büchel 2010a). The conflict between immediate-observed and future-imagined rewards was directly implemented in a recent study where choice options could be presented either as pictures or as texts (Lebreton et al. 2013). Both the hippocampus volume and activation predicted the individual propensity to favor imagined future outcomes. Moreover, patients with damage to the hippocampus (due to Alzheimer’s disease), but not with damage to the prefrontal cortex (due to fronto-temporal dementia), were specifically more impulsive when the delayed option had to be simulated (because presented as a text and not as a picture). It is plausible that poverty of imagination induces not only impulsivity but also apathy, since goal representation would not be attractive enough to drive the behavior.

11.3.3 Social Cognition System

There is a particular class of objects that have a huge impact on our values: this is the social domain. Social representations, such as the characteristics or the mental states of other people, are processed in a dedicated brain system that includes superior temporal sulcus (STS), temporoparietal junction (TPJ), and medial prefrontal cortex (Frith and Frith 1999; Saxe 2006). These regions have been shown to interact with valuation regions and to influence the behavior. For instance, activity in the STS and TPJ was related to participants making more altruistic choices, toward charities or toward game partners (Hare et al. 2010; Morishima et al. 2012). A recent study revisited the classical finding that, when collaborating to achieve a common goal, participants typically reduce their effort in proportion to group size (an effect termed “social loafing”). This can be interpreted as an effect of diminishing the marginal utility of effort exertion, as each individual effort has a lesser impact on group performance if there are more participants. However, beyond social loafing, participants who departed from utility maximization and invested more energy in collaboration had both higher functional activity and higher gray matter density in their TPJ (Le Bouc and Pessiglione 2013).

These last studies illustrate how social brain regions influence our behavior toward other people. The opposite link, through which others’ behavior can influence our preferences, has also been investigated. For instance, explicit information about others’ preferences biases our own valuation toward social conformity, an effect that was shown to involve BVS regions (Campbell-Meiklejohn et al. 2010; Klucharev et al. 2009). A more basic mechanism would involve the mirror neuron system, which represents actions at an abstract level, such that a given action can elicit the same neural activity, whether it is being performed by the subject or by an actor whom the subject is observing (Gallese et al. 1996; Rizzolatti et al. 1996; Rizzolatti et al. 2001). It has been shown that the recruitment of this system during action observation is not neutral for the observer: it can affect her/his motivational values. More precisely, the interaction between the mirror neuron system and the BVS resulted in subjects perceiving as more desirable the objects taken as goals by actors in a video (Lebreton et al. 2012). This mechanism could implement a primitive form of mimetic desire, possibly important in preverbal humans and other species, allowing values to propagate implicitly across individuals (Bayliss et al. 2006). This might be adaptive, as it would save some time and avoid some risk inherent to learning values by experience (i.e., by trial and error). It might also be considered as detrimental, since it would direct several people toward the same goal, and therefore generate rivalry and/or herding behavior (Girard 1979).

11.4 Unresolved Issues

Although appealing, the idea of a single brain system devoted to valuating any object that comes to mind is not without raising issues. In this section, we mention some of the problems that should be the focus of research in the next years.

11.4.1 Value Representation at a Lower Scale

Although subjective value was repeatedly observed to correlate with BVS hemodynamic signal, the link with electrophysiological activity remains to be established (Logothetis 2008). In other words, the neural code for subjective value has not been cracked yet. Most single-unit activities have been recorded in the primate lateral (not medial) orbitofrontal cortex. Although many neurons in this lateral region exhibited sensitivity to visual cues predicting juice rewards (Hikosaka and Watanabe 2000; Kennerley et al. 2011; Padoa-Schioppa and Assad 2006; Tremblay and Schultz 1999; Wallis and Miller 2003), it is not the case that they would all activate in proportion to subjective value. In binary choices, three types of neurons have been identified (Padoa-Schioppa and Assad 2006): neurons that encode the expected value of a particular juice ("offer cells"), neurons that encode the value of the chosen option whether it is juice A or juice B ("chosen-value cells"), and neurons that signal the chosen juice irrespective of its value ("taste cells"). Such a careful taxonomy has not been established for the medial orbitofrontal cortex (which would be homologous to the human VMPFC). It has nonetheless been suggested that neurons in medial regions would be more sensitive to internal factors such as satiety, possibly encoding more subjective values (Bouret and Richmond 2010). In any case, how a distribution of various single-unit activities can give rise to a value signal measurable with fMRI remains to be understood. One attractive possibility is a population code analogous to that seen in the motor cortex (Georgopoulos et al. 1986; Pouget et al. 2000), with different neurons voting for the values of different features.

11.4.2 Construction of the Value Signal

A related point is how the uncertainty over value estimate is incorporated in neural activity. Effects of uncertainty have been mostly investigated in choice situations, with subjects being faster when option values are more distant. Several studies have reported that the hemodynamic signal in the VMPFC reflects this distance (chosen minus unchosen value), which is linked to choice confidence (De Martino et al. 2013; Hare et al. 2011b). However, we also have feelings of confidence about the valuation itself (i.e., we can be unsure of whether we like something). It is likely that neural activity in the BVS encodes not one scalar value but a probability distribution over values. Further research is needed to uncover how this distribution is biologically implemented. A straightforward hypothesis is that uncertainty corresponds to the variance of activities over the neuronal population. Another (nonexclusive) possibility is that value takes time to be extracted, for instance by sampling and integrating input signals. This sort of sequential sampling models has been widely used in perceptual decision making, where the task is to categorize an ambiguous stimulus (Gold and Shadlen 2007; Ratcliff and Rouder 1998; Shadlen and Newsome 2001). The idea is that integrating over time enables extracting signal from noise. In drift diffusion models, evidence is accumulated until it reaches a predefined threshold triggering a given response. The same principle has recently been applied to value-based decision, with the aim of disambiguating internal signals that participate to subjective value (Basten et al. 2010; Hunt et al. 2012; Krajbich et al. 2010; Lim et al. 2011). In this framework, uncertainty could be reduced to the temporal variance of value signals, or to the time taken to reach the threshold. Of course it raises the question of which signals exactly are integrated in the construction of subjective value, which certainly deserves further consideration. It also raises the possibility that the activity preceding option presentation affects value judgment, as it could place the system more or less close to the threshold. The influence of pre-stimulus activity on behavioral response has already been demonstrated in perceptual decision tasks (Fox et al. 2007; Hesselmann et al. 2008a; Hesselmann et al. 2008b; Sadaghiani et al. 2009) and could be extended to value-based decision.

11.4.3 How Many Value Signals?

The issue is further complicated when the options to be valuated have multiple attributes on independent dimensions. The integration over dimensions is a process that has received little attention so far. It is not clear whether all value signals integrate all dimensions. For instance, the VMPFC appeared to incorporate the costs due to temporal delay but not those linked to the required effort (Prévost et al. 2010). When a choice must be made, one may wonder whether the integration over attributes is done before or after comparing the options. The locus of the comparison process itself is subject to lively debate, some authors suggesting that values are directly compared within the VMPFC (Rushworth et al. 2012), others that values are passed on to other systems dedicated to comparison, such as the dorsomedial prefrontal cortex (Rangel and Hare 2010). Another issue under intense scrutiny is how option values are normalized with respect to the number of alternatives (Louie and Glimcher 2012; Rangel and Clithero 2012).

The specific role of the various BVS components is also matter to debate. It has been suggested for instance that the distinction between goal value (the expected reward associated to one option), decision value (the net difference between option values), and experienced value (the pleasure provided by the outcome) could match the anatomical parcellation of the BVS (Hare et al. 2008). The distinction of goal and experienced values is reminiscent of the distinction between wanting (how much a potential reward is desirable) and liking (how much an obtained reward is pleasurable) forged by Kent Berridge (Berridge 2004). However, no consensus has been reached so far about whether these quantities have separable neural substrates. On the contrary, much evidence suggests that the same BVS components reflect the values of potential and obtained rewards. Another current opinion is that relative to the VMPFC, the VS is more involved when the valuation concerns a familiar or subconscious representation, and/or when it must be connected to a motor process such as effort production (Knutson et al. 2001; Pessiglione et al. 2007, 2008; Schmidt et al. 2009, 2012).

It is also possible that different brain systems assign different values to a same object, creating a conflict for the control of behavior. Theories involving dual valuation systems have been proposed for instance to explain inter-temporal choices. One system, including the VS, would be more impulsive and give priority to immediate rewards, whereas the other system, including the dorsolateral prefrontal cortex, would be more patient and favor long-term rewards. This theory would explain the "now effect" captured with quasi-hyperbolic discount function, which accords a special bonus to immediate rewards relative to all delayed rewards (McClure et al. 2007; McClure et al. 2004a). It has been contradicted however by studies showing that a same brain system, including both the VMPFC and VS, reflects subjective values irrespective of whether options are immediate or delayed (Kable and Glimcher 2007; Peters and Büchel 2010a). One way to reconcile these views is to consider that all values are indeed encoded in the usual BVS, with the values of delayed options being under the upregulating influence of dorsolateral regions (Hare et al. 2009). Similar top-down influence (from the dorsolateral onto the VMPFC) has also been evidenced in the case of cognitive regulation (Hare et al. 2011a; Hutcherson et al. 2012).

Finally, several teams have started to search for an opponent system signaling aversive value. A good candidate for such a system is the anterior insula (as illustrated in Fig. 11.2b), which has been shown to reflect unexpected punishments (including monetary losses) in associative learning paradigms (Palminteri et al. 2012; Seymour et al. 2004). This putative opponent role is supported by consistent findings that the anterior insula activates with negative events or feelings, such as pain, disgust, or risk (Craig et al. 2000; Craig et al. 1996; Critchley et al. 2001; Preuschoff et al. 2006). Other neural dissociations for rewards and punishments have been suggested, such as medial versus lateral orbitofrontal cortex (Grabenhorst et al. 2007; Kringelbach 2005; O'Doherty et al. 2001; Small et al. 2001). It does not mean however that the BVS would be exclusively responding to positive events and the opponent systems only to negative events. The idea is rather that both systems signal both types of events, but with an opposite sign. It has been shown for instance that the VMPFC also reflects negative value (of food items that participants would not eat) through deactivation level (Plassmann et al. 2010). There is also evidence for the converse relation in the anterior insula, in which deactivation might represent higher value (Palminteri et al. 2012; Seymour et al. 2004). However, the dissociation of appetitive and aversive systems is not uncontroversial: Positive activations in response to negative events have been reported in all BVS components, including the VMPFC and VS (Baliki et al. 2006; Bartra et al. 2013; Laxton et al. 2013). Further investigations should aim at explaining these discrepancies.

11.5 Conclusion and Perspectives: Toward Clinical Applications

In this chapter, we have exposed how behavioral economists, experimental psychologists, and cognitive neuroscientists joined their efforts and merged two fields of investigation: reward learning and choice behavior. This collaboration was made possible by technical progress—the availability of brain imaging scanners, and conceptual links—the use of motivational value as a key variable. We have then presented evidence that motivational values are encoded in a so-called BVS, which essentially comprises the ventral parts of the prefrontal cortex and basal ganglia. Some fundamental properties of the BVS have been uncovered: it encodes values that are personal (subject- and not object-specific), generic (expressed in a common neuronal currency), and automatic (generated even during distractive tasks). Next, we have seen example situations where the BVS interacts with other brain systems (such as the perceptual, motor, executive, episodic, and mirror systems) that can impact on, or be impacted by, motivational values. These neural interactions might explain a number of psychological phenomena, for instance, incentive motivation (why we put so much effort in a task), delay discounting (why we can resist the temptation of immediate pleasures), or mimetic desires (why we often pursue the same goals as others). Last, we have pointed to unsolved issues, such as how values are encoded at the single-cell level, how the value code incorporates uncertainty, how the values of different features are integrated, how the values are different options are compared, how negative values are represented relative to positive values, etc.

Although our understanding of the value computations implemented by our brains remains extremely limited, we have made substantial progress that can already explain some cases of irrational behavior. For instance, the fact that the BVS is both generic and automatic means that it will inevitably aggregate the value of many contextual features. Because brain signals are strongly auto-correlated in time, this is likely to affect subsequent choices. This simple mechanism would be sufficient to explain a number of priming effects, and more generally, to account for observation that our decisions are context dependent.

Beyond economic theory of choice, knowledge of brain value computations could be useful for understanding clinical conditions. Damage to the VMPFC was shown to result in inconsistent choices, as if inducing noise in subjective value representations (Camille et al. 2011; Fellows and Farah 2007). The apathy due to dopamine depletion or basal ganglia lesions could be explained by a down-weighing of expected rewards (Adam et al. 2013; Rochat et al. 2013; Schmidt et al. 2008). Impulsivity, defined as the propensity to go for immediate pleasures, could be reduced to overdiscounting rewards with delays. These examples suggest that many pathological features could be captured by parameters of value functions being out of the normal range. Several clinical studies have begun to use behavioral tasks that enable inferring key parameters of value computation. Results will tell us whether these parameters can be used for identification of neural dysfunction, or for prediction of therapeutic effects.

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Neural Foundations of Motivational Orientations

12

Eddie Harmon-Jones and Cindy Harmon-Jones

12.1 Introduction

Motivational direction, the urge to approach versus avoid, is a fundamental motivational dimension present in most living organisms (Schneirla 1959). Indeed, major theories of self-regulation typically include approach–avoidance as one of the most basic dimensions (Carver and Scheier 2001; Kuhl and Koole 2008). Approach–avoidance motivational impulses are the primary targets of self-regulatory attempts, and conflicts between these basic motivational impulses (and even approach–approach conflicts) need to be regulated. These basic motivational impulses are often the basis of approach–avoidance goals, which regulate behavior. Moreover, self-regulatory failure increases approach motivation, adding to the challenges of voluntarily regulating these urges (Schmeichel et al. 2010).

The basic motivational orientations toward approach and withdrawal are often associated with emotions. Most of the neuroscience research is predicated on models that assume approach motivation and responses to rewards involve a positive affective system, whereas avoidance motivation and responses to punishments involve a negative affective system. As will be reviewed later, however, this assumption has come under question with recent evidence.

This chapter provides a selective review of research on the neural bases of approach and avoidance motivation, with a particular focus on asymmetrical frontal cortical activity as much research has associated this neural variable with approach/withdrawal. Approach and withdrawal motivational processes likely involve brain systems and not only specific brain structures. However, the investigation of the dynamic unfolding of motivational processes within neural structures and chemicals has not yet been well investigated because of the difficulties of mapping these micro-processes over the microseconds in which they occur. As a result, in this chapter, we review research on brain regions that have received the most scrutiny by motivation scientists. Figure 12.1 shows the main locations of these regions within the human brain. In doing so, we also review research from both the nonhuman and human research literatures, as the nonhuman research is more precise neuroanatomically and neurochemically because it can be more invasive than research with humans. It is important to note that it is difficult to demonstrate that one psychological process maps perfectly onto one physiological process. For example, greater activity within the amygdala could reflect several psychological variables, including uncertainty (Whalen 1998), positive affect (Anderson et al. 2003), and motivational relevance (Cunningham et al. 2008). These issues will be considered more fully within this chapter.

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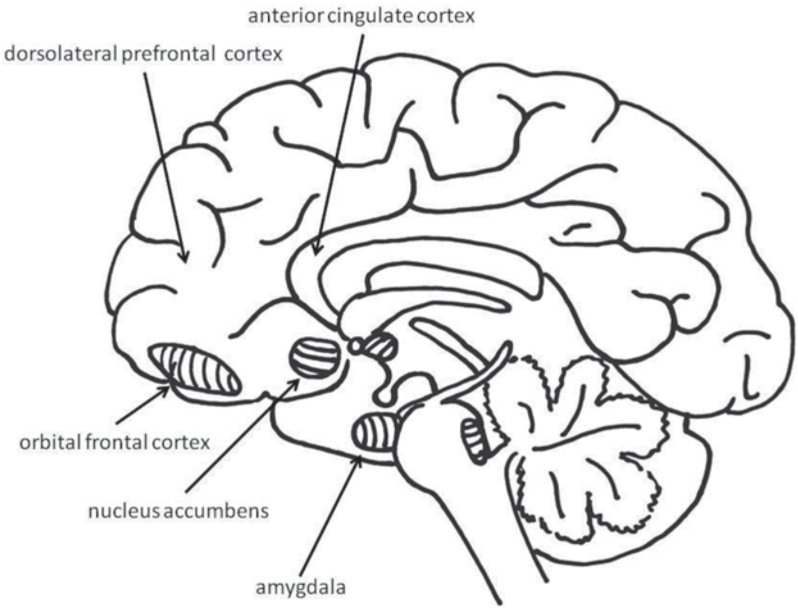

Fig. 12.1 A rough illustration of the locations of the brain regions reviewed in this chapter

12.2 Amygdala

The amygdala is one important brain structure involved in the avoidance and approach motivations that are often the target of self-regulation efforts. Laypersons and psychologists who are not familiar with the neuroscience literature often believe that the amygdala is only involved in fear. However, research has revealed the amygdala to be involved in a variety of emotive processes. The amygdala consists of approximately a dozen nuclei (Freese and Amaral 2009). Three of these nuclei have been found to be involved in fear—the lateral nucleus, central nucleus, and basal nucleus. The lateral nucleus receives input from thalamic and cortical regions. The lateral nucleus is connected to the central nucleus directly and also indirectly through projections to the basal nucleus. The lateral nucleus is critical for the acquisition and storage of fear conditioning, and the basal nucleus and central nucleus are critical for the expression of fear (Cain and LeDoux 2008).

The amygdala is also involved in positive emotional reactions, such as reward-seeking. Amygdala lesions cause rats to not work for salty rewards even when they are in states of sodium depletion (Schulkin 1991). Amygdala lesions also cause rats to not consume salt that is freely given to them, even though they show positive reactions to salty tastes once placed in their mouths (Schulkin 1991). Amygdala lesions also disrupt reward learning (Everitt and Robbins 1992). After amygdala damage, male rats will not perform a learned task to gain access to sex, even though the same rats will copulate if access to the female is freely granted (Everitt 1990).

Destruction of the amygdala is not sufficient to eliminate emotional learning, because aspects of learned reward and learned fear exist after removing the amygdala. Monkeys with bilateral amygdala destruction express fear to strong stimuli (Kling and Brothers 1992). Humans with bilateral amygdala damage also show normal recognition of vocal expressions of fear (Anderson and Phelps 1998), and normal patterns of daily mood (Anderson and Phelps 2002).

Findings on amygdala activity in humans are largely consistent with findings obtained from nonhuman animals. One major difference between human and animal experiments is the spatial resolution of the measurement of neural activity. The most often used technique for measuring amygdala activation in humans is functional magnetic resonance imaging (fMRI). With a 3 T magnet, spatial resolution is approximately 3 mm per cube or voxel. However, a voxel contains hundreds to thousands of neurons. Moreover, areas containing neurons tightly packed together, such as the hypothalamus or amygdala, do not allow detailed measurements of subpopulations of neurons within the regions. Finally, fMRI relies on blood flow, blood volume, and blood oxygenation associated with recent neuronal activation, whereas the animal research directly measures electrical activity of the neurons.

As with the animal research, human neuroimaging research has revealed that the amygdala region activity is increased by a variety of emotive stimuli in addition to fear-provoking ones. In humans, positive stimuli evoke greater amygdala activity than neutral stimuli (Breiter et al. 1996). Moreover, other experiments have manipulated valence and intensity independently, and found that the amygdala region responds more to affective intensity than to any specific valence (Anderson et al. 2003). Other research has found that the processing goals of motivationally relevant evaluative information influence amygdala activity (Cunningham et al. 2008; Sander et al. 2003). In the experiment by Cunningham et al. (2008), participants provided positive to negative ratings (i.e., bivalent) of famous persons, only positive ratings (from none to very good) of famous persons, or only negative ratings (from none to very bad) of famous persons. When participants provided bivalent evaluations, both positive and negative names caused amygdala activation. When participants provided only positive evaluations, positive names caused amygdala activity, and when they provided only negative evaluations, negative names caused amygdala activity. This research indicates that the amygdala flexibly processes information motivationally in line with current processing goals.

12.3 Nucleus Accumbens/Ventral Striatum

The nucleus accumbens, which is at the front of the subcortical forebrain, is rich in dopamine and opioid neurotransmitters, and well known for being involved in positive affect (Ashby et al. 1999). Thus, the nucleus accumbens is involved in many of the appetitive processes toward which self-regulation results are directed. In addition, research has found that the nucleus accumbens is involved in more than only positive affect.

Dopamine cells within the ventral tegmental area project to the nucleus accumbens, amygdala, ventral pallidum, and prefrontal cortex, and these regions project back to the ventral tegmental area both directly and indirectly. Some have theorized that this mesolimbic dopamine system provides the motivation to direct behavior toward reward-related stimuli (Berridge 2000, 2007). This system is posited to be involved in the "wanting" of stimuli and not the hedonic impact or "liking" of rewarding stimuli. Consistent with this hypothesis, human functional neuroimaging research has found that the nucleus accumbens is activated by pre-goal positive emotion but not by post-goal positive emotion (Knutson and Wimmer 2007).

Dopamine and the nucleus accumbens, however, have been found to be involved in more than "wanting." Specific regions of the nucleus accumbens together with specific neurotransmitters may be involved in "liking." When morphine, which activates opioid receptors, is injected into posterior and medial regions of the accumbens shell, it increases positive affective responses to sweet tastes (Peciña and Berridge 2000). Additionally, the nucleus accumbens is involved in regulating effort: Lever-pressing schedules that require minimal work are not affected by depletions of dopamine within the accumbens, but lever-pressing schedules that require much work are affected (Salamone et al. 2007).

Aversive stimuli also activate nucleus accumbens (Salamone 1994), depending on the region of accumbens and the chemicals involved. When substances that increase GABAergic neural transmission are injected into the rostral (front) shell of the nucleus accumbens, appetitive behaviors increase (e.g., eating, place preference, orofacial expressions of taste-elicited liking). In contrast, when the same substances are injected into the caudal (back) shell of the nucleus accumbens, fearful defensive behaviors increase (e.g., place avoidance, orofacial expressions of taste-elicited disliking; Reynolds and Berridge 2001, 2002). Human fMRI research has found a similar rostral–caudal distinction in the nucleus accumbens (Seymour et al. 2007). Also, dopamine and acetylcholine have differing functions in the nucleus accumbens: Dopamine enhances approach and acetylcholine enhances inhibition or avoidance (Hoebel et al. 2007). Manipulated stressful environments cause the caudal fear-generating zones to expand rostrally, filling approximately 90 % of the nucleus accumbens shell. Manipulated preferred environments cause appetitive-generating zones to expand caudally, filling approximately 90 % of the shell (Reynolds and Berridge 2008). This latter research demonstrates how environments modify brain regions involved in emotive processes.

12.4 Orbitofrontal Cortex

The orbitofrontal cortex is the bottom (ventral) one-third of the prefrontal cortex. It receives inputs about gustatory, olfactory, somatosensory, auditory, visual, and visceral information. Moreover, it has direct reciprocal connections with the amygdala, cingulate cortex, insula/operculum, hypothalamus, hippocampus, striatum, periqueductal gray, and dorsolateral prefrontal cortex (Kringelbach and Rolls 2004).

Neurons in the orbitofrontal cortex fire when monkeys taste desired foods and also when they simply see desired foods or associated stimuli (Rolls 1997, 2000; Rolls et al. 1990). These neurons stop firing once monkeys have eaten their fill of the desirable foods (Rolls et al. 1988). Thus, these neurons respond to affective properties and not simply the sensory quality of the taste. The orbitofrontal cortex is activated by other rewarding stimuli (Chang et al. 1998) as well as punishing stimuli (Berridge 2003).

Human neuroimaging experiments have conceptually replicated these results, and found different regions of the orbitofrontal cortex are involved in reward and punishment responses. Rewards and pleasant stimuli activate the medial orbitofrontal cortex, whereas punishments and unpleasant stimuli activate the lateral orbitofrontal cortex (see O’Doherty 2004, for review). In addition, a posterior–anterior distinction exists: complex reinforcers (such as monetary gain and loss) activate anterior regions, whereas simple reinforcers activate posterior regions (see Kringelbach and Rolls 2004, for review).

Loss of the orbitofrontal cortex is not sufficient to eliminate emotive responses (Damasio 1994, 1996). Persons with lesions to the orbitofrontal cortex seek some simple pleasures (e.g., palatable foods) and avoid unpleasant events. Similar results have been observed in animals (Berridge 2003).

12.5 Anterior Cingulate Cortex

Stimuli may directly cause behavior via passage through sensory processing areas to neural substrates involved in approach or avoidance. At other times, stimuli may be processed more deeply and/or multiple responses may be possible. At these times, neural substrates involved in decision making determine whether approach or avoidance occurs. The anterior cingulate cortex is one neural region involved in this process and it has thus received much research attention. That is, the anterior cingulate cortex is proposed to be critically involved in monitoring action tendencies for potential conflicts, so that other processes, presumably engaged by the dorsolateral prefrontal cortex, can promote the desired goal-directed response (Botvinick et al. 2001; van Veen and Carter 2006). Thus, the anterior cingulate cortex may trigger the conscious, deliberate components of self-regulatory behavior by detecting conflicting motivational responses that require regulation.

In one set of studies illustrating the functions of the anterior cingulate cortex, the event-related potential (ERP) known as the “error-related negativity” was used to measure anterior cingulate cortex activity (Gerhing et al. 1993). When individuals who were low in racial prejudice accidentally committed responses that indicated they might possess racial stereotypes, they had greater anterior cingulate cortex activity (Amodio et al. 2004a). Subsequent research found greater anterior cingulate cortex activity associated with racially biased responses particularly for individuals who had strong personal motivations to respond without prejudice (Amodio et al. 2008a).

These studies support the idea that the anterior cingulate cortex responds to conflicts between responses such as approach–avoidance conflicts.

12.6 Asymmetric Frontal Cortical Regions

One pattern of neural activity that has often been found to relate to approach and avoidance motivation is asymmetrical activity over the frontal cortical regions. Goldstein's (1939) observations of persons who had suffered damage to the right or left prefrontal cortex suggested that these regions were differentially involved in positive affect (or approach motivation) and negative affect (or withdrawal motivation). Subsequent observations confirmed these results: persons with left hemisphere damage showed depressive symptoms, whereas persons with right hemisphere damage showed manic symptoms (Robinson and Price 1982).

Much of the more recent evidence has been obtained with electroencephalographic (EEG) measures of brain activity, or more specifically, alpha frequency band activity derived from the EEG. Research has revealed that alpha power is inversely related to regional hemodynamic activity (Cook et al. 1998). Source localization of EEG signals (Pizzagalli et al. 2005) and fMRI results suggest that the dorsolateral prefrontal cortex is the primary region involved (Berkman and Lieberman 2010).

12.6.1 Trait Affective Styles and Resting Asymmetric Frontal Activity

Some of the initial support for the idea that positive affect and approach motivation were associated with greater left than right frontal cortical activity (referred to as relative left frontal activity) came from studies examining resting, baseline EEG activity over several minutes. These studies found that individuals with depression had relatively less left than right frontal brain activity (Jacobs and Snyder 1996; see meta-analysis by Thibodeau et al. 2006).

Subsequent studies found that trait approach motivation was related to greater relative left frontal activity (Amodio et al. 2004b; Amodio et al. 2008b; Harmon-Jones and Allen 1997), suggesting that asymmetric frontal cortical activity is with motivational direction. However, because avoidance and approach motivation are often associated with negative and positive affect, respectively (Carver and White 1994), it was difficult to determine whether motivational direction or affective valence was primarily responsible for the relationship of these emotive traits with asymmetric frontal activity. In other words, the research had confounded emotional valence with motivational direction. However, researchers suggested that relative left frontal cortical activity reflected greater approach motivation and positive affect, whereas relative right frontal cortical activity reflected greater withdrawal motivation and negative affect. This interpretation was consistent with theories that associated positive affect with approach motivation and negative affect with withdrawal motivation (Watson 2000).

However, approach motivation is not always associated with positive affect. Consider anger, a negative emotion that is associated with approach motivation (for review, see Carver and Harmon-Jones 2009). For instance, studies have found that trait behavioral approach sensitivity is positively related to state and trait anger (Carver 2004; Harmon-Jones 2003; Smits and Kuppens 2005). Because evidence suggests that anger is often associated with approach motivation, research has used anger to test whether asymmetric frontal cortical activity best relates to emotional valence, motivational direction, or a combination of emotional valence and motivational direction. If asymmetric frontal cortical activity reflects motivational direction, then anger should relate to relative left frontal activity, because anger is associated with approach motivation. However, if asymmetric frontal cortical activity reflects affective valence, then anger should relate to relative right frontal activity, because anger is associated with negative valence.

Harmon-Jones and Allen (1998) assessed trait anger and asymmetric frontal activity by measuring baseline, resting EEG activity. Results indicated that trait anger related to increased left frontal activity and decreased right frontal activity. Anger related only to frontal asymmetries and not to other region asymmetries, as has occurred in all subsequent studies on anger. Studies have replicated these initial results (Hewig et al. 2004; Rybak et al. 2006) and found they are not the result of anger being evaluated positively (Harmon-Jones 2004).

12.6.2 Manipulations of Asymmetric Frontal Cortical Activity and Emotion

To provide more causal evidence for the role of asymmetric frontal cortical activity in emotive processes, researchers have manipulated asymmetric frontal cortical activity and observed the effects of the manipulation on emotive responses. Some experiments have used neurofeedback training (e.g., Allen et al. 2001). With this method, participants are given "reward" feedback when brain wave activity over a particular cortical region changes in a desired direction; participants are given negative or no feedback when brain wave activity does not change in a desired direction. Rewards may be the simple presentation of a tone. In one experiment, neurofeedback training was used to increase or decrease relative left frontal activity over several days (Harmon-Jones et al. 2008). Then, on the last day following training, participants' attitude change toward decision alternatives was measured following a difficult decision. Consistent with predictions derived from the action-based model of dissonance (Harmon-Jones 1999), results indicated that individuals who experienced a manipulated decrease in relative left frontal cortical activity showed less attitude change in favor of the decision than individuals who experienced a manipulated increased in relative left frontal cortical activity.

Other research has had participants contract their left or right hand to manipulate asymmetric frontal cortical activity (Harmon-Jones 2006). These unilateral body contractions (e.g., right-hand) likely influence activity in the contralateral hemisphere (e.g., left hemisphere), particularly in the motor cortex, and these motor cortex activations may spread to the frontal cortex. One experiment manipulated hand contractions and then exposed participants to a mildly positive, approach-oriented radio editorial (Harmon-Jones 2006). Results indicated that unilateral contractions of the hand increased contralateral hemisphere activity, as measured by EEG alpha suppression, over the central and frontal regions. The hand contraction manipulation also influenced self-reported positive activation. Specifically, the right-hand contractions caused greater positive activation than left-hand contractions.

In another experiment, hand contractions were to manipulate asymmetric frontal cortical activity, and then participants received insulting feedback ostensibly from another participant. Next, they played a competitive reaction time game against the other ostensible participant, so that the motivation to harm the other participant with noise blasts (i.e., aggression) could be measured. Results revealed that right-hand contractions caused more aggression than left-hand contractions (Peterson et al. 2008). Also, within the right-hand contraction condition, greater relative left frontal activation correlated with more aggression.

Repetitive transcranial magnetic stimulation (rTMS) has also been used to manipulate asymmetrical frontal cortical activity. One experiment by d'Alfonso et al. (2000) used slow rTMS to inhibit the left or right prefrontal cortex. Results indicated that rTMS to the right frontal cortex caused selective attention toward angry faces, whereas rTMS to the left frontal cortex caused selective attention away from angry faces. van Honk and Schutter (2006) conceptually replicated these results, and suggested that they indicated that the inhibition of the right frontal cortex led to an increase in left frontal activity that caused participants to attentionally approach angry faces, similar to how one might behave in an aggressive encounter.

Other research has used transcranial direct current stimulation (tDCS) to manipulate asymmetric frontal cortical activity. With tDCS, one electrode, the anodal, increases cortical excitability, whereas the other electrode, the cathodal, decreases cortical excitability (Nitsche and Paulus 2000). Because of this feature of tDCS, it is ideal for investigating the influence of asymmetric frontal cortical activity on psychological and behavioral processes. In one tDCS experiment, individuals were given tDCS to increase relative left or increase relative right frontal cortical activity (a sham control condition was also run). Then, after tDCS, the individuals were given insulting feedback and then given an opportunity to aggress against the person who had insulted them. Results indicated that the manipulated increase in relative left frontal cortical activity increased aggressive behavior in the individuals who were most angry (Hortensius et al. 2012).

12.6.3 State Manipulations of Affect and Asymmetric Frontal Cortical Responses

Research has found that asymmetric frontal brain activity is influenced by state emotive manipulations. Newborn infants have increased left frontal activation when tasting sucrose (Fox and Davidson 1986), and 10-month-olds have increased left frontal activation while viewing happy facial expressions as compared to sad facial expressions (Davidson and Fox 1982).

Other experiments have investigated emotional processes and asymmetric frontal activity using ERPs. Reward cues cause greater left frontal cortical activity (Ohgami et al. 2006), as do photographs of desirable desserts (Gable and Harmon-Jones 2010).

Do positive affects regardless of their approach motivational intensity cause increases in relative left frontal activation or do only approach-motivated positive affects cause these increases? One experiment addressed this question by having individuals write about a neutral day (*neutral mindset*), a goal they intended to achieve in the next 3 months (*high-approach-positive mindset*), or something exceptionally positive that happened to them (*low-approach-positive mindset*; Harmon-Jones et al. 2008). After writing about one of these events, participants recalled and reexperienced the event while EEG was recorded. The two positive mindset conditions caused participants to report feeling more positive affect. More importantly, the high-approach-positive mindset caused greater relative left frontal cortical activity than the other conditions. These results suggest that it is the approach motivational character of some positive affects, and not positive valence per se, that causes greater relative left frontal cortical activity. These results have been conceptually replicated. When adults form facial expressions of determination, they show increased left frontal activity (Price et al. 2013). However, when they form facial expressions of satisfaction, they do not.

State Anger In the first experiment to manipulate anger and measure asymmetric frontal activity, individuals who were insulted responded with greater relative left frontal activity than individuals who were not insulted (Harmon-Jones and Sigelman 2001). Moreover, within the insult condition, self-reported anger and behavioral aggression were positively correlated with relative left frontal activity. Subsequent experiments have conceptually replicated these results by finding that social rejection increases relative left frontal activity that is associated with anger (Peterson et al. 2011) and jealousy (Harmon-Jones et al. 2009). Also, impersonal stressors (high-pressure air blasts assigned by a computer) cause increased relative left frontal activity, which is associated with aggression in an “employee-supervisor” laboratory task (Verona et al. 2009). Other experiments have revealed that this anger-related increase in relative left frontal cortical activity is reduced when individuals are first induced to feel sympathy for the person who insults them (Harmon-Jones et al. 2004).

12.6.4 Independent Manipulation of Approach Motivation Within Anger

In previous experiments, the anger evoked was one that was oriented toward approach. That is, participants knew of ways in which they could act on their anger. However, all instances of anger may not evoke approach motivation, and the intensity of approach motivation evoked may depend on the perceived difficulty of acting on the anger (Brehm 1999; Brehm and Self 1989). That is, when individuals expect to be able to act with moderate effort to resolve an angering situation, they should have greater approach motivation than when they expect to be unable to act.

Two experiments have supported this prediction. In each, participants who were angered and expected to be able to engage in the approach-related action had greater left frontal activity than participants who were angered and expected to be unable to engage in approach-related action (e.g., Harmon-Jones et al. 2006; Harmon-Jones et al. 2003). These results suggest that relative left frontal activity likely taps approach motivational intensity and not anger per se.

These results do not, however, indicate that greater relative left frontal activity will only occur when there is an explicit approach motivational opportunity. That is, explicit approach motivational opportunities may not be necessary, but may only intensify left frontal activity. For example, individuals who scored high in trait anger evidenced increased left frontal activity in response to subtle anger inductions even when there were no explicit opportunities for action (Harmon-Jones 2007).

Another experiment has provided support for the idea that it is the approach motivation often associated with anger and not anger per se that causes increased relative left frontal activity (Harmon-Jones and Peterson 2009). Based on the observation that we often lie back after consumption of desired objects, it was predicted that being in a supine body posture would reduce approach motivation. In the experiment, participants received neutral or insulting feedback while sitting upright or in a supine position. When participants received the feedback while sitting upright, those who were insulted responded with greater relative left frontal activation than those who received the neutral feedback, and more importantly, those who received insulting feedback while in a supine position. These latter two conditions did not differ statistically.

12.6.5 Anger and Withdrawal Motivation

The research reviewed thus far has indicated that greater relative left frontal activation is associated with anger because anger is often associated with approach motivation. The experiments in which anger was manipulated independently of approach motivation provide the strongest evidence for this conclusion. Indeed, in these experiments, self-reported anger was equal between the "high approach" and "low approach" motivation conditions, suggesting that the experience of anger is not necessarily always associated with an urge to approach.

These results lead to the idea that anger may be associated with right frontal activation if the experienced anger is associated with withdrawal motivational tendencies. In particular, anger may be associated with withdrawal motivation when the situation also evokes concerns about punishment. For example, if expressing anger is perceived to be socially inappropriate, individuals may withdraw from the situation rather than express approach-oriented anger.

One correlational study tested these ideas by placing individuals in a social context where they were expected to behave without racial prejudice (Zinner et al. 2008). Based on observations that some individuals become angry when socially pressed to behave in a nonracist way coupled with the fact that it would have been inappropriate to express anger, it was expected that individuals who became angry in such a social situation would respond with an anger that was associated with withdrawal motivation (i.e., "I am angry about this situation but want to leave it."). In this study, self-reported anger related to greater relative right frontal cortical activity. In line with the idea that the anger was associated with concerns about punishment, anger was also associated with anxiety. Taken together, these results suggest that anger was associated with relative right frontal activation because of withdrawal motivation.

Another experiment provides support for the idea that anger associated with right frontal activation causes behavioral inhibition or withdrawal motivation. In this experiment, individuals received tDCS to increase relative right or increase relative left frontal cortical activity (or sham stimulation). Then, they received insulting feedback from another individual but could not act upon their anger. Under these circumstances, the manipulated increase in relative right frontal cortical activity caused more rumination (Kelley et al. 2013). These results are conceptually consistent with the previous study by Zinner et al. (2008) in suggesting that when angry expressions are inhibited, relatively greater right frontal activation may be associated with more angry feelings.

Conclusion

In this chapter, we provided a selective review of several key neural substrates involved in approach and avoidance motivation, chosen because they have received the most attention, to date, in human motivation research. A basic understanding of these brain regions is important to the study of self-regulation because regulation efforts are often either in opposition to, or in support of, the motivational tendencies associated with activation in these regions.

Neural networks involve regions that appear to serve specific functions. One of the key functions of the amygdala is the determination of motivational relevance. The nucleus accumbens appears to be involved in both approach and avoidance motivation, with the anterior regions more involved in approach processes and the posterior regions more involved in avoidance processes. The orbitofrontal cortex also appears to be involved in both approach and avoidance motivation, with the medial areas more involved in approach processes and the lateral areas more involved in avoidance processes. The anterior cingulate cortex is involved in detecting response conflicts and thus assists in resolving conflicts between motivational orientations.

Much research has revealed that the dorsolateral prefrontal cortex is involved in motivational direction, with the left dorsolateral region being more involved in approach processes and the right dorsolateral prefrontal region being more involved in withdrawal processes. This large body of evidence on motivational functions could be viewed as standing in contrast to other research that has emphasized the role of the prefrontal cortex in cognitive control, which is often defined as “the ability to orchestrate thought and action in accordance with internal goals” (Miller and Cohen 2001, p. 167). Scientists who study cognitive control often go further to propose that the prefrontal cortex “is not critical for performing simple, automatic behaviors” that are “determined largely by the nature of the sensory stimuli” (Miller and Cohen, p. 168). Viewing the prefrontal cortex as only involved in “cognitive control” seems to be inconsistent with evidence of newborn infants showing increased left frontal cortical activation when tasting sucrose (Fox and Davidson 1986). It also seems inconsistent with the evidence linking approach-motivated anger and behavioral aggression to increased left frontal cortical activation (e.g., Harmon-Jones and Sigelman 2001). The simplest resolution to this inconsistency is the realization that the prefrontal cortex occupies roughly one-third of the adult brain and it is therefore likely involved in a vast array of psychological processes, some of which may appear to be in conflict with one another.

In addition, conscious processes may serve to coordinate plans and actions *in the service of* approach or avoidance motivations, rather than in opposition to them. That is, self-regulation efforts in response to an anger provocation might be related to planning for revenge and mobilizing aggressive responses, rather than downregulating anger responses. In order to fully understand self-regulation, theorists must consider various sources of approach and avoidance motivation, the circumstances in which these motivations conflict with versus enhance one another, and to what degree conscious decision making is involved in regulatory processes.

Before ending, it is important to note that each neural region is densely connected with other regions and infused with multiple neurochemicals. These neural connections and chemicals will ultimately be important in revealing how the brain does motivation. Further advances in understanding these complex processes await the development of better techniques to assess the rapid communications among neurons and chemicals, particularly in research on humans.

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13 Motus Moderari: A Neuroscience-Informed Model for Self-Regulation of Emotion and Motivation

Jordan L. Livingston, Lauren E. Kahn and Elliot T. Berkman

13.1 Introduction

The Latin word *motus* refers to movement. It is the root of common English words including motion, momentum, and commotion. It is also the root of the words emotion and motivation, and provides a compelling explanation of the link between the two: both are for action. Emotion and motivation, to borrow a phrase from William James, are for the sake of doing (James 1890). Contemporary thinkers largely agree with this view, and have placed emotion and motivation immediately before action in some of the most powerful theories of behavior including reinforcement sensitivity theory (Gray 1970) and feedback control theory (Carver and Scheier 1980), not to mention a range of functionalist accounts of emotion and motivation (Cosmides and Tooby 2000; Fredrickson 1998; Frijda 1986; Izard and Ackerman 2000). Each of these theories is backed by robust evidence of a role for emotion and motivation in regulating, moderating, guiding, or anticipating action if not directly causing it (Baumeister et al. 2007). Research aside, the subjective experience of each demonstrates a strong link to the other. What is fear without the accompanying urge to run or hide? And what is the longing to be with a loved one without the feelings of affection and desire?

Despite the clear connections between emotion and motivation in both science and everyday experience, the research on the self-regulation of each of these topics is an island unto itself. Early studies of emotion regulation (e.g., Gross 1998) focused narrowly on the modification of basic emotions such as fear and disgust, and research on the self-regulation of motivation typically examines a specific motive (e.g., food craving; Ward and Mann 2000) to the exclusion of other types of motivation. There is little cross talk between the two lines of research, even when there are clear parallels such as between reward motivation and positive emotion. (The domain of self-regulation of behavior takes an even more extreme position, studying "behavior" in terms of button presses using purely cognitive models of executive control that have no place for emotion or motivation (e.g., Aron 2008; Miyake and Friedman 2012), but that is beyond the scope of our argument here.)

The present disconnect between these bodies of research on self-regulation in different domains is not intentional but rather reflects a natural trajectory in the development of the field. Early studies were isolated because they were

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pioneering new territory, and many of their design choices (e.g., to use standardized stimuli known to reliably elicit specific emotions) reflected this. Building upon these studies, researchers have begun to assemble an argument that self-regulation of emotion, motivation, and behavior are related even perhaps to the point of being interchangeable (Cohen et al. 2013; Heatherton and Wagner 2011; Volkow et al. 2008). Emotions, motivations, and actions may be qualitatively distinct from one another, but the top-down processes that regulate them are likely shared across domains (Heatherton and Wagner 2011). The central aim of this chapter is to review evidence for and against this position.

13.1.1 A Role for Neuroscience in Developing Self-Regulation Theory

The psychological science community has been engaged in a conversation about the usefulness of neuroscience methods (Diener 2010; Poldrack 2010; Shimamura 2010). The central questions are whether neuroscience data can advance psychology theory, and if so, under what conditions. We and others have argued that indeed it can (Berkman et al. 2014; Cunningham 2010; Mitchell 2009). Specifically, neuroscience methods can distinctly answer four types of questions about mental processes: "brain-mapping" questions about which structures in the brain support a given process, "prediction" questions seeking to foretell specific behaviors based on a pattern of neuroscience data, "divergence" questions about whether two or more processes rely upon different neural systems even though those processes may feel qualitatively alike (e.g., different forms of learning), and "convergence" questions about whether two or more processes rely upon the same neural systems even though the processes seem distinct (Berkman et al. 2014). Our working hypothesis here about various domains of self-regulation sharing a common neural pathway is a "convergence" question in that it asks whether processes that have been traditionally studied separately by different theoretical camps actually draw upon the same neurobiological machinery. However, in the present review we also entertain the idea that unexpected divergences may emerge that could have value for informing theory about self-regulation.

The advantages of uncovering a possible neural convergence and divergences across several aspects of self-regulation are numerous. From a theoretical perspective, it would provide additional information about which types of self-regulation are related to which other forms and how. It would also begin to suggest the possible mental processes that underlie those relationships. For example, suppose that there is a neural distinction not between "emotion regulation" and "motivation regulation" but rather between the regulation of positive/appetitive stimuli and negative/aversive ones. This would suggest that regulation varies as a function of the eliciting stimulus more so than the nature of the mental process being regulated. Identifying convergences allows scholars to import theoretical constructs from one domain into another. For example, the theories on emotion regulation are highly developed relative to those on motivation regulation (Gross and Thompson 2009), but if it turns out that both kinds of self-regulation rely on the same neural systems, then it would be reasonable to apply the more elaborated emotion regulation theory to models of motivation regulation. From a practical perspective, convergences would enable researchers to share experimental paradigms across the (perhaps) artificial boundaries between these fields and leverage existing knowledge into new territory.

13.1.2 Organizing Principles: Domain, Direction, Process, and Agency

As implied above, the field of self-regulation is currently fractionated around distinctions between "emotion," "motivation," and "action." We have referred to these as "domains" of self-regulation and made the case that there might be "cross-domain" similarity in the neural systems of self-regulation (Cohen et al. 2013). Beyond domain, several other distinctions have been investigated to some extent and will be reviewed here: direction, process, and agency.

The first organizing principle—and the one used to structure the main sections in this chapter—is *direction*. For our purposes here, direction encompasses both the automatic action tendency with respect to the stimulus (toward vs. away) and the valence of the stimulus (appetitive vs. aversive). Thus, in the following review, studies of "approach" include those investigating regulation of positive basic emotions (e.g., happiness) and of approach motivational impulses (e.g., cravings for food). Similarly, studies of "avoidance" include those investigating negative basic emotions (e.g., sadness) and of avoidance motivational impulses (e.g., loss aversion). We note that positive/negative valence and approach/avoidance motivation are not interchangeable and indeed that some have studied cases under which people approach negative stimuli and avoid positive stimuli (e.g., Berkman and Lieberman 2010). However, for the purposes of simplicity, we have focused our review on self-regulation of approach to positive stimuli (e.g., delicious foods, happy faces) and of avoidance to negative stimuli (e.g., aversive foods, fear faces). For a review of the neural systems of the approach and avoidance motives per se, as opposed to the systems involved in regulating them, see Chap. 12 in this volume.

A second organizing principle that has been noted informally by researchers but proposed systematically only recently (McRae et al. 2012) is *process,* or the specific cognitive process targeted by a regulation strategy. The idea that different cognitive processes can support the same ultimate goal of self-regulation goes back at least to Gross's (1998) process model, but has been somewhat lost in practice. For example, reframing, distancing, and distraction have each been described as "antecedent-focused" types of cognitive reappraisal, even though the mental calculations involved in each may be entirely different (in a process analysis sense; see Bilder et al. 2009): Reframing involves making new meaning from the same concrete information, distancing involves altering the visual representation of the scene or shifting visual perspectives, and distraction involves shifting attention in a controlled way to different properties of the stimulus or to a different internal or external stimulus altogether. It is particularly important to consider mental process when using functional neuroimaging, as that class of tools is presumably optimized to detect neural activity at the level of the mental process (e.g., attention) rather than at the level of the broader psychological construct which may involve a collection of more basic processes (e.g., reappraisal; see Davis and Poldrack 2013 for a more detailed discussion of this issue). In the present review, we note differences and similarities in the processes likely deployed in various self-regulation strategies where appropriate.

The final distinction we consider throughout the chapter is *agency,* which encompasses two distinct yet closely related ideas. First, as the name implies, agency refers to choice during the regulation process, either of regulation strategy or of the target being regulated. Our general hypothesis here is that regulation strategies that are self-chosen will be more effective than those that are experimenter-assigned because of previous practice, comfort, or mere cognitive dissonance. Second, we also use agency to refer to whether or not the self-regulation effort results in a self-relevant behavior. In other words, is there an implied behavior or decision that will have real consequences for the person engaging in regulation (see also Chap. 14, in this volume for further discussion of self-processes in self-regulation). Considerable evidence suggests that self-processing is distinct from other forms of processing (Heatherton 2011), perhaps because it requires a unique convergence of processes including memory, valuation, emotion, decision making, and action selection (Legrand and Ruby 2009). The experimental paradigms employed in studies of emotion and motivation regulation vary in how self-relevant or self-referential they are. In some cases, participants regulate generic emotional stimuli that are self-relevant only because they tend to evoke certain emotions in most people; in other cases, participants regulate personalized stimuli with actual behavior at stake (e.g., a purchase or consumption of a food). We hypothesize that the degree of agency as such would generate quantitative and possibly qualitative differences in the patterns of neural activity during regulation, and will use this chapter as a vehicle to explore that hypothesis.

13.1.3 The Present Review

In the following two sections, we review neuroimaging studies on the regulation of "approach" and "avoidance" emotions, motivations, and impulses. For each, we describe the methods with particular attention to how the paradigm relates to the distinctions described above of domain, direction, process, and agency. We then describe the results, using neuroanatomical labels as consistently as possible to allow for comparisons across studies. We also note research gaps and open questions where appropriate. Finally, we conclude by synthesizing the general results with respect to each distinction and providing several recommendations for future studies on self-regulation of emotion and motivation.

13.2 Approach

In this section, we focus specifically on the overlap between regulation of approach motives and positive affect. For example, it would be logical if similar brain regions were involved in both craving for a stimulus (a motivational state) and the enjoyment of consuming it (an emotional state). To the end of uncovering possible connections between them, this section reviews and synthesizes the functional neuroimaging literatures on the regulation of these two types of experiences.

A ubiquitous daily experience is to approach stimuli in the environment such as food, money, or other potential rewards. This experience is sometimes goal directed (e.g., striving toward a desired professional outcome) but often more stimulus driven (e.g., impulsively reaching for a high-calorie snack that one otherwise does not want to eat). Thus, regulating the motivation to approach these types of stimuli has been the focus of a large body of research. For a little over a decade, research has investigated the neural systems underlying the regulation of cigarettes, food, monetary reward anticipation, risky behavior, and sexual arousal.

In addition, some high-arousal emotions such as excitement or anger elicit approach motivation, and these emotions may likewise be the target of regulation. Although positive emotions (like happiness or excitement) are usually not the target of regulation, there are some situations where positive emotion can be inappropriate, either due to social contexts (e.g., laughing at an inappropriate time) or in the case of bipolar disorder, where excessive positive emotion can be maladaptive (Gruber et al. 2008). (However, emotion regulation in clinical populations is outside the scope of the present review.) Though some recent work has begun to examine the behavioral mechanism supporting regulation of positive emotion in these contexts (Giuliani et al. 2008), very few studies have investigated the neural mechanisms supporting regulation of positive emotion (Kim and Hamann 2007). In contrast, the utility of regulating negative approach emotions is perhaps more obvious. Expressing anger in an inappropriate context (e.g., at your coworker in a meeting) may lead to negative consequences. Only a few studies have begun to investigate the neural underpinnings of anger regulation (e.g., Pietrini et al. 2000), making this a fruitful area for future research. Understanding the mechanisms underlying regulation of approach emotions, when combined with knowledge about the regulation of avoidance emotions, may help us understand whether the same neural systems underlie both types of regulation.

In this section, we review existing studies that investigate how the brain supports regulation of motivation toward appetitive stimuli and positive emotion. We review the brain regions that are commonly involved in approach regulation which significantly increase or decrease during the attempt to regulate. We also discuss whether the cognitive regulation strategy deployed and the nature of the stimulus being regulated (e.g., food vs. cigarettes) influence the specific neural systems recruited during approach/positive affect regulation.

13.2.1 Brain Regions That Increase During the Regulation of Approach Motivation and Positive Affect

A variety of regions have been found to be more active during attempts to regulate versus naturally viewing appetitive stimuli such as cigarettes, food, and monetary rewards. Though active regions vary between different paradigms, perhaps due to a difference in strategies deployed to effectively regulate (see below), there are some regions that commonly appear during this kind of regulation. Several studies have found activity in the dorsal anterior cingulate (Brody et al. 2007; Martin and Delgado 2011), which has often been associated with conflict monitoring and cognitive control more generally (Botvinick et al. 2004). Another region frequently observed during regulation is the ventrolateral prefrontal cortex (vlPFC; Kober et al. 2010; Hutcherson et al. 2012; Delgado et al. 2008a; Hollmann et al. 2012), which has often been implicated in response inhibition (for a review, see Aron et al. 2004). A range of other regions have been observed as well, though less consistently than the dorsal anterior cingulate cortex (dACC) and vlPFC, including dorsomedial PFC (dmPFC; Hollmann et al. 2012; Kober et al. 2010), inferior parietal lobe (Delgado et al. 2008a), posterior parietal cortex (Hollmann et al. 2012; Hutcherson et al. 2012; Staudinger et al. 2011), posterior cingulate cortex (Brody et al. 2007), dorsal striatum (Hollmann et al. 2012), lateral orbitofrontal cortex (lateral OFC; Hollmann et al. 2012; Siep et al. 2012), and anterior PFC (Siep et al. 2012). Many of these regions are recruited across a variety of types of approach regulation, suggesting that approach regulation may employ a system that is at least partially domain-general. However, a formal test of this hypothesis—eliciting multiple forms of approach regulation and assessing the similarity among the neural correlates—has yet to be conducted. The only study that directly examined regulation of positive affect (Kim and Hamann 2007) supports a domain-general account of emotion/motivation regulation in finding similar regions (e.g., dmPFC, vlPFC, and lateral OFC) to those reviewed above. See Table 13.1 for a summary of these regions.

One puzzling result is that activity in some regions has been found to increase with regulation in some studies but to decrease in others. For example, activity in the dorsolateral PFC (dlPFC; including parts of the middle frontal gyrus) increased in some studies (Kober et al. 2010; Delgado et al. 2008a; Staudinger et al. 2011; Hollmann et al. 2012; Siep et al. 2012; Beauregard et al. 2001; for regulation of positive affect, see Kim and Hamann 2007) but decreased in others (Hutcherson et al. 2012). Similarly, one study found increases in subgenual ACC (sgACC) activation during regulation (Delgado et al. 2008a), but another found decreases (Westbrook et al. 2013). Next, we discuss several possible explanations for these discrepancies through the theoretical lens of heterogeneity among the cognitive strategies deployed for regulation and in the targeted stimuli.

13.2.2 Are the Neural Systems of Regulation Consistent Across Cognitive Strategies?

Although the tasks in the studies described in this section can all be classified as “regulation,” the cognitive strategy deployed by participants varies greatly. In some studies, participants are given very narrow instructions (e.g., “imagine a calming ocean”) and other times, they are told to regulate their motivation toward the stimuli without being given specific tactics to accomplish this. Examples of nonspecific instructions include the instruction to resist feelings of cravings (Brody et al. 2007), to distance or disengage from their emotions (Staudinger et al. 2011), to inhibit emotional reactions (Beauregard et al. 2001), or to use whatever strategy allows them to regulate their motivation (Hutcherson et al. 2012; Kim and Hamann 2007).

The specific instructions used in different studies vary, but several general categories of strategies emerge among the studies that provide them. First, in some paradigms, participants are asked to focus on the consequences of engaging

Table 13.1 Involvement of brain regions in self-regulation of approach and avoidance motives and emotions

	Lateral cortex				Medial cortex				Subcortex
	Prefrontal cortex			Parietal	Prefrontal cortex		Cingulate		Striatum
Target	Dorsal	Ventral	Anterior	IPL	Dorsal	Ventral	Dorsal anterior	Posterior	Dorsal
Approach	–	xx	x	x	x	–	xx	x	x
Avoidance	xx	xx	x	x	xx	x	x	–	–

xx = frequent involvement; x = some involvement; – = no involvement
IPL inferior parietal lobule

in regulation (Kober et al. 2010; Hollmann et al. 2012; Siep et al. 2012). However, even among paradigms where participants are asked to focus on consequences, there are many variants that may or may not be qualitatively different. For example, several paradigms use negative long-term consequences of eating food as a strategy to downregulate cravings (Siep et al. 2012; Hollmann et al. 2012). One study compares thinking about (presumably negative) long-term versus (presumably positive) short-term consequences of smoking (Kober et al. 2010). An open question about consequence-focused regulation is whether regulation that is motivated by the drawbacks of failure relies on different neural regions than regulation motivated by the gains of success. Though both strategies are cognitive and future-oriented, they are different in terms of their direction (i.e., approach-avoidance focus).

Another set of strategies uses mental imagery to regulate approach motivation. In a study by Delgado et al. (2008a), participants were asked to think of a calming scene as a method of downregulating their desire for the upcoming monetary reward, rather than thinking of the potential reward itself. A similar strategy was used in a decision-making task in which participants were instructed to imagine either a calming scene or an exciting scene before making a choice between a risky and safe financial option (Martin and Delgado 2011). One interesting aspect of these two studies is that, besides just causing participants to employ mental imagery, these strategies may also manipulate physiological arousal. Imagining a calming scene may literally change physiological arousal, and accordingly, skin conductance responses reflected this manipulation (Delgado et al. 2008a). Given its central role in affect and motivation, regulation strategies that alter peripheral physiology may be qualitatively different from those that do not.

It is difficult to draw firm conclusions about how brain activity varies from strategy to strategy because of the relatively small number of studies on the neural correlates of regulating approach motivation. However, we note there are similarities between these strategies that may ultimately lead to similar results. At a high level, most of these strategies involve some sort of attention manipulation, by way of intentionally directing attention either to calming mental imagery or to long-term consequences. This may explain why most of these studies report increased activation in attention and executive control networks during regulation. However, it remains unclear if those regions are involved in regulation per se, or if some kinds of regulation require attentional focus, which in turn recruits those regions. One unique study used mindfulness practice—attention to thoughts, feelings, and sensations in a nonjudgmental fashion—as a manipulation of cigarette craving regulation (Westbrook et al. 2013). Revealingly, this is one of the few studies in this body of literature that did not report increased prefrontal cortical activation during the regulation of approach motivation. In our view, a plausible explanation for this discrepancy is that this type of regulation reduces reactivity to the cigarette cues in a bottom-up fashion by reducing cue reactivity, thus not requiring top-down control from PFC. This supports the theoretical prediction that attention modulation is but one of many forms of emotion regulation (Gross and Thompson 2009).

An important future target for research is the differences between various strategies. Not only may some strategies recruit different brain networks but also some strategies may simply be more effective than others. One study investigated this hypothesis by directly comparing suppression and reappraisal (Siep et al. 2012). Interestingly, suppression was more effective at regulating reactivity in classical reward regions, despite the fact that suppression is generally found to be less effective than reappraisal (Gross 2002). This result highlights the need to link laboratory findings to real-life outcomes by increasing the ecological validity of neuroimaging studies.

13.2.3 Brain Regions that Decrease in Activation with Regulation of Approach Motivation and Positive Affect

Along with identifying the brain regions that are engaged during regulation, it is also interesting to consider the brain regions whose activation decreases during regulation, presumably as the level of appetitive motivation or positive affect they support decrease. These regions are revealed using the opposite contrast from the one described above, namely the contrast of natural viewing > regulation. This contrast provides a tight control for regulation, since natural viewing involves the same visual processing and motor responses as regulation. Importantly, if the regions in the viewing > regulation contrast also come online during viewing of appetitive stimuli compared to rest, it suggests that these regulated regions were initially involved in reactivity, and that regulation results in a decrease of activation in those regions that would otherwise be active.

Most studies of approach regulation report which brain regions show less activity during regulation versus passive viewing, and they find a variety of regions including those involved in sensory processing, reward, and value computation. In a study of cigarette craving regulation, Brody et al. (2007) found that activation in somatosensory and occipital regions decreases as a function of regulation, suggesting that the sensory and visual salience of the rewards decreases with regulation. By contrast, other studies find that activation in reward-related regions such as ventral striatum (Kober et al. 2010; Martin and Delgado 2011; Delgado et al. 2008a; Siep et al. 2012), the closely connected ventral tegmental area (Kober et al. 2010; Siep et al. 2012), and the amygdala (Kober et al. 2010) decrease during regulation. Two studies have also found decreased activity in sgACC as a result of regulation (Kober et al. 2010; Westbrook et al. 2013). Interestingly, during regulation using mindful attention, sgACC activity decreased its coupling with activity in several regions including caudate, insula, dlPFC, IPL, and precuneus (Westbrook et al. 2013). These studies suggest that regulatory processes in the brain indeed act to decrease activity supporting affective reactivity.

A second and more precise way of investigating decreases in activation during regulation is by using a method called "parametric modulation," in which regions whose activity scales with a particular metric (in this case, stimulus value) can be detected. In other words, the activity in these regions should correspond to the subjective value the participant places on that stimulus. Regions responding parametrically to stimulus value include ventromedial PFC (vmPFC) and dlPFC (Hutcherson et al. 2012; Westbrook et al. 2013; Siep et al. 2012). Interestingly, within the same study those regions also show regulation-related decreases (Hutcherson et al. 2012; Westbrook et al. 2013; Siep et al. 2012). Furthermore, these two prefrontal regions demonstrated functional connectivity with other regulatory regions, further supporting the claim that these decreases are systematically linked with regulation and not just coincidental (Hutcherson et al. 2012). Future research will be strengthened by more network-based analyses in order to make stronger claims about how different regions may be associated with one another during regulation.

In summary, regions that show less activity during regulation than during passive viewing have been linked to a variety of psychological functions, including sensory perception, reward (Knutson et al. 2001), motivational salience (McClure et al. 2003), and value computation (Chib et al. 2009). However, the common link between all these processes is that they provide salience or vividness to the appetitive stimulus being regulated. By this logic, a compelling interpretation of these results is that regulation causes change in affect and motivation through a salience or value modulation mechanism, which in turn drives behavior. In other words, regulation alters the salience or value of a stimulus, and the decision that follows results from the ultimate level of salience, which is a product of a competitive interaction between some initial evaluation of the salience and a regulatory process.

An open question is whether the target of regulation (e.g., cigarettes, food, money) changes which "reactive" regions must be decreased in order for regulation to occur (Heatherton and Wagner 2011). It is possible that the particular regions observed to decrease in any given paradigm may be a function of the particular target of regulation. In the studies reviewed above, however, no clear pattern emerges. For example, ventral striatum, which is commonly associated with reward processing, decreases during regulation of motivation toward cigarettes (Kober et al. 2010), food (Siep et al. 2012), and potential financial rewards (Martin and Delgado 2011; Delgado et al. 2008a). However, other regions (e.g., visual cortex) decrease in some paradigms (Brody et al. 2007) but not others, perhaps due to the nature of the particular stimuli. An alternative technique to interrogate the data such as multivoxel pattern analysis, which reveals what kind of information a brain region is representing at the pattern level rather than detecting general heightened activation across a broad region, may lead to a better understand of how the brain regulates motivation toward different types of appetitive stimuli.

13.2.4 Downregulation Versus Upregulation

In all of the studies discussed in this section, the term "regulation" has referred to the process of reducing approach motivation. However, one might ostensibly want to increase approach motivation as well. These two types of regulation have been referred to as down- and upregulation, respectively. There are far fewer studies investigating the neural mechanisms of upregulation, perhaps because practically, we are generally interested in how to counteract reactive processes, not how to heighten them. However, understanding the mechanisms of upregulation is important because there are many situations in which upregulating emotions is encouraged (e.g., artful expression) and because knowledge about the differences between up- and downregulation at a neural level may reconcile previous questions regarding the involvement of certain brain regions in regulation in general. For example, vmPFC has been commonly found as a region with parametric representations of value (Chib et al. 2009; Hutcherson et al. 2012). Hutcherson et al. (2012) observed increased value signals in vmPFC during upregulation, and these signals had more influence over behavior during upregulation as well. However, during downregulation, this pattern was observed in dlPFC instead: decreased value signal due in dlPFC to regulation, and increased influence of the dlPFC value signal on behavior. These results suggest that multiple value signals (vmPFC, dlPFC) compete for control, and that part of effective regulation (up or down) is linking behavior with appropriate value signal. Without examining upregulation separately from downregulation, an important neural dissociation between those two processes would have gone unnoticed.

13.2.5 Future Directions for Regulation of Approach Motivation and Positive Affect

Above we have described how the brain supports regulation of approach motivation toward appetitive stimuli like cigarettes, food, money, sexual arousal, and risky behavior. One relevant and interesting extension to this work is into the area of social reward regulation. For example, social psychologists have regarded the motives to belong and to be accepted as fundamental to healthy functioning (Baumeister and Leary 1995). To what extent do people regulate these motives, and how? Another relatively unexplored area is the regulation of approach emotions like excitement and anger. Some work on these topics has come from the clinical literature in terms of anger regulation among individuals with aggression disorders (Coccaro et al. 2011). Some neuropsychological evidence suggests that medial OFC (mOFC) lesions cause aggressive behavior, perhaps due to a lack of regulation (Grafman et al. 1996). Furthermore, simply imagining restraining aggressive behavior seems to engage mOFC (Pietrini et al. 2000). Unfortunately, almost no research has further investigated this possibility. Fully understanding regulation of negative approach emotions like anger would not only help us understand those with problems regulating such emotions, but also might enlighten us of the differences between regulating negative and positive approach emotions.

The growing body of work investigating regulatory processes on approach emotion and motivation has thus far yielded only a preliminary view of how the brain supports the regulatory processes described above. As the field moves forward, we hope that this view is refined with a careful consideration and comparison of what is being regulated, and with what strategies the regulation is being implemented. As such, we now turn our attention to review what is known about how people regulate avoidance motivation and negative emotion, which are different constructs from approach motivation and positive emotion, but nonetheless may be regulated with similar neural machinery.

13.3 Avoidance

As noted previously, the literatures on the regulation of approach- and avoidance-type reactions evolved in parallel and without much interchange. We juxtapose our reviews of them here, acknowledging that there may be a vast gulf between the two, with the hope that merely connecting them theoretically through their neural systems and some shared constructs (e.g., process, agency) might encourage others to do the same.

Our working definition of regulation of avoidance emotions and motivations encompasses the processes of overcoming or controlling the reaction to a negative or aversive stimulus that can be either emotional or motivational in nature. For example, one may desire to overcome one's fear of the barking dog next door (regulation of negative emotion) or to overcome one's dislike of broccoli (regulation of avoidance motivation). To date, the large majority of studies investigating the neural systems responsible for regulating avoidance reactions have focused on the regulation of negative emotions rather than motivations. For this reason, this section emphasizes the regulation of emotions over the regulation of motivation, but does note important and recent developments in the regulation of avoidance motivation.

13.3.1 Regulation of Negative Emotion

Emotion regulation has traditionally been defined as "the processes by which individuals influence which emotion they have, when they have them, and how they experience and express these emotions" (Gross 1998), and a number of comprehensive reviews detailing the neural systems responsible for regulating negative affect, in particular, have emerged in recent years (e.g., Buhle et al. 2013). Interestingly, these reviews have generally focused on comparing and contrasting the various cognitive strategies used when regulating negative affect (e.g., reappraisal). Thus, we begin with a review of these various strategies with a particular eye toward the cognitive processes engaged by each, but we conclude by considering other potentially important constructs that have emerged from the literature on avoidance regulation and its neural substrates, with a particular eye toward the role of agency.

By far, the most studied regulation strategy to date has been cognitive reappraisal, in which participants "reinterpret […] the meaning of a stimulus, including one's personal connection to it, to change one's emotion response" (Ochsner et al. 2012). One reason for the popularity of this strategy is that it generalizes to other types of regulation (Ochsner et al. 2012). Undoubtedly, such an emphasis on reappraisal has been fruitful: One recent meta-analysis of cognitive reappraisal, alone, included 48 separate neuroimaging studies (Buhle et al. 2013).

From such a large wealth of data, a number of consistencies in terms of the neural regions recruited by this strategy have emerged (Table 13.1). At the broadest level, most studies have found that cognitive reappraisal utilizes regions typically implicated in cognitive control (e.g., lateral PFC) in order to downregulate emotional responding in the amygdala (Ochsner and Gross 2008). More specifically, dlPFC (typically involved in selective attention and working memory), vlPFC (typically involved in goal selection and inhibition), and dmPFC (typically involved in attributing mental states and self-reflection) seem to be consistently recruited during studies of cognitive reappraisal (Ochsner et al. 2012; Buhle et al. in-press). Additionally, reductions in amygdala activation are nearly always found, suggesting a strong relationship between PFC and amygdala. In studies where connectivity between PFC and amygdala is measured (e.g., Banks et al. 2007), PFC activation is inversely related to amygdala activation.

However, the magnitude and location of PFC activations and amygdala deactivations vary to some extent across different forms of reappraisal. For example, whereas reinterpretation of a stimulus recruits a more dorsal, left-lateralized region of the PFC, mentally distancing oneself from a scene recruits a more medial, right-lateralized region of the PFC (Ochsner and Gross 2008). Such distinctions likely result from the different cognitive processes involved in each strategy (e.g., left-lateralization required for using language during reinterpretation; right-lateralization required for using imagery-based attentional control), and perhaps due to overarching differences in attentional focus as noted in the review of approach/positive emotion above.

Similarities and differences between cognitive reappraisal per se and other strategies such as distraction and suppression have also emerged. Distraction involves “the use of selective attention to limit the extent to which the emotionally evocative aspects of an event are attended and appraised“ (McRae et al. 2010), and two studies have now directly compared the brain systems involved in distraction with those involved in cognitive reappraisal. Both studies found that distraction and reappraisal led to deactivation in the amygdala as well as recruitment of inferior parietal cortex, medial PFC, and lateral PFC for regulation, but that distraction led to greater increases in parietal regions and greater decreases in the amygdala than did cognitive reappraisal (McRae et al. 2010; Kanske et al. 2011). One interpretation of these divergences is that the distraction requires more allocation of attention away from negative emotions, and therefore less emotional processing than reappraisal.

Reappraisal can also be compared and contrasted with suppression, a strategy “directed towards inhibiting behaviors associated with emotion responding” (Goldin et al. 2008). Previous behavioral studies have shown that suppression effectively reduces emotionally expressive behavior but have also noted that suppression does not result in meaningful change in subjective reports of emotion (Goldin et al. 2008). Recent studies have suggested that suppression engages prefrontal activation, particularly in lateral PFC (Vrticka 2013; Shimamura 2013). In a study directly comparing suppression with cognitive reappraisal, researchers found that although both reappraisal and suppression activated similar regions in the PFC (e.g., lateral PFC), the activation of these regions was early during reappraisal but late during suppression (Goldin et al. 2008). Additionally, whereas reappraisal was associated with decreased amygdala responses, suppression was associated with increased amygdala responses, highlighting that the two strategies draw upon similar regions but in different ways.

A recent review of the emotion regulation literature expanded upon these direct comparisons to note that the right ventrolateral PFC is recruited for distraction, suppression, and reappraisal, but that the time courses for the strategies differ such that distraction and reappraisal recruit relatively early activation, whereas suppression recruits relatively late activation (Cohen et al. 2013). Thus, a comparison of all three strategies reveals that there may be some commonalities across various forms of negative emotion regulation, at least in their location if not their timing. However, a broad conclusion is not yet comprehensive because other emotion regulation strategies that are also effective at reducing negative emotion need to be included.

Specifically, mindfulness meditation has been an emotion regulation strategy on the rise that has yet to be integrated into the frameworks described above. Mindfulness meditation can be described as "paying attention in a particular way: on purpose, in the present moment, and non-judgmentally" (Kabat-Zinn 1994). Because affective neuroscience is only beginning to study mindfulness, direct comparisons of mindfulness with other, more commonly studied forms of emotion regulation are limited. Although no quantitative meta-analyses have yet been able to synthesize the growing number of studies comparing the neural correlates of mindfulness and other forms of emotion regulation, the field is moving in that direction, allowing for a more thorough understanding of the similarities and differences between these two types of strategies.

Recent studies have revealed a number of convergences in the neural systems involved in mindfulness and other, more cognitively based forms of emotion regulation. One recent study (Lutz et al. 2014) found increased prefrontal activation in both dlPFC and dmPFC during anticipation of negative images during a mindfulness task, mirroring the activity found during studies of cognitive reappraisal. Furthermore, participants who used a mindfulness strategy for regulation demonstrated reduced amygdala activation during perception of the negative emotional images (Lutz et al. in-press). This finding is consistent with our earlier discussion of mindfulness for craving regulation, where (approach motivation) regulation effects seemed largely to be due to reduced reactivity. Other similarities between mindfulness and traditional emotion regulation have also emerged within the context of pain regulation, particularly within the ACC (Zeidan et al. 2012). See Chap. 10 for more discussion of the self-regulatory effects of mindfulness and their neural underpinnings.

Even after considering the various forms of cognitive reappraisal, distraction, suppression, and mindfulness meditation, a complete comparison among emotion regulation strategies is nowhere near complete. For example, Gross and Thompson's (2009) description of emotion regulation includes a variety of strategies such as situation selection and directed attention that have received little to no empirical attention. In the meantime, it is important to consider that emotion regulation also varies across a variety of other characteristics such as direction (e.g., up- vs. downregulation) and agency (e.g., self-relevant vs. generic) that are likely relevant to any attempt to understand and organize the neural signatures of emotion regulation (Ochsner et al. 2012; McRae et al. 2012). A careful theoretical taxonomy of such factors might prove informative in our understanding of the neural processes involved in emotion regulation.

The discussion about the role of the vmPFC in emotion regulation illustrates the need for such additional considerations. Recently, it has been proposed that vmPFC may act as a mediator between prefrontal and subcortical regions (Ochsner et al. 2012; Etkin et al. 2011). In fact, in a meta-analysis of studies investigating placebo effects, fear extinction, and emotion regulation, Diekhof et al. (2011) suggest that the *only* common region involved in modulating negative affect is vmPFC. In turn, Buhle et al. (2013) performed a meta-analysis of emotion regulation studies investigating whether vmPFC mediates the relationship between cognitive control regions and the amygdala. Results yielded no support for this claim, leading the authors to suggest that perhaps the vmPFC, commonly found in a number of studies on "fear extinction, reversal learning, and regulation of social behavior," is also involved in cognitive reappraisal of emotion but does not emerge in such studies because the vmPFC is recruited during both emotion regulation tasks and the comparison conditions. Here, we consider a variety of mental processes with established neural correlates, such as vmPFC, that are likely involved in emotion regulation to illustrate how such a process analysis of emotion regulation can inform this specific debate and emotion regulation theory more broadly.

Based on our reading of recent work in the field, we argue that the degree to which a target or a strategy is valued by or relevant to the self is a critical factor in emotion regulation studies that is rarely considered. Though the precise function of the vmPFC is a hotly debated topic, studies have shown it to be involved in valuation (Rangel and Hare 2010; Schoenbaum et al. 2011) and self-reflection (Kelley et al. 2002; Northoff and Bermpohl 2004), both of which are processes that might be involved in emotion regulation when the target of regulation or strategy deployed is valued by or highly relevant to the self.

One way "value to the self" can be construed is with regard to the value of the target being regulated. Though few emotion regulation studies have made distinctions among the specific negative emotions being regulated, the regulation of fear has been an exception. Researchers investigating the regulation of fear (as separate from other negative emotions such as disgust or anger) have consistently found that vmPFC plays a role in dlPFC's regulation of the amygdala regardless of the specific strategy that is deployed (Delgado et al. 2008b; Schiller and Delgado 2010; Hartley and Phelps 2009), a finding which has generally not been true for the regulation of other emotions. Bringing the construct of value to the self into the discussion might explain why vmPFC is active for regulation of fear but not necessarily other emotions: Fear is a basic emotion perhaps most central to human survival, and thus might be personally valued more than other emotions. In fact, certain negative emotions such as fear and anger have proven desirable if they help people attain their goals (Tamir 2009). In other words, fear may be more "affectively meaningful" because of its relatively higher value to the self across an entire sample, leading to a greater involvement of vmPFC in the regulation of this emotion over others (Roy et al. 2012).

Agency in some part of the emotion regulation process is another way in which value to the self may help in understanding and organizing the neural correlates of emotion regulation. Kuhn et al. (2014) recently found that regulation (versus passively experiencing) recruits dmPFC for endogenous (i.e., self-chosen) cues but lateralized regions for exogenous (i.e., experimenter-provided) cues. One reason dmPFC may be involved in the endogenous condition is because of the self-reflective, volitional nature of this condition. This fits well with the differences between self-chosen and experimenter-provided regulation strategies discussed above. Though studies investigating the role of choice in regulation are just emerging, the topic provides a promising way in which to directly test the extent to which self-relevance and self-value plays a role in emotion regulation.

However, choice need not be involved in order to invoke self-value. Rather, value may be instantiated by the success or failure of the regulatory act. A number of studies have suggested that vmPFC (and/or the overlapping Brodmann's area 10) is only recruited during *successful* regulation (Urry et al. 2006; Johnstone et al. 2007; Denny et al. 2014) and, complementarily, that *unsuccessful* regulation is reflected in a disruption of the otherwise inverse relationship between the vmPFC and the amygdala (Wagner and Heatherton 2013). In this view, successful regulation relies on motivation derived in part from self-value (Baumeister 1986; Wicklund and Gollwitzer 1982), and the involvement of vmPFC speculatively implies that success or the anticipation of success might play an important role.

Together, this evidence suggests that factors beyond the specific cognitive strategy or target emotion may be worth considering when investigating the neural patterns of emotion regulation. This is particularly true in resolving the debate over the role of vmPFC in emotion regulation, but presumably applies to many other regions involved in emotion regulation. We have considered how the regulation target, temporal duration, choice to regulate, and success or failure of regulation may all contribute to varying patterns of activation in vmPFC and related regions. Importantly, we speculate that differing patterns across emotion regulation, particularly but not only in vmPFC, may result from different ways in which various components of the emotion regulation experience are valuable to the self.

13.3.2 Motivation

Though the majority of studies investigating regulation of avoidance emotions or motives have centered on the regulation of negative affect, the field will need to extend beyond this narrow framework to provide a more comprehensive picture of avoidance regulation. To date, the literature extending beyond emotion regulation and into regulation of avoidance motivation is sparse, but there is some work on the regulation of the motive to avoid losses. A number of studies have now demonstrated that cognitive emotion regulation strategies can decrease loss-aversive behavior (Grecucci et al. 2013; Heilman et al. 2010; Sokol-Hessner et al. 2012), providing support for the theoretical notion that the neurocognitive systems involved in regulating emotion and motivation may be quite similar.

Neuroimaging provides one way of establishing whether different processes such as regulation of motivation versus emotion share similar neurocognitive substrates. For example, Sokol-Hessner et al. (2012) showed that when emotion regulation decreased loss aversion during financial decision making, both dlPFC and vmPFC were engaged, and amygdala activity to losses decreased. Similarly, Hare et al. (2009) showed that regulation of aversion for healthy foods during food-related decision making involved the modulation of vmPFC by dlPFC. In both studies, the same regions that consistently emerge during emotion regulation (e.g., dlPFC) also appear in the regulation of motivations. Intriguingly, both studies also suggest that vmPFC may only be involved in regulation to the extent that the goal is valuable to the self. Because these studies again provide evidence that value to the self may play an important role in the neurocognitive differences amongst regulation strategies, studies investigating regulation of motivation may be particularly suited to inform the debate over the role of vmPFC in emotion regulation. However, because of the sparse literature within this domain, these conclusions remain speculative.

13.4 Conclusion

Our goal in this chapter was to compare and contrast the neural systems engaged during the regulation of emotions and motivation. We argued that comparing these two domains of regulation could have the potential to broaden existing knowledge about the neural correlates of self-regulation, which in turn would inform theoretical accounts of both. In general, a number of similarities seem to exist between these two forms of regulation (e.g., recruitment of prefrontal regions; downregulation of amygdala), suggesting that more commonalities than differences may exist within the broader domain of self-regulation (Heatherton and Wagner 2011). A second goal was to review factors that are relevant in driving the observed patterns of neural activity during self-regulation. In addition to the distinction between the regulation of emotion and motivation (which did not account for much variance across studies), we noted differences in the mental processes associated with various strategies, the direction of the emotion or motivation being regulated, and the extent to which self-value was involved in a given experimental paradigm. Below, we synthesize our findings regarding each of these distinctions, then provide some future directions for research in this area.

13.4.1 Emotion Versus Motivation

We deliberately juxtaposed results from lines of research that have evolved separately: regulation of emotion and regulation of motives. We are struck by the similarities between the two, particularly in terms of recruitment of lateral prefrontal regions. The overall similarity was consistent with domain-general models of self-regulation (Cohen et al. 2013; Heatherton and Wagner 2011), but still raises some important questions. For example, if all regulation recruits the same regions, why did we observe differences in terms of strategy? Or in terms of the target of regulation? More research will be needed to conclusively answer these kinds of questions.

This review highlighted some factors that might be important, which we discuss in turn below. In the interim, we see no need to make fine distinctions between "emotional" and "motivational" targets when it comes to regulation. These two constructs are highly overlapping and may be identical in terms of top-down control. Indeed, other factors such as the cognitive strategy used to target them or their value to the self may be more influential on the neural systems of regulation than the mere distinction between basic emotions and motivational states per se.

13.4.2 Approach Versus Avoidance

Early neuropsychological investigations using electroencephalography focused on a lateral distinction between approach and avoidance motivation, with approach being associated with increased relative left prefrontal activation and avoidance with increased relative right activation (Coan and Allen 2004; Sutton and Davidson 1997). However, with few exceptions (Berkman and Lieberman 2010; Herrington et al. 2005), studies using fMRI have failed to find such a distinction, perhaps because they typically do not directly compare activity based on laterality. The studies we reviewed are no exception; none of them compared activation in, say left to right dlPFC. Nonetheless, comparing the results of approach versus avoidance in a qualitative way, we note that regulating approach is much more likely to elicit activation in traditional reward regions including dorsal striatum, OFC, and, at times, sgACC. Contrasts tapping approach regulation also tended to reveal more stimulus-driven attention systems such as posterior parietal and cingulate cortices more often than contrasts targeting avoidance regulation. On one hand, this trend may not be surprising given the much greater appetitive value of the stimuli typically used in studies of approach (e.g., delicious-looking food) versus avoidance (e.g., contamination) regulation. On the other hand, the presence of reward system activation in conditions wherein participants are effortfully trying to regulate reward motivation seems to belie the general claim that "bad is stronger than good" (Baumeister et al. 2001); perhaps a more accurate description is that "bad motivates disengagement more than good." This description explains this finding, and also suggests that regulating approach/positive emotion might be inherently more difficult than regulating avoidance/negative emotion because there is more at stake in a failure to regulate the latter compared to the former.

13.4.3 Process Distinctions

As noted throughout, the precise cognitive strategy or tactic (McRae et al. 2012) deployed has a strong impact on the neural systems recruited during regulation. From a cognitive neuroscience perspective, this is entirely unsurprising; emotion regulation is a psychological construct that can be instantiated in a number of ways through varying neurocognitive processes. The results here support an emerging trend within the field of emotion regulation to focus more on the nature and quality of those processes rather than on emotion regulation per se, which can be conceived of as the goal or outcome of the processes. Indeed, one of the principal strengths of neuroimaging is its ability to inform upon the neurocognitive processes that underlie mental phenomena such as emotion regulation.

Along those lines, one theme that emerged from our review is the importance of attention (and attention regulation) for emotion regulation. It remains an open question in our minds whether most forms of emotion regulation studied thus far reduce to simple attention manipulations. Is the "active ingredient" in emotion regulation just effortful regulation of attention toward one stimulus (internal or external) and away from another? The only possible exception to this question is mindfulness, which can produce emotion regulation-like effects but in the absence of activation in frontoparietal regions typically engaged in attention regulation (e.g., Westbrook et al. in-press). The possibility that mindfulness represents a distinct class of emotion regulation strategies—more "bottom-up" than "top-down" like nearly all other forms—is an intriguing possibility that is beginning to receive extensive empirical attention. When we next review this literature, we hope to have more data to directly speak to that issue.

Another process-level distinction that emerged from our review is the role of value modulation in self-control (Hare et al. 2009). Given that vmPFC appeared across a range of emotion/motivation regulation studies—usually when the regulation was successful—and the well-established role of that region in global value computation (Hare et al. 2011), it seems plausible that altering the value attached to a particular stimulus (positive or negative) is the proximal effect of emotion regulation that drives its downstream affective/motivational and behavioral consequences. For example, perhaps successful regulation of food craving is caused by a decrease in the subjective value of consuming the food relative to not consuming it. This proposition seems simple enough, but it is a radically different way of viewing emotion regulation than the traditional dual process (e.g., top-down control vs. bottom-up impulse) view. In the value modulation account, there is only one process—value computation—and the outcome of a controlled or impulsive action is determined not through a competition between two types of processes (e.g., controlled vs. automatic or cognitive vs. emotional) but rather through integration of various inputs to the value computation (e.g., short-term and long-term value). As is the case with mindfulness, this is presently a robust area of research and we anticipate having extensive relevant data in the near future.

13.4.4 Agency and Choice

A final theme that cut across several types of regulation and emerged throughout as important is the role of agency and choice. Emotions and motivations can be intensely personal, and so, it turns out, are the strategies that we use to regulate them. An ongoing challenge in social and affective neuroscience is to blend the tradition of ecological validity from social psychology and affective science with the rigor and experimental control of cognitive neuroscience. In this case, that means using stimuli with personal relevance and meaning, and regulation strategies over which participants feel ownership and control, even when homogenizing the stimuli and strategies might be more convenient. Studies are beginning to emerge that directly compare the effects of constructs such as personal relevance, agency, and choice on neural systems related to self-regulation (e.g., Giuliani et al. in-press). Studies like this will provide better knowledge than we currently have about how our brains actually engage in emotion/motivation regulation in our daily lives.

Another way that agency is important in emotion regulation is though the behavioral implications of the regulation or lack thereof. Most of the paradigms used to study emotion/motivation regulation rely upon participants to remain engaged in a task that ultimately has no meaning for them; participants typically have nothing at stake. For example, in a standard reappraisal of negative emotion task, participants know that the aversive image will be removed within a matter of seconds regardless of how well or poorly they are able to regulate their emotion. Even in a study of food craving reduction, dieting participants presumably are aware that, unlike in real life, they will not actually eat the appetitive foods shown in the images if they fail to regulate their craving for it. We argued here that one reason for the presence or absence of activation in the vmPFC, a region likely involved in the computation of value for the ultimate purpose of making a decision, is the relevance of choice on a given task. As noted in the introduction, William James's (1890) position was that "thinking is for the sake of doing," and we tend to agree. An important consideration for future studies of emotion and motivation regulation is the degree of "doing" involved in the task; the less there is, the lower the quality of the "thinking" is likely to be.

13.4.5 Future Directions

We have reviewed studies on the regulation of emotions and motivations, intentionally juxtaposing the two as a way of highlighting the extensive similarities between the cognitive and neural processes involved in regulating each. Interestingly, most of the research on motivation is related to approach states (e.g., craving), and most of the research on emotions is related to negative affect (e.g., sadness), with large research gaps in regulation of avoidance motives and positive emotions. Those gaps are logical given the relative infrequency of those kinds of regulation, but still are substantively interesting (e.g., regulation of loss aversion or joy) and theoretically meaningful. Other high priority research topics include the role of value modulation in emotion/motivation regulation, the component neurocognitive processes of regulation (particularly control processes vs. mindfulness), and the ecological validity of the neural systems of regulation in terms of the strategies people actually choose and the degree to which they are predictive of actual choices and behaviors in vivo.

We began this chapter by noting the etymological relationship between emotion and motivation. Now we close by noting that the root of the word "regulate," *moderari,* relates to the English words restrain, control, moderate, govern, and guide, among others. The breadth of the connotations of these words underscores the diversity of possibilities when it comes to guiding affective and motivational responses. We have many options for guiding these responses, and just as many ways of studying them. We have learned a lot in a short time, but are still only at the beginning.

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14

More than the Medial Prefrontal Cortex (MPFC): New Advances in Understanding the Neural Foundations of Self-Insight

Jennifer S. Beer and Taru Flagan

14.1 Introduction

At 9:04 p.m., on August 6, 1926, Gertrude Ederle completed a swim across the English Channel, a choppy 21 mile-wide stretch of water that separates Britain from the northwestern tip of France. Swimming the English Channel is quite a feat: Ederle was the first woman and only the sixth person to accomplish it, she beat the previous record holder by 2 h, and, despite placing in three swimming events in the 1924 Olympics, Ederle's historic swim across the channel was actually her second attempt.

Ederle's accomplishment illustrates the heights of self-regulation, that is, a person's ability to monitor and change their behavior to reach their goals. When we hear about feats of self-regulation, it is easy to focus on the discipline and effort that go into changing behavior to meet one's goals. However, an equally important aspect of self-regulation is self-insight, that is, accurate knowledge of your own behavior, attributes, and beliefs. Insight reflects the extent to which you are aware of the consistency between behavior and goals. In other words, it can be the (conscious or subconscious) recognition of when behavior is inconsistent with goals that must precede efforts to change behavior. For example, Ederle had to have insight into the factors that caused her first attempt to fail and, during her second attempt, she had to constantly monitor those factors in relation to her physical capabilities. Whereas psychological models of self-regulation typically include some component of self-insight (Carver and Scheier 2011; Shah and Higgins 2001), the centrality of self-insight to self-regulation has virtually been ignored in neuroscience discussions of self-regulation as well as broader neuroscience discussions of self.

To address this shortcoming, this chapter will integrate the newly emerging body of research that has begun to investigate the neural underpinnings of self-insight. Although the medial prefrontal cortex (MPFC) has gained much attention for its role in self-evaluation, research suggests it plays only a small role in self-insight. Instead, other regions along the midline of the cerebral hemispheres, the medial orbitofrontal cortex (MOFC) and ventral anterior cingulate cortex (VACC), appear to play roles in self-insight that have implications for self-regulation.

14.2 A History of the Association Between MPFC Function and the Self

MPFC is not importantly involved in self-insight, yet has received much attention as the "seat" of the self in the brain. This notion has likely

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arisen from the fact that neuroscience research on self-processes is still quite new and not many self-processes have actually been studied. The first inklings of how the self may be represented in the brain came from observations of soldiers with brain damage returning from war. Clinicians noted that frontal lobe injuries were often associated with personality changes that included poor self-insight. As empirical work began to complement the historical neuropsychological observations, researchers discovered that a region of the frontal lobes, the MPFC, showed increased activation when encoding information in relation to the self. These studies and their presumed consistency with neuropsychological observations of impaired self-insight may have given rise to the expectation that MPFC plays an important role in self-insight rather than other self-processes or social-cognitive processes more broadly. However, this expectation has not been supported.

The MPFC is involved in encoding information in relation to the self and it plays a similar role in encoding information in relation to a close other person. Additionally, studies that include paradigms that actually measure self-insight (i.e., rather than the self-reference effect) do not find robust associations with MPFC. However, there is some evidence that an MPFC subregion typically associated with the self may play a role in self-regulation. Research suggests two possibilities: a ventral region of the MPFC may support either the cognitive or affective mechanisms that mark the importance we place on the actions of ourselves and those close to us (e.g., Flagan and Beer 2013).

14.2.1 Historical Beginnings: Neuropsychological Observations of Frontal Lobe Damage

Not too many years after Ederle made her historic swim across the English Channel, neuropsychologists were already discussing the importance of the frontal lobes for self-processes. Classically, neuropsychologists noted that frontal lobe damage was often associated with a disruption in a variety of self-processes including impaired self-insight (for a review, see Blumer and Benson 1975). Early observations came from clinicians who were eager to understand how brain function related to behavior. They began to document their patients' specific brain injuries and note their associated behavioral changes.

Changes in personality were most often accompanied by damage to the frontal lobes in comparison to other brain regions. In fact, in some cases of frontal lobe injury, the predominant consequence is a change in personality rather than deficits in memory, language, or motor ability (see Stuss and Benson 1984 for a review). Perhaps most relevant to the current chapter, one variant of the "frontal lobe personality" was a tendency for patients to exhibit grandiose beliefs about themselves (Blumer and Benson 1975). In other words, damage to the frontal lobes appeared to disrupt self-insight such that evaluations of the self began to diverge from reality in a way that was much more positive than warranted by others' observations. These observations of impaired self-insight in patients with frontal lobe damage are mirrored in more contemporary neuropsychological work that associates disorders of the frontal lobes with grandiose self-beliefs (e.g., unwarranted beliefs of control over relapse in substance abusers: Goldstein et al. 2009; grandiose confabulation of patients who have sustained traumatic brain injury: Fotopoulou et al. 2008).

This work has laid the foundation for thinking about how the brain may support the self-insight that is so central to self-regulation but neuropsychological observations make it challenging to draw strong conclusions (Beer 2009). Patients rarely sustain brain damage in a perfectly circumscribed subregion of the brain (e.g., Brodmann's areas or meaningful functional subdivisions), which makes it difficult to delineate how behavior maps onto the function of particular brain subregions. Furthermore, an association between brain damage and change in behavior does not establish the necessity of that brain region for that behavior. Instead, the function of the damaged region may depend on communication that passes through that region. Fortunately, these early observations are now being complemented by a wave of neuroimaging techniques, such as functional magnetic resonance imaging (fMRI), which permit the investigations of the association between behavior and function in particular brain regions.

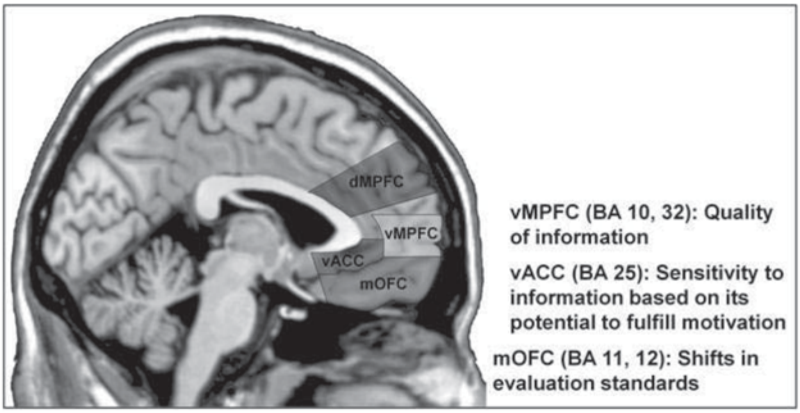

Fig. 14.1 Cortical midline structures implicated in self-evaluation. *dMPFC* dorsomedial, prefrontal cortex; *vMPFC* ventromedial prefrontal cortex; *mOFC* medial orbitofrontal cortex; *vACC* ventral anterior cingulate cortex. The functions of the vMPFC, vACC, and mOFC in supporting self-insight are discussed in the chapter

14.2.2 A Brief Note About Nomenclature for Brain Regions

The manner in which neuroscientists refer to brain regions can sometimes be confusing to readers who are new to the literature. This chapter focuses on functional differences in regions that span the frontal lobe section of the midline between the cerebral hemispheres so it is worth taking some time to unpack the relevant nomenclature. There are two typical ways in which brain regions are described: Brodmann's areas and a name to indicate theorized functional subdivisions (e.g., OFC, VACC). This practice can lead to confusion because multiple functional names can be associated with the same Brodmann area. For example, Brodmann area 25 can be paired with a multitude of functional names such as the frontal lobes, the MPFC, the anterior cingulate cortex (ACC), or the VACC. All these names are correct; they just indicate different levels of differentiation at the functional level of analyses. It is also important to note that there is a lot of variance in how researchers conceptualize the boundaries of functional subdivisions in relation to the Brodmann's areas (e.g., Fuster 2001).

Therefore, we include Fig. 14.1 to provide a visual depiction of the nomenclature used in this chapter. The MPFC broadly refers to the medial wall of the frontal lobes, that is, the portion of the frontal lobes that are visible along the midline between the two cerebral hemispheres. The MPFC is typically divided into at least two sections: a dorsal region (DMPFC) and a ventral region (VMPFC). In the case of self-evaluation research, there are specific portions of the DMPFC and VMPFC that receive a lot of attention (see Fig. 14.1). In this literature, the most typical subregion of the DMPFC includes Brodmann's areas 9/32. The most typical subregion that is labeled as the VMPFC includes portions of Brodmann's areas 10/32. Other important regions that we discuss include the VACC, which is the ventral portion of the ACC (BA 25/32). Additionally, the OFC includes the ventral surface of the brain that lies above the eye orbits (BA 11). It is important to note that in other literatures, particularly those interested in emotion, the label VMPFC is used to refer to all of the VMPFC, VACC, and OFC regions in Fig. 14.1 (i.e., the functional label can be used to refer to a much bigger portion of the brain).

It can also be confusing for new readers to understand why they sometimes read about the medial frontal lobe and other times about the middle frontal gyrus. These are completely distinct brain regions. In contrast to the medial wall of the frontal lobes discussed above, the lateral convexity of the frontal lobes includes three gyri: superior, middle, and inferior (not pictured in Fig. 14.1). Therefore, the middle frontal gyrus is on the "outside" or the region of the frontal lobes that lies closest to the scalp, whereas the medial prefrontal cortex lies on the "inside" midline wall between the hemispheres of the brain.

14.2.3 Empirical Investigations of the Self-Reference Effect Reveal that MPFC is not Specific to Self-Processes and Do Not Have the Capability of Measuring Self-Insight

The first wave of empirical investigation into the neural underpinnings of the self- focused on the neural underpinnings of the self-reference effect, that is, the tendency to have superior memory for information encoded in relation to the self (e.g., Ochsner et al. 2005; Symons and Johnson 1997). The early 2000s saw a burst of studies that asked participants to judge whether a series of trait words described themselves and a famous person such as a politician. Participants were then given a surprise memory test and, consistent with the self-reference research, they were most likely to remember the traits they had judged in relation to themselves than the traits they had judged in relation to the politician. Activation in an MPFC subregion (BA 9/10/32) changed in relation to both self-evaluation and evaluations of a political figure but the change was greatest for self-evaluation (e.g., Kelley et al. 2002; Macrae et al. 2004; Ochsner et al. 2005). Furthermore, changes in MPFC activation found in relation to judging information about oneself predicts subsequent memory for that information (Macrae et al. 2004). These findings gave rise to the speculation that MPFC performed some kind of selective process that was important for self-evaluation. However, this impression may have arisen because studies were comparing self-evaluation to the evaluation of other people who were not personally known to the participants.

Recent meta-analyses found that MPFC (BA 9/10/32) modulation is not specific to tasks involving self-evaluation. An overlapping MPFC subregion is modulated by both self-processing and processing about other people (Murray et al. 2012; Ochsner et al. 2005; Qin and Northoff 2011; Roy et al. 2012). There is a close other (e.g., a significant romantic partner) versus non-close-other (e.g., a public figure) distinction instead of a broader self versus other distinction. The ventral region of the MPFC activation typically found in self-reference studies (BA: 10/32, see Fig. 14.1) is associated with both evaluations of self and close others (Murray et al. 2012; Ochsner et al. 2005; Qin and Northoff 2011). The more dorsal portion of the MPFC region typically found in self-reference studies (BA 9/32, see Fig. 14.1) is associated with evaluations of both self and non-close-others (Murray et al. 2012; Ochsner et al. 2005; Qin and Northoff 2011). These studies therefore do not establish the MPFC as the “seat” of the self. Furthermore, the benefit of conceptualizing the self as relying on a “neural module” is questionable (Beer and Ochsner 2006). Regardless, the region most often associated with self-evaluation is also similarly engaged for evaluating other people.

It is also important to recognize that the typical self-reference paradigm cannot test other aspects of self-processing such as self-insight. If someone rates themselves as having a trait, there is no way of knowing whether this rating indicates self-insight or not. In other words, when measuring self-insight, it is necessary to have an external criterion that serves as a benchmark for assessing the accuracy of the self-evaluation (Beer 2007; Beer and Hughes 2010). But is it the case that MPFC plays no role in the processes we know to be important for self-regulation? It is possible that the VMPFC is involved but not because of self-insight. Instead, it may play a role in self-regulation because VMPFC is sensitive to things and people that are important to us based on our idiosyncratic goals and beliefs.

Meta-analyses show that VMPFC is similarly modulated by self-evaluation and evaluations of close others (i.e., those people who are important to us). It is also the case that VMPFC activation found during self-evaluation is predicted by the extent to which a participant is judging a trait they considered to be important to their self-identity (D’Argembeau et al. 2012). One predominant hypothesis about this pattern of findings is that VMPFC marks an affective aspect of “self-relatedness,” that is, the socioemotional importance of the trait or person for the self (Krienen et al. 2010; Murray et al. 2012; Northoff et al. 2006; Roy et al. 2012). Self-relatedness is a socioemotional variable reflecting the extent to which the evaluation process draws on affectively rich self-representations. The extent to which another person is considered to be a close other has been characterized by the extent to which the representations of that person are associated with self-representations (Aron et al. 1992). It is not the case that the self-representation is theorized to serve as a starting point for evaluating the close other (i.e., a self-projection-like process, which is then subject to correction). Instead, the evaluation draws on a representation of the close other that is emotionally charged because of its association with the self-representation. From this perspective, VMPFC is modulated by self-evaluation and the evaluation of close others because those evaluations have a unique affective or socioemotional significance. Self-regulation involves modifying or controlling behavior to achieve desired outcomes and, therefore, VMPFC may play a role in representing the importance of self and close others.

However, it may not be that VMPFC marks whether social evaluations are "self-like" in a socioemotional sense. In the existing research, socioemotional relation between the self and another person has always been confounded with the quality of information (e.g., cognitive representation) used to make an evaluation. We simply have a different class of information to draw on when we evaluate ourselves and people we actually know (e.g., greater complexity, abstraction, actual experience) compared to unknown others. A novel person and a romantic partner elicit not only different emotional reactions but also different cognitive representations. For both the self and romantic partners, there is a long history of storing person information which creates a more elaborated representation that includes both abstract and biographical information when compared to representations that could be used to evaluate someone who is relatively unknown (e.g., Kihlstrom et al. 2003; Sherman and Klein 1994).

A brain region that indexes one or more cognitive qualities that are emphasized in the representations of people we know well (i.e., self, close other) would also behave like the VMPFC across these social evaluation tasks as reviewed above (i.e., similar modulation across self-evaluation and evaluation of close others but less modulation for unknown others: Krienen et al. 2010; Murray et al. 2012; Ochsner et al. 2005; Qin and Northoff 2011; Roy et al. 2012). This raises the possibility that the contribution of VMPFC to social cognition is more a cognitive (rather than affective) "self-relatedness." From this perspective, VMPFC may mediate a quality of the kind of information that feeds into self-evaluations that is also available for evaluations of people we actually know (but not as much for unknown others). Future research is needed to disentangle whether the self-relatedness aspect of VMPFC function is affective, cognitive, or both.

14.3 The Role of MOFC and VACC in Self-Insight

Although the neuroscience research on the self has been dominated by investigations of self-referent encoding, there is a growing body of research that is beginning to understand the neural basis of self-insight. This research has mostly sought to understand the neural basis of relatively self-enhanced perceptions by comparing them with relatively more calibrated self-perceptions (Beer 2007; Flagan and Beer 2013). This line of research suggests that the brain supports self-insight processes necessary for self-regulation in different ways depending on the self-regulation goal at hand. If people's goal is simply to sharpen thinking such that self-insight is relatively calibrated to external criterion of one's behavior, then this self-insight is associated with increased MOFC activation in the context of an extensive network of neural regions that span the frontal lobe and beyond (Flagan and Beer 2013). However, when people use enhanced self-perceptions to regulate their self-esteem in the face of an attack, then the MOFC (working within a more specific network of the lateral frontal lobe and caudate) and the VACC support different component processes that feed into the self-enhanced views. In other words, one clear finding emerging from this research is that the same neural region, the MOFC, supports self-regulation either by promoting relatively calibrated self-insight or self-enhanced self-views by working within different neural networks depending on the self-regulation goal at hand.

14.3.1 First Steps Toward Investigations Into Self-Insight: Transitioning Away from the Self-Reference Effect

The dominance of the self-reference paradigm influenced the very earliest attempts to empirically investigate the neural basis of self-insight. These paradigms do not have the capability to directly measure self-insight, so researchers instead focused on neural regions that tracked the extent to which participants were presented with socially desirable (or undesirable) things to say about themselves. For example, participants evaluated the self-descriptiveness of traits or the likelihood of future events that varied in their desirability (Beer and Hughes 2010; Moran et al. 2006; Sharot et al. 2007). These studies found convergent evidence that VACC differentiates judgments of desirable attributes from judgments of undesirable attributes. Furthermore, the role of VACC in differentiating desirable from undesirable attributes is especially true for traits that people claim as highly self-descriptive (Moran et al. 2006).

However, the VACC results are difficult to translate into an understanding of the self-insight needed to self-regulate because there is no external criterion that serves as a benchmark for evaluating the calibration of the self-evaluation (Beer 2007; Beer and Hughes 2010; Chambers and Windschitl 2004). People may genuinely be highly characterized by a desirable quality or they may not be. When you simply ask people to rate the self-descriptiveness of a quality, there is no way to establish whether this is an enhanced claim or not. Therefore, this research provided strong evidence that the VACC is sensitive to whether a trait or future event is something that a person can claim to portray themselves in a positive light, but there was no way to assess whether the claim reflected accurate or impaired self-insight. Paradigms other than the self-reference effect were hence needed to investigate whether MPFC, VACC, or other neural regions show significant modulation when self-insight is more directly measured.

14.3.2 Self-Insight in the Absence of Self-Esteem Threat: A Boost from the OFC

Research has now robustly shown that rather than the MPFC or VACC, the medial OFC, working within an extended neural network, is an important region for supporting self-insight so long as self-esteem is not under attack. Both neuroimaging studies and studies of patients with selective lesions support this conclusion. This line of research typically focuses on situations in which cognitive shortcuts or incomplete information drives unrealistically positive self-evaluations (rather than self-esteem protection as the underlying motivation, e.g., Beer et al. 2013; Chambers and Windschitl 2004; Paulhus et al. 1989).

The association between improved self-insight and increased OFC engagement has been found across numerous operationalizations: discrepancies between self-confidence and actual task performance (Beer et al. 2010), discrepancies between base rates and self-rankings in social-comparative judgments (Beer and Hughes 2010), and discrepancies between self-perceptions and other perceptions (Beer et al. 2006). For example, relative insight into one's success on a trivia task is associated with increased OFC activation (Beer et al. 2010). In this study, participants answered trivia questions about average July temperatures and then estimated how confident they were that their answers were correct. In other words, the experiment required participants to report their insights into their chances of being correct. When participants had answered the trivia question correctly, a region of OFC was positively modulated by confidence level. In other words, people tended to recruit OFC activation the most on the trials where they answered correctly, and the magnitude of this activation was driven by their accurate confidence in their answer. Additionally, participants who tended to be more confident about their performance on the task were the most likely to activate OFC.

OFC activation is also increased when people make relatively calibrated social comparisons (Beer and Hughes 2010). In this study, participants compared themselves to their average peer on 200 personality traits. Each person is likely to have some traits that compare favorably and others that compare unfavorably to the average peer. Therefore, averaged self-rankings across the 200 traits are considered to reflect relatively accurate self-insight to the extent they indicate similarity between the self and the average peer (Chambers and Windschitl 2004; Moore and Small 2007). The more participants rated themselves as similar to their average peer, the more likely they were to activate OFC during the social-comparative judgments (Beer and Hughes 2010). Connectivity analyses were conducted on this dataset to understand the network in which OFC activation was being modulated. The analyses found that OFC increases and decreases its functional connectivity (i.e., covariation in activation) with numerous regions in the frontal lobes and beyond (Flagan and Beer 2013) when supporting self-views that are more optimally calibrated in relation to external criterion such as base rates of an average peer.

Finally, if OFC activation is important for relatively calibrated self-insight, then it is reasonable to expect that self-insight becomes impaired when the region is damaged. Research supports this conclusion: patients with OFC damage overestimate their social skills on a social interaction task when compared to judges' ratings of their social skills (Beer et al. 2006). This overestimation was not found in patients with other kinds of brain damage (i.e., dorsolateral prefrontal cortex: DLPFC) or healthy control participants. In this study, participants reported on their understanding of the social norms governing conversations between strangers. All participant groups reported similar understanding that certain kinds of personal information are considered inappropriate to be discussed with strangers. Participants then had to engage in a semi-structured conversation with a stranger. Judges who were blind to the participant group rated patients with OFC cortex damage as the most likely to introduce inappropriate personal information into the conversation. When questioned about their performance on the conversation task, patients with OFC damage were much less likely to note the inappropriateness of their conversation in comparison to blind judges' perceptions.

Together, this research shows that regardless of how you measure self-insight, OFC activation working in the context of a broad neural network (Flagan and Beer 2013) is important for boosting the self-insight that can be so critical for self-regulation. This region is helpful for accurately assessing one's qualities or task performance as indicated by external criterion such as task performance, base rates, and social consensus. That kind of insight is helpful for monitoring whether behavior is meeting one's goals or necessitates change. However, if the self-regulation goal is to protect self-esteem through positively inflated self-evaluation, then the OFC takes on a different role. Furthermore, the VACC may play an important role in boosting self-enhancement used to regulate self-esteem.

14.3.3 When Self-Regulation Rests on Self-Enhancement Rather than Self-Insight

Gertrude Ederle's record-breaking swim is an example of self-regulation that benefits from calibrated self-insight; overestimations of her ability to handle the rough sea conditions could be deadly. But what about cases where self-regulation is aimed not at using self-insight to achieve a goal, but to defend a positive self-image that is under attack? In this case, people tend to self-enhance, that is, produce uncalibrated self-evaluations for the purpose of defending self-esteem. How are these uncalibrated self-evaluations produced at the neural level? It is not the case that there is simply a dialing down of the neural activation associated with self-insight described above. Research suggests that self-enhancement also draws on increased OFC activation albeit within the context of a different neural network. Furthermore, the VACC is also implicated in promoting self-enhancement used to regulate self-esteem.

Specifically, OFC may support the adjustment of evaluation thresholds needed to promote self-enhancement (i.e., top-down processing) whereas VACC may play a more preliminary role through its sensitivity to opportunities with the potential to achieve a positive self-evaluation (i.e., motivational influences on bottom-up processing).

14.3.4 MOFC: Self-Regulatory Influences on Top-Down Processing

One considerable self-regulatory task is maintaining self-esteem; it can be threatened by any number of things including negative feedback about their personality, academic abilities, or skills (Baumeister et al. 1993; Leary et al. 1998; vanDellen et al. 2011). People may self-enhance in order to cope with these threats (Beer et al. 2013 and see Sedikides and Gregg 2008; vanDellen et al. 2011 reviews). The lesion and fMRI research reviewed above did not include any manipulations to threaten self-esteem. What do we know about the neural basis for these self-enhanced views used to regulate self-esteem? The most direct answer to this question comes from an fMRI study that used the very same social comparison evaluation as a previous study (Beer and Hughes 2010) but added in a self-esteem threat manipulation (Hughes and Beer 2013). In this study, participants were asked to evaluate how their personality traits compared to their peers. However, these judgments were interspersed with false feedback about whether other students had found the participant either likable or unlikable. Self-enhancement was used to regulate self-esteem in the face of this negative feedback: participants evaluated their personalities in a much more flattering way after learning that others found them unlikable (compared to learning that others found them likable). Increased OFC activation predicted the extent to which participants boosted the favorability of their social-comparative judgments in the face of self-esteem attack (Hughes and Beer 2013). Connectivity analyses on this dataset found that the region of OFC associated with self-enhancement tended to increase its functional connectivity with the striatum and reduced functional connectivity with the middle frontal gyrus (Flagan and Beer 2013). Therefore, whereas increased OFC activation predicted calibrated self-insight in the studies described earlier, this line of research found that increased OFC activation predicts self-enhancement but the region is working within the context of a different neural network.

The social comparison studies (Beer and Hughes 2010; Hughes and Beer 2013) permitted a clear test of the neural association of self-evaluation as a function of self-esteem threat but they were not designed to pinpoint the underlying psychological process that explained the association. This issue is just now beginning to be addressed. One study used signal detection theory (SDT) to investigate the neural associations of self-evaluations used to protect one's self-esteem (Hughes and Beer 2012b). Just as people tend to inflate their social standing on personality traits, they also tend to claim knowledge about concepts beyond what they actually know or could know in order to maintain self-esteem (Paulhus et al. 2003). However, when self-esteem is potentially at stake (i.e., their false claims of knowledge could be discovered), people protect self-esteem by reducing the extent to which they overclaim knowledge (Paulhus et al. 2003). More specifically, people reduce their overclaiming to protect their self-esteem by adopting a different standard (i.e., decision threshold) for claiming knowledge. An fMRI study found that OFC was modulated to the extent that participants adopted a more conservative standard for claiming knowledge to protect self-esteem (Hughes and Beer 2012b). In this study, participants were asked to rate their familiarity with different knowledge items (e.g., famous authors, scientific concepts). Although the lists they rated all contained fake items, participants were only warned that some of the items did not exist for half of the lists. Consistent with previous research (Paulhus et al. 2003), participants did not want to look foolish and therefore adopted a more conservative decision threshold when claiming knowledge in the condition where they were warned some items might not exist (Hughes and Beer 2012b). OFC activation increased to the extent that participants adopted a conservative decision threshold when they knew any false claims could be exposed. Furthermore, this region of OFC showed functional connectivity that was similar to the connectivity found in the study investigating the effect of threat on social-comparative judgments (Flagan and Beer 2013): increased covariation with a striatal region and decreased covariation with middle frontal gyrus.

Taken together, these studies and subsequent connectivity analyses suggest that OFC aids top-down influences on social cognition by adjusting evaluation standards as a function of motivational state. When we want to protect self-esteem, OFC may be engaged to maintain positive self-evaluations in the face of threat and may support the flexible adjustment of evaluation thresholds depending on whether positive self-evaluations are maintained by more conservative (reducing the overclaiming of knowledge) or loose (inflating claims of desirable personality traits) thresholds. Furthermore, the connectivity results converge: OFC increases covariation with regions within the striatum and decreases covariation with the middle frontal gyrus when protecting self-esteem.

14.3.5 VACC: Self-Regulatory Influences on Bottom-Up Processing

However, the function of OFC in promoting self-enhancement is not the whole story about the neural basis of self-enhancement used to regulate self-esteem. As noted earlier, VACC was initially suspected to be a region that might be involved in self-enhancement because of its sensitivity to traits or events that could cast the self in a positive light but these studies did not have the potential to directly measure self-insight, only what people claimed about themselves (Moran et al. 2006; Sharot et al. 2007). Further research has built on these findings and suggests a different role than expected for VACC in self-enhancement. VACC activation does not predict the extent to which someone reports a self-enhanced evaluation (i.e., unrealistically flattering social-comparative judgments: Beer and Hughes 2010; Hughes and Beer 2012a). Instead, research suggests that VACC may be modulated by earlier bottom-up processes that can feed into self-enhancement: marking opportunities that have the potential to cast yourself in positive light (Flagan and Beer 2013; Hughes and Beer 2012a).

The reason VACC may be implicated in marking opportunities that have the potential to carry out self-regulatory goals is that its activation is modulated by how much you care about the target you are evaluating. Specifically, the studies that have asked people to evaluate traits sometimes include targets beyond the self. When people evaluate well-liked social targets (e.g., the self, romantic partner, well-liked roommate), VACC activation is associated with trials where affirmative claims would cast the target in a positive light (i.e., desirable personality traits, likelihood of a positive future) from trials where affirmative claims would cast the target in a negative light (i.e., undesirable personality traits, likelihood of a negative future: Beer and Hughes 2010; Hughes and Beer 2012a; Moran et al. 2006; Sharot et al. 2007). However, when there is reduced motivation to portray the target in a positive light (i.e., personality traits that are not considered central to one's self-view: Sedikides and Gregg 2008; a non-close other: Suls et al. 2002), VACC activation is less likely to differentiate trials on the basis of how affirmative claims would affect the impression of the target (i.e., the self: Moran et al. 2006; an assigned college roommate: Hughes and Beer 2012a). Taken together, these studies suggest that VACC activation is sensitive to opportunities that afford the possibility of casting someone in a positive light. However, its activation does not predict whether the opportunity is exploited (i.e., leads to a self-enhanced judgment, Hughes and Beer 2012a).

Functional connectivity analyses also support the hypothesis that VACC may play a signaling opportunity for self-enhancement and further suggest a possible connection between VACC and OFC (Flagan and Beer 2013). For example, the VACC region that is sensitive to trials involving desirable (versus undesirable) traits shows relatively more positive covariation with the OFC subregion that regulates the extent to which social comparative evaluations are better calibrated. The direction of functional connectivity cannot be determined by connectivity analyses. However, taken together, the current research suggests that VACC may play a role in analyzing the content of an evaluation on the basis of whether an affirmative claim (i.e., endorsing a desirable trait) has the potential to achieve a desired self-evaluation. That information may then be fed forward to the OFC, which conducts further analyses before an evaluation is expressed.

14.4 Conclusions and Future Considerations

The dominance of the self-reference paradigm in neuroscience research on the self has left researchers interested in self-regulation with many questions about the neural basis of self-insight and few answers to those questions. Early clinical observations have pointed to the broad expanse of the frontal lobes as the seat of self-processes. Empirical research is shedding light on how specific regions within the frontal lobes support various self-processes including the self-insight that precludes control efforts over behavior and the self-enhancement used to regulate self-esteem. MPFC, the region most often associated with the self in self-reference research is likely not important for self-insight. Instead, a subregion of the MPFC, the VMPFC, may play a role in self-regulation by indicating the socioemotional significance of the self and close others through either cognitive or affective mechanisms. The OFC supports self-insight or self-enhancement depending on whether it is functioning within a broad neural network or within a network involving the striatum and middle frontal gyrus. The VACC may be important for detecting opportunities where self-enhancement is possible. Future research is needed to further deepen our understanding of self-regulation.

For example, more research is needed to investigate the role of VMPFC in the evaluation of social targets. Is this region implicated in the affective or cognitive qualities shared by the evaluation of the self and close others? One avenue for addressing this question is whether VMPFC is similarly modulated by the evaluation of a person who evokes an emotional association with self but no actual firsthand experience to draw. If VMPFC modulation was similar for the self and such a person, then it would suggest that VMPFC is important for mediating the socioemotional aspect of self-relatedness rather than some cognitive aspect of the knowledge we have about ourselves and people close to us.

A very important step will be investigating the psychological significance of the OFC in self-insight, and the OFC and VACC in self-enhancement. Virtually nothing is known about what psychological computation is reflected by the association of OFC function to self-insight. Future studies need to carefully test possible computations to better understand why OFC is called upon to support self-insight. Furthermore, it will be useful to replicate the connectivity analyses. Does the OFC work within a broad network to support self-insight or do more specific regions emerge across studies? In contrast, there is convergent evidence that increased OFC activation in concert with increased positive covariation with striatum and reduced covariation with middle frontal gyrus is associated with changing self-evaluation thresholds in order to protect self-esteem (Flagan and Beer 2013). However, future research is needed to better understand the psychological significance of the striatum and middle frontal gyrus in self-enhancement.

Additionally, more research is needed to clarify the possibility that VACC is sensitive to opportunities for self-enhancement. Does VACC mediate sensitivity to self-enhancement or does it play a broader role in detecting opportunities that are simply consistent with the regulation goal at hand? This question is important: the motivation to see oneself in a positive light is not the only motivation that influences self-evaluation. For example, some people regulate their feelings through self-verification, or the motivation to confirm an established self-view regardless of whether it is positive or negative (Swann et al. 1989). When self-verification is the goal at hand, people may become vigilant for opportunities that have the potential to verify their current self-evaluations. For people with negative self-views, the opportunity to evaluate the self-descriptiveness of negative traits (rather than positive traits) would have the potential to affirm the way in which they want to see themselves but not the opportunity to self-enhance. If VACC mediates sensitivity to opportunities relevant to self-regulation goals, then it should be modulated by opportunities to affirm a negative self-evaluation for people who are motivated to confirm a negative self-view. Furthermore, more research is needed to replicate and understand the psychological significance of the connectivity between VACC andMOFC.

Finally, as a clearer picture of the neural basis of self-insight emerges, it will be critical to integrate this work with the research on control efforts. In other words, how does the self-insight and self-enhancement functions of OFC and VACC relate to the function of regions known to be involved in controlling or changing one's behavior to meet a self-regulation goal? Neuroscience research that takes all of the psychological components of self-regulation into account will be beneficial for creating a more complete understanding of how the brain supports self-regulation from extreme feats such as Ederle's historic swim to relatively everyday occurrences such as directing attention back to one's work when it has strayed.

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Self-Control in Social Decision Making: A Neurobiological Perspective

15

Daria Knoch and Kyle Nash

15.1 Introduction

The social world is becoming ever more integrated and connected (Friedman 2006); decisions thus have more of an impact on a greater number of people. Social norms are standards of behavior that help regulate such complicated group functioning, and people who indulge in selfish whims that flout social norms risk a range of negative outcomes (Kurzban and Leary 2001). Critical in overcoming selfish urges to act in the interest of others is self-control—the process in which thoughts, emotions, or prepotent responses are inhibited to efficiently enact a more focal goal. This is evident in many everyday situations. Patiently listening to an in-law's insipid tale, volunteering time and resources to a social cause, or remaining faithful in a long-term relationship all constitute a social dilemma that requires self-control of selfish impulses. And in contrast with work on the nonsocial forms of self-control (Cohen and Lieberman 2010), evidence about the underlying neural mechanisms of self-control in social decision making has only recently begun to emerge. Researchers have consequently combined neuroscience methods with social interaction games to elucidate the complexities of this unique mental ability displayed in a social context.

We had two aims in writing this chapter. The first was to outline research on self-control in social decision making with a particular focus on research that converges on a seemingly common neural substrate—the lateral prefrontal cortex (PFC). The second aim was to review newly developing opportunities and challenges unique to this field. Thus, we first outline the combination of neuroscience methods and social interaction games in researching self-control in social decision making (Sect. 15.2). We then examine functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) research from three social decision-making domains—norm compliance, costly punishment, and moral decision making—that all highlight the involvement of the lateral PFC in self-control in social decisions (Sect. 15.3). Research is then reviewed in which neural traits, such as baseline cortical activation in the lateral PFC, explain sources of individual differences in self-control capacity (Sect. 15.4). We then examine how basic neurobiological processes involved in stopping a motor response appear to be involved in self-control in social decision making (Sect. 15.5). Finally, key research questions are discussed to help further research that investigates the processes that allow people to maintain and realize stable goals in a dynamic and often uncertain social environment (Sect. 15.6).

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15.2 Examining Self-Control in Social Decision Making: Neuroscience and Social Interaction Games

Neuroscience methods can help reveal the neurobiological systems that implement social behaviors (for a review, see Rilling and Sanfey 2011). The researcher can both image and modulate brain activity to provide a unique window into neural processes that mediate decision making and choice. Self-control in social decision making is thus well suited to neuroscience methods. Because self-control is the process in which thoughts, emotions, or prepotent responses are inhibited to efficiently enact a more focal goal (Thaler and Shefrin 1981), successful self-control processes are not directly observable. Researchers have been forced to infer self-control from other theoretically relevant variables. For example, response-inhibition processes are often inferred from failures to inhibit a response (e.g., number of errors committed) or the speed of correct responses. Such indirect measures, however, can fail to differentiate between patients who have poor self-control, i.e., those characterized by a disinhibited pathology, and healthy controls (e.g., Kemner et al. 1996; Karayanidis et al. 2000). Neuroscience methods allow the researcher to directly image and even modulate brain processes that underlie self-control.

Similarly, social interaction paradigms have certain features that make them ideally adaptable to the study of self-control in social decisions. First, most games involve a cost. That is, participants must sacrifice, often money, to behave in certain ways. For example, in the ultimatum game (UG), one player (often called the proposer) is given a sum of money (or points that will be exchanged for money at the end of the game) and must decide how much to share with another player (i.e., the responder). The responder can either accept the offer or reject it and ensure both players get no money at all. Thus, the responder can punish the proposer for an unfair offer, but at a personal cost. In comparison to hypothetical scenarios or questionnaires, behaviors in these social interaction games have real, easily quantifiable consequences. Additionally, social interaction paradigms are highly malleable. They are readily and precisely modified to suit different research questions or to operationalize a number of social phenomena; for example, games in which each trial involves a new interaction partner controls for reputational concerns. Games that involve repeated trials with the same interaction partner elucidate longer term, iterative social processes. Anonymity, cost, reputation, etc. are all precisely manipulated within the social interaction paradigm.

Together, these features equip the researcher with a set of tools with which to examine self-control in social decision making. Behaviors in social interaction paradigms involve a direct conflict between selfish actions and actions that benefit others. Combining social interaction games that involve a social dilemma with neuroscience methods thus provides a paradigm that can precisely operationalize self-control in a social context and discern the underlying neural processes. We focus our chapter on research that has used social interaction paradigms like the UG and brain stimulation techniques that allow causal inferences about the neural mechanisms of self-control. These studies reliably point to the lateral PFC.

15.3 Self-Control in Social Decision Making: The Lateral PFC

Observations of patients with PFC lesions were the first to suggest that the PFC may play a critical role in self-control in a social context. In general, frontal PFC lesions were associated with poorer social behavior (Damasio 1996; Shallice and Burgess 1991; Stuss and Benson 1986). For example, patients with PFC lesions demonstrate socially inappropriate behavior and personality disturbances associated with impulsiveness (Tranel et al. 2002; Clark et al. 2003). Such findings indicate that the PFC may be involved in self-control abilities. However, it is difficult to experimentally test this hypothesis in lesion patients under controlled conditions. Moreover, lesion studies often have a low number of patients and the possibility of functional reorganization after brain lesions may cast doubt on the interpretation of the results (Rorden and Karnath 2004).

Functional neuroimaging has been used to extend lesion research by noninvasively measuring brain activity in healthy individuals during social decision making. These studies have provided critical correlational evidence on PFC involvement in self-control in social decision making (e.g., Sanfey et al. 2003; Spitzer et al. 2007). Imaging methods, however, do not allow causal inferences to be made about changes in brain activity or mental processes. A direct investigation of causal brain–behavior relationships requires controlled modulation of brain activity with direct measurement of changes in behavior. One method that allows such an investigation is TMS. TMS noninvasively increases or decreases cortical excitability in targeted brain regions by pulsed magnetic fields through a contiguous scalp location. If TMS is applied at a low frequency for several minutes, the function of a stimulated area can be temporarily disrupted (Robertson et al. 2003), producing a kind of "transient lesion" in the healthy brain. The behavioral impact of disrupting this region can then be observed. Using TMS, researchers have begun to examine whether modulation of prefrontal brain functioning impacts self-control in healthy individuals. In the next section, we review evidence from different social situations that require self-control, including norm compliance, costly punishment, and moral dilemmas, first in adults (Sect. 15.3.1) and second in samples from across the life span (Sect. 15.3.2). This evidence converges to demonstrate the importance of the lateral PFC. Note, we use the term lateral PFC to refer to both dorsolateral and ventrolateral regions. Certainly, somewhat different regions of the lateral PFC may be activated in the separate studies. However, we provide an inclusive, rather than divergent, overview of research grounded by the consistent involvement of the lateral PFC.

15.3.1 Evidence in Healthy Adults

15.3.1.1 Norm Compliance

The threat of punishment is an important factor in norm compliance (Boyd et al. 2003; Fehr and Gächter 2002). For example, when there is no threat of punishment, people are generally more selfish, whereas when the threat of punishment looms, people are more cooperative and giving, e.g., more compliant with the norm for fairness (Fehr and Gächter 2002). To avoid punishment for norm violation, then, people must implement self-control to override selfish interest. Spitzer et al. (2007) used fMRI to examine the neural mechanisms associated with such norm compliance under the threat of punishment. In this study, participants played as a proposer in a social interaction game that was required to split a sum of money with a playing partner (the responder). There were two conditions; one in which the proposer could be punished by the responder and another where he or she could not be punished. During these interactions, participants' brain activity was measured with fMRI. The authors found that in comparison to the nonpunishment condition, the punishment condition elicited greater activation in the left and right lateral PFC and this activation correlated with the degree to which participants increased their offers under the threat of punishment. Because the threat of punishment prompts increased compliance with the norm for fairness, the authors suggested that lateral PFC activation represented increased self-control implemented to override the impulse to keep the money and make a low offer.

Norm compliance is not merely enacted to avoid punishment, however. Social rewards can also motivate normative behavior. Reputation, for example, is a kind of social currency accrued over time by engaging in actions valued by the group, particularly those that comply with norms. These behaviors that garner reputation are often costly. That is, they signal to other people that the individual is willing to sacrifice in order to cooperate or reciprocate trust in a social interaction. Though defection or breaking trust may be more rewarding in the short term, a good reputation is more beneficial over the long term. Reputation building thus requires self-control as people must forego immediate selfish temptations for the longer-term payoff of favorable social standing. Because reputation building does indeed involve self-control, one would expect that this ability involves the lateral PFC. To examine whether the lateral PFC was causally involved in reputation building, Knoch et al. (2009) conducted a brain stimulation study with TMS. In this study, participants played a modified trust game in which they could return or not return money to an investor. There were two game conditions, a reputation condition in which the investor could see prior decisions made by the participant and an anonymous condition in which no interaction history was visible. Thus, building a good reputation of trustworthy behavior would increase the likelihood that the investor would transfer money in the reputation condition, thereby increasing the participant's payoff. Participants were randomly assigned to one of the three TMS conditions, right lateral PFC disruption, left lateral PFC disruption, and a sham TMS condition. Results showed that right lateral PFC disruption caused a decrease in returning the investment when interaction history was visible, even though participants across TMS conditions were still equally aware of the benefits of building a good reputation. Thus, right lateral PFC disruption specifically antagonized the ability to resist the temptation to keep the money.

15.3.1.2 Costly Punishment

As demonstrated by the Spitzer et al. (2005) study, the threat of punishment guides norm compliance. Costly punishment—the degree to which people sacrifice personal resources to reprimand norm violators—is central to maintaining social norms. People are willing to sanction wrong doers at their own expense. Delivering costly punishment thus requires self-control in order to overcome the self-interested choice of keeping personal resources. This social dilemma is neatly captured by the UG. In this game, two people interact, one as a proposer who is instructed to offer the other person a division of real money, the other as a responder who is instructed to reject or accept the proposed division. A rejection decision ensures that both parties get no money. Thus, the responder can punish the proposer for an unfair offer, but such behavior is costly. In a landmark neuroimaging study, Sanfey et al. (2003) examined costly punishment in the UG. Participants played this game in the role of the responder as brain activity was measured with fMRI. The researchers found that unfair monetary offers prompted rejection of the offer and elicited left and right lateral PFC and anterior insula activation (Sanfey et al. 2003). Knoch et al. (2006) directly extended this evidence by manipulating activity in the lateral PFC with TMS. As in the Sanfey et al. (2003) study, they had participants act as responders in the UG. However, subjects were randomly assigned to one of three TMS conditions, right lateral PFC disruption, left lateral PFC disruption, and a sham TMS control. Knoch et al. found that right, but not left, lateral PFC disruption caused a decrease in the rejection of unfair offers. Because the rejection of unfair offers involved losing money to enact normative behavior, these results indicated that the right lateral PFC implemented self-control to mute selfish concerns in favor of punishing the proposer for unfair offers. This same effect of right lateral PFC disruption on the rejection rates of unfair offers has been demonstrated in separate studies (Baumgartner et al. 2011; van 't Wout et al. 2005) and with a different method used to modulate frontal activity (i.e., with transcranial direct current stimulation, Knoch et al. 2008).

One might suggest, however, that the complex processes of self-control in social decision-making tasks involve a distributed neural network and not just the lateral PFC. Neural imaging identifies neural correlates but does not identify causal roles of those brain regions. Brain stimulation identifies causal relationships between brain regions and decision making but does not identify changes to the broader neural network. However, if these two methods are combined, one can overcome the separate limitations of each method. That is, the researcher can examine how modulated brain activity implements changes in a neural network to cause the behavior of interest. With this benefit in mind, Baumgartner et al. (2011) combined TMS with fMRI to examine the effect of right and left lateral PFC disruption on neural activity and costly punishment behavior. Participants first had either the left or the right lateral PFC disrupted and then played the same UG in the role of the responder, during which brain activity was measured. Results demonstrated that TMS of the right PFC disrupted recruitment of the right lateral PFC to unfair offers and increased acceptance rate of those unfair offers. Additionally, participants who made more costly punishment decisions to unfair offers showed increased activation in and connectivity between the right lateral PFC and the ventromedial PFC after receiving an unfair offer. TMS over the right lateral PFC, however, eliminated these effects. By combining brain stimulation with brain imaging, the authors identified a prefrontal network consisting of the right lateral PFC and the ventromedial PFC as the drivers of costly punishment, a social behavior that requires self-control.

15.3.1.3 Moral Decision Making

Moral choices are inherently social and would appear to also require self-control. Tough decisions must be made as emotions and opposing moral values clash with cold, calculated logic. Tassy et al. (2012) examined whether the right lateral PFC was causally involved in moral dilemmas using TMS. Participants were randomly assigned to either a right lateral PFC disruption or sham TMS condition and then read scenarios that required the participant to select one of two outcomes that contrasted important moral values (e.g., killing is wrong vs. letting innocent people die is wrong). One option typically required a morally wrong act that nevertheless caused a much better outcome (i.e., a utilitarian choice). Results demonstrated that compared to the sham condition and to nonmoral decisions, TMS disruption of the right lateral PFC caused a reduction in subjective utilitarian choices (but an increase in objective utilitarian choices). In other words, disrupting the right lateral PFC reduced the preference to personally engage in difficult actions that benefited more people (e.g., killing one person to save many more lives). Although the authors interpreted these findings as demonstrating that right lateral PFC disruption knocked out the ability to integrate emotional information into the decision-making process, these results also fit the notion that the lateral PFC implements self-control to inhibit the automatic emotional reaction to engage the choice that benefits more people (e.g., save more people) but is personally costly (e.g., engage in a difficult behavior to save more people).

15.3.2 Evidence Across the Lifespan

Social decision making, and the ability to restrain selfish choices, appears to develop throughout childhood and adolescence (Garon et al. 2008) in conjunction with a growing regard for others (van den Bos et al. 2011). For example, children increasingly share more over childhood (Benenson et al. 2007), inequity aversion emerges between the ages of 3 and 8 (Fehr et al. 2008), and development shows a general trend from marked selfish behavior to increased perspective taking and relational concern (Steinberg 2009). Recent efforts have begun to unravel the development of self-control behavior by examining the underlying cognitive or neuronal mechanisms.

Steinbeis et al. (2012) examined the development of norm compliance in childhood by examining cortical activity and structure changes associated with offers made in the UG versus the dictator game (DG) in children ranging in ages from 6 to 13. The DG is similar to the UG in that a proposer decides how much money to share with another person. However, in the DG, the other person cannot accept or reject the proposer's offer. Functional and structural scans were acquired to examine both brain activity and anatomical differences associated with increased norm compliance under the threat of punishment (e.g., higher offers in the UG vs. the DG). Results showed that increasing age was associated with both higher offers in the UG versus the DG and greater activity elicited in the lateral PFC when making offers in the UG compared to in the DG. Moreover, this lateral PFC activity was correlated with larger offers under the threat of punishment. Similarly, cortical thickness in the left lateral PFC was also correlated with the same shift to higher offers in the UG compared to the DG. Thus, younger children appeared less able to engage the lateral PFC to implement control over tempting selfish desires under the threat of punishment.

Van den Bos et al. (2011) examined adolescent neural development and trust reciprocation in three different groups chosen based on key developmental stages, a 12–14 group, a 15–17 group, and an 18–22 group. Participants played a modified trust game in the role of a trustee as fMRI was acquired during the game. Participants could return or keep an investment made by an investor under conditions of low or high risk. A high-risk investment thus signaled greater trust in the participant to return the money, a signal that could be reciprocated by returning the investment. Thus, under high risk, self-control was required to override the selfish impulse to keep all of the money in order to reciprocate trust and return the investment. Results showed that participants reciprocated more as age increased. Additionally, among the 18–22 group, right lateral PFC activation predicted increased reciprocity. These findings demonstrate that increasing engagement of the lateral PFC across adolescence is associated with prosocial behavior in social decision making.

As compared to the increase in self-control across childhood and adolescence, in old age there is a general decline in self-control and a decline in PFC function and structure (Dempster 1992). Moreover, there is evidence that reduced self-control in older adults appears to be specifically attributable to changes in lateral PFC functioning (Sharp et al. 2006). In a review article, von Hippel (2007) directly related the reduced self-control that is associated with aging to deficits in social conduct. Older adults, who show deficits in nonsocial self-control, such as inhibiting nonrelevant stimuli to efficiently implement motor or vocal responses, show more overt prejudice against minorities, display increased socially inappropriate behavior, and show poorer regulation of social emotions (von Hippel 2007). Given that previous research has associated self-control decline with the lateral PFC, whether or not these social deficits are specifically due to atrophy in or disruption of the lateral PFC is an intriguing open question in need of future study.

In any case, evidence across the life span generally corroborates the evidence from healthy adults that the lateral PFC is integral in implementing self-control in social decision making. Specifically, the development of the lateral PFC over the life span tracks and predicts the developmental trajectory of self-control in social contexts.

15.4 Neural Traits Explain Individual Differences in Self-Control Capacity

One person struggles with sexual temptations, another person effortlessly resists the same enticement. One person keeps a cool comport under social stress, another is mercurial under the same pressure. One person shows seemingly boundless consideration for other people, another person shows little to no regard for others. People appear to have stark differences in the capacity for self-control across social contexts. But from where do these differences originate? To answer that question, the neural trait approach holds unique promise (Nash and Knoch in press). A neural trait may be defined as a quantifiable brain-based characteristic that is stable over time. In the field of social neuroscience, most studies that have employed the neural trait approach have focused on the characteristics of brain structure, using anatomical MRI, or resting-state brain activity, using electroencephalography (EEG) or fMRI. Generally, the neural trait approach involves indexing task-independent, brain-based differences and examining whether these indices predict behavior or psychological processes of interest. Neural traits can explain how and why people display a remarkable amount of variance in self-control capacity in social choices. The neural trait approach carries with it a further advantage. Because resting EEG and structural MRI can be measured separately from behavioral performance, researchers can then measure behavioral performance in more ecologically valid environments—that is, outside of the MRI scanner or without being hooked up to EEG electrodes.

As such, given that the lateral PFC appears integrally involved in implementing self-control in social decision making, one might expect that neural traits involving the lateral PFC might explain sources of the significant heterogeneity found in costly punishment behavior. Knoch et al. (2010) specifically explored this possibility by using resting-state EEG. Frequency-based measures of resting-state EEG in healthy adults are stable, heritable, and unique to the individual (Dunki et al. 2000; Näpflin et al. 2007). In fact, patterns of baseline cortical activation appear idiosyncratic as they can predict who the individual is at up to a 99% recognition rate (Dunki et al. 2000; Näpflin et al. 2007), suggesting that baseline cortical activation powerfully captures individual differences in characteristic neural function, akin to identifying a "neural fingerprint." In the Knoch et al. (2010) study, participants first had resting-state EEG measured. After that, participants played the role of the responder in the UG. A whole-brain correlational analysis between source-localized baseline EEG activity and costly punishment behavior revealed that the costly punishment behavior was predicted by baseline cortical activation in the right lateral PFC. That is, higher baseline cortical activation in this area predicted higher levels of costly punishment behavior. Moreover, this baseline cortical activation explained approximately 50% of the variance in costly punishment, demonstrating the potential power of the neural trait approach. Thus, based on fMRI and TMS research in which the lateral PFC was integral in implementing self-control to enact costly punishment, these findings are consistent with the idea that resting-state activation in the lateral PFC reflects self-control capacity.

Individual differences in self-control capacity may also be examined by assessing potential genetic contributions (e.g., Boettigger et al. 2007; Kuhnen and Chiao 2009). The *intermediate phenotype model* holds that genes impact behavior through neural mechanisms (Meyer-Lindenberg and Weinberger 2006). To be an effective, brain-based intermediate phenotype, certain criteria have been articulated, such as the characteristics of stability and heritability (Gottesman and Gould 2003; Green et al. 2008; Kanai and Rees 2011). Baseline cortical activation and brain anatomy are both highly stable and heritable in healthy adults, as noted above. Neural traits are thus ideal intermediate phenotypes. As an example, Gianotti et al. (2012) employed the intermediate phenotype approach in examining delay discounting—the degree to which people overlook or "discount" future rewards in favor of smaller, sooner rewards, depending on the amount of delay of the future reward. Delay discounting has direct relevance to self-control and social conduct (Beck and Triplett 2009; Casey et al. 2011; Mischel et al. 2011; Reimers et al. 2009). In this study, participants were genotyped on the COMT Val158Met polymorphism, which has been associated with delay discounting in past research (Boettiger et al. 2007; Paloyelis et al. 2010). Participants also had resting EEG measured and then completed a task in which they made a series of decisions between smaller-sooner rewards and later-larger rewards that differed in magnitude and delay. Results demonstrated that participants with more Val alleles (greater COMT activity and lower dopamine levels in the PFC) exhibited greater delay discounting. This effect was mediated by the baseline cortical activation levels in the lateral PFC: Higher numbers of Val alleles lead to lower baseline activation in the left lateral PFC which, in turn, biases choices toward greater impatience. These findings thus converge with the costly punishment findings to support the idea that dispositional differences in the lateral PFC might reflect differences in a general self-control capacity.

15.5 Connecting Self-Control in Nonsocial and Social Domains

To summarize the above research, it is apparent that across correlational and causal research, at different stages of development, the lateral PFC is consistently involved in implementing self-control in social decision making in a variety of social contexts. Given this, it is reasonable to assume that this brain area is a common mechanism for self-control in social decision making. However, self-control is invoked across a wide range of other, nonsocial, regulatory processes, including motor inhibition, delaying gratification, and inhibiting cognitions or emotions (Heatherton 2011). Further, self-control in one nonsocial domain can impact self-control in subsequent, unrelated domains (Berkman et al. 2011; Muraven and Baumeister 2000). Individual differences in self-control have been shown to be relatively stable throughout the life span and across a variety of situations (Casey et al. 2011) and a range of psychopathological disorders characterized by motor inhibition deficits often co-occur with impulsive social conduct (Aron and Poldrack 2005; Heatherton and Wagner 2011; Robbins et al. 2012).

Together, these studies further suggest that self-control involves a common process across social and nonsocial contexts, a notion buttressed by cutting-edge neuroscience research. Tabibnia et al. (2011), in a research paradigm that used the neural trait approach, specifically examined whether there were common anatomical substrates that could predict performance in motor and affective control using structural MRI. They found that gray matter volume in a region in the right lateral PFC predicted both better inhibitory control and better emotion regulation. Berkman et al. (2009) found neural evidence of self-control "spill-over." In this study, participants completed an emotional Go/NoGo task while brain activity was indexed with fMRI. The Go/NoGo stimuli were faces that were either male or female with positive or negative emotion. Importantly, participants only responded to gender to initiate or inhibit a response. However, inhibiting a response caused unintended reductions in emotion-related brain activity. That is, engaging self-control in a motor control task engaged the right lateral PFC, caused unintended reductions in activation in the amygdala, and increased negative connectivity between these regions. Thus, the degree to which the lateral PFC was engaged during motor control was associated with unintended affect regulation. And in a recent review of the neuroscience literature on self-control, it was concluded that the self-control of motor responses, emotions, desires, and cognitions reliably involve the right lateral PFC (Cohen and Lieberman 2010). In sum, nonsocial and social forms of self-control have been linked to the same brain area. However, evidence for the link between nonsocial and social forms of self-control is unclear.

To explore whether basic self-control processes, such as motor-response inhibition, could predict self-control in a complex social context, Nash et al. (2013) had participants first complete a Go/NoGo task as EEG was recorded. To index motor control processes, two established electrophysiological indices were measured: the NoGo Anteriorization (NGA; Fallgatter and Strik 1999) and peak amplitude of the NoGo-P300. Participants then played a social interaction game in which they promised whether or not they would return money to ostensibly real partners, but were later given the opportunity to break that promise. Recall that a response requires self-control if a prepotent impulse must be inhibited at the decision point (Thaler and Shefrin 1981). The game was designed to ensure that the prepotent response was to follow through with the promise to return money. Thus, the response that required self-control was breaking the promise. Results demonstrated that a larger NGA and larger NoGo-P300 peak amplitudes both predicted more broken promises. This study provides some of the first evidence that connects nonsocial with social forms of self-control.

15.6 Future Opportunities and Challenges

This chapter has explored research that combined neuroscience methods with social interaction paradigms to discern the underlying processes of self-control in social decision making. A noteworthy feature is evident—one that has been noted by several others (Cohen and Lieberman 2010; Frith and Singer 2008; Tabibnia et al. 2008)—in that self-control appears to involve a common mechanism. The lateral PFC is involved in the implementation of both nonsocial and social forms of self-control. In the next section, we consider the opportunities and challenges presented by these and other relevant findings.

15.6.1 Potential Applications

What, then, is the significance of the notion that self-control, in both social and nonsocial domains, appears to involve a common neural substrate? We would suggest that exciting avenues for future research are afforded, particularly if such study draws upon findings from its parent disciplines of neuroscience, behavioral economics, and social psychology. For example, a considerable amount of social psychological research indicates that self-control is limited in some fashion. Self-control can be temporarily disrupted or exhausted through continued use (Lopez et al. 2014, this volume, Chap. 4). Prospective research could explore whether training manipulations that boost basic forms of self-control over the long term (Houben and Jansen 2011; Klingberg 2010) could potentially promote lasting improvements in the regulation of social behavior. Additionally, a number of psychopathological disorders are characterized by chronic self-control problems (Aron and Poldrack 2005). As these disorders are often comorbid with social difficulties (Robbins et al. 2012), this chapter further supports the idea that diminished self-control may produce these social deficits (Heatherton and Wagner 2011). As self-control has been related to specific neural traits, such as baseline cortical activation in the lateral PFC (Knoch et al. 2010; Gianotti et al. 2012), training manipulations of specific neural traits might allow researchers to effect longer-lasting changes to even the most complex of preferences or decision-making behaviors, such as adherence to social norms. For example, techniques such as neurofeedback, meditation, or repeated practice of certain skills have the capacity to increase baseline cortical activation or cortical volume in specific brain regions (e.g., Ghaziri et al. 2013; Lazar et al. 2005; Takeuchi et al. 2010). Using these techniques, enduring neural changes could be made to the lateral PFC structure and function, which could impact self-control capacity. Such findings could improve social conduct and perhaps aid efforts to understand predispositions toward self-control deficits.

15.6.2 Self-Control for Selfish and Prosocial Impulses

The classic example of self-control in social decision making is that of restraining base, selfish instincts to enact prosocial behaviors. An overarching assumption has been that selfish impulses are automatic first reactions, whereas prosocial motives are second, requiring self-control to implement, as demonstrated by the bulk of the research reviewed above. However, certain studies cast doubt on this assumption. For example, one fMRI study demonstrated that accepting, and not rejecting, unfair offers involves the lateral PFC (Tabibnia et al. 2008). Similarly, another fMRI study found that choosing to not cooperate with an untrustworthy partner (a selfish behavior) activates the right lateral PFC (Suzuki et al. 2011). In these studies, the lateral PFC appeared to implement self-control to mute prosocial impulses to enact more egoistic choices. In a recent review of these studies and the broader self-control literature, Zaki and Mitchell (in press) concluded that such divergent evidence suggests that we should explore not only whether prosocial impulses can be prepotent but also the situational factors that shift prosocial/selfish impulses into prepotency.

In line with this recommendation, we would suggest (as others have, see Declerck et al. 2013; Frith and Singer 2008; Zaki and Mitchell in press) that in self-control in social decision making, there is no one impulse that is universally prepotent or “default.” Rather, what determines a person’s prepotent impulse is personality and the environment. Such a view adheres to classic ideas in social and personality psychology (e.g., Lewin 1946) and can parsimoniously reconcile the divergent and sometimes contradictory findings explored above without the need to posit some universal impulse. For example, recall that Knoch et al. (2006) found that right lateral PFC *disruption* caused increased acceptance of unfair offers, whereas Tabibnia et al. (2008) found that right lateral PFC *activation* was associated with increased acceptance of unfair offers. Rather than claim that one study involved self-control and the other did not, one could argue that self-control was differentially employed due to individual or situational differences.

We propose that preferences may determine prepotency. Thus, people who require the most self-control in social decision making are those who have strong preferences that conflict with the more focal goal. Conversely, people will not need self-control to enact a goal that coincides with a strong preference. For example, a person with strong prosocial preferences should not need self-control to act in a prosocial way, whereas a strongly egoistic individual should need self-control to act in a prosocial way. If individual differences in preferences are critical in determining whether self-control is involved in certain social decisions, then effective measurement of such preferences seems equally critical. Examples of measures that may capture selfish and prosocial preferences include measures of social value orientation (Van Lange et al. 1997) and the Honesty–Humility subscale of the HEXACO personality inventory (Ashton and Lee 2007).

Importantly, preferences are not immutable. The contours of the situation can shift and augment personal preferences, even at implicit levels (Bargh and Chartrand 1999). People become more selfish in a competitive environment and more compassionate in a cooperative environment (Bargh et al. 2001). For example, merely displaying images of money or presenting symbols associated with money can make people significantly more egoistic (Vohs et al. 2006). On the other hand, basic representations of facial features elicit more cooperative behavior in the DG (Rigdon et al. 2009). Given this, it is plausible that mere differences in study design, context, or sample could shift the prepotency of a given impulse (e.g., did the instructions emphasize winning/making money or social, cooperative concerns? Is the sample drawn from a hypercompetitive business school or a progressive arts school?). Future research should thus take into account the baseline preferences and situational affordances in order to determine which impulse is prepotent for whom and thereby determine what behaviors require self-control.

Preliminary neuroscience evidence for this view of self-control can be found. Based on our contention that whether self-control is required or not is (partially) determined by individual preferences, one might hypothesize that if an action opposes a dominant preference, regardless of what that preference is, then the individual should require more self-control to engage in that act. Rilling et al. (2007) conducted a study in which brain activity was measured as participants played a trust game. Participants were grouped into high and low scoring on a psychopathy measure. Results showed that those low in psychopathy tended to cooperate, whereas those high in psychopathy tended to defect. Critically, trials were also examined in which participants acted against their preferred tendency. When low psychopathy people defected and when high psychopathy people cooperated, greater lateral PFC activation was elicited. This is consistent with the idea that acting against prepotent impulses, regardless of the impulse type, required increased self-control.

15.6.3 Other Brain Regions

We are careful to note that the lateral PFC is not only involved in self-control and has been related to a number of different processes. Additionally, brain areas do not act in isolation. This should be particularly true in the case of self-control in social decision making because of the presumably complex and abstract processes involved. A neural network should be engaged. Research does suggest additional brain regions. For example, whereas the preponderance of evidence suggests the right lateral PFC is the integral structure in self-control, in some of the studies above, the left was coactive with the right lateral PFC or appeared more involved in self-control than the right (Steinbeis et al. 2012). In addition to the lateral PFC, response-inhibition activation (NoGo vs. Go) has been related to activation in the dorsomedial PFC and the anterior cingulate cortex (Brass and Haggard 2007; Fallgatter et al. 2002; Kuhn et al. 2009).

Future research could examine how modulated brain activity implements changes in a neural network to cause the behavior of interest. The aforementioned Baumgartner et al. (2011) study is a prime demonstration. In this study, it was found that the right lateral PFC and the ventromedial PFC showed increased activation and connectivity after participants received an unfair offer, though TMS over the right lateral PFC disrupted this neural network. Because the ventromedial PFC encodes the value of choice options (Chib et al. 2009), the authors suggested that the right lateral PFC implements self-control by increasing the value of the normative decision to reject unfair offers, which is processed in the ventromedial PFC. These findings demonstrate that the combination of correlational (fMRI) and causal (TMS) neuroscience methods is capable of precisely determining causal neural networks of self-control in social decision making.

Conclusion

Historically, the study of self-control has been most heavily researched in nonsocial domains, including motor-response inhibition, memory and thought suppression, and emotion regulation (Aron and Poldrack 2005; Cohen and Lieberman 2010). Yet, social dilemmas confront us daily and self-control is critically involved in deciding between options that benefit ourselves and options that benefit others. In this chapter, we reported research in which neuroscience methods combined with social interaction paradigms reveal the neural mechanisms of self-control in social contexts. Moreover, it was revealed that self-control in social decision making reliably involves the lateral PFC, the same region involved in a host of other nonsocial forms of control. Such research highlights the potential for making long-lasting changes to lateral PFC structure and function, which could in turn change self-control capacity and help researchers better understand predispositions toward self-control problems in social conduct. Future research can turn to researching how individual differences and situational affordances interact to impact self-control in social decision making.

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Part IV

Self-Regulation of Effort

Mental Effort: Brain and Autonomic Correlates in Health and Disease

16

Eugenia Radulescu, Yoko Nagai and Hugo Critchley

16.1 Overview

Mental effort is an affective experience that encompasses subjective, physiological and behavioural dimensions. This chapter focuses on how mental effort is reflected in regional brain activity, as measured using functional neuroimaging techniques in humans, and how mental effort and regional brain activity is coupled to peripheral autonomic responses. These observations are discussed in the context of conceptualizations of the nature and function of mental effort, and with respect to clinical disorders in which mental effort capacity appears impaired. Particular attention is given to the mental effort deficit in schizophrenia, due to the profound impact of this symptom on the individual's personal and social functioning.

Mental effort can be intentional (self-generated) and/or reactive to external challenges and cognitive demands, and is ultimately directed at enhancing problem-solving and subsequent behavioural performance and related also to the achievability of the intended goal. As with stress, the relationship of mental effort to performance is non-linear. With increasing mental effort, attention is tuned to components of the task. This is accompanied by the recruitment of additional brain regions to those engaged in the absence of effort, putatively to provide extra cognitive capacity and inhibitory control. The increased range of mental resources that are deployed is also supported by changes within task-related, sensory and integrative brain regions and shifts in underlying functional connectivity. Mental effort is also embodied: There are concurrent changes in bodily physiology, i.e. alterations in the level of autonomic arousal that are mediated by cortically driven modulation of subcortical and brainstem homeostatic centres (Critchley 2009). These changes in physiological arousal can facilitate goal-directed cognitive processes and feedback to contribute to feelings state of perceived difficulty, control and achievement. The encoding of these affective experiences can thus motivate and shape future effortful performance.

Disturbances of mental engagement, sustained attention and motivation are common across neurodevelopmental (e.g. attention-deficit hyperactivity disorder (ADHD) and schizophrenia), neurodegenerative (e.g. Parkinson's disease) and psychosomatic conditions (fibromyalgia, chronic fatigue syndrome). Mental fatigue raises the perceived intensity of effort and undermines

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the motivation for, and maintenance of, effortful behaviour. Heightened fatigue is also a symptom of inflammation, pain syndromes and a range of other medical and neurological disorders. There is therefore a clinical need to understand the nature and mechanisms of mental effort, as revealed through cognitive neuroscience, human psychophysiology and neuroimaging. Improving the capacity for mental effort is a target for strategies to optimize intellectual performance across patient groups and in non-clinical populations, where strategies may be geared towards both educational goals. This chapter provides a perspective on the present state of biomedical knowledge about mental effort, and its clinical relevance.

16.2 Conceptualizations of Mental Effort

Mental effort is viewed as a requirement for generating increased information processing capacity (Kahneman 1973). It has been described as a feeling state (rather than an action or emotion) related to the conscious appraisal of one's cognitive and physiological state (Damasio 1999). However, this definition appears impoverished if mental effort contributes actively to goal-directed cognitive processes. Mental effort has correlates in autonomic changes, notably increased cardiovascular sympathetic activity, that can be interpreted as an action-ready bodily state. The magnitude of this sympathetic arousal reflects both the feeling of effort and likelihood of goal attainment (e.g. Richter et al. 2008).

In some definitions of mental effort, a distinction is drawn between the reactive task-driven engagement of cognitive resources (i.e. passive effort) and the active intentional mobilization of attentional and cognitive resources linked to volition. Correspondingly, the neural correlates of this distinction have been explored (Mulert et al. 2008). Effort mobilization can be viewed as an investment of energy towards a better performance (goal success). Hence, effort is driven by motivation intensity in a way that is closely coupled to metabolic regulation (Fairclough and Houston 2004). The control and selection of attention is a core feature in this mobilization and can be engaged by perceptual novelty or context unfamiliarity as a top-down cognitive perceptual set (Hars et al. 2011).

Anatomical and functional neural correlates of mental effort are currently explored with neuroimaging techniques, especially functional magnetic resonance imaging. So far, neuroimaging studies have attempted to dissociate brain processes supporting mental effort from those engaged in information processing. Thus, during enhanced working memory load, increases in the neural activity within lateral ventral-prefrontal cortex and decreases in activity within ventral anterior cingulate are associated with the extra mental demand and effort. In contrast, regions of dorsolateral prefrontal and dorsal anterior cingulate cortices appear to be more sensitive to the informational content of the stimuli (Jansma et al. 2007). Moreover, the investment of mental effort, particularly when expressed in the form of volitional increases in attentional concentration, depends on knowledge regarding the target outcome: Here, the motivational value of an outcome is proposed to take into account (i.e. deducts) the amount of effort invested and the exertion associated with attaining that outcome. Correspondingly, brain activity within the dorsal anterior cingulate cortex and dorsal striatum anticipates the effort, while ventral striatal regions reflect the final computed value (Botvinick et al. 2009; Kurniawan et al. 2013).

Objective measures of effort can be derived from the engagement of autonomic arousal responses, notably pupillary dilatation, blood pressure or the cardiac pre-ejection period (Kahneman et al. 1969; Mulder 1986; Richter et al. 2008). One theory designed to explain the way in which mental effort is engaged is the 'motivational intensity theory' which encapsulates the notion that effort is mobilised proportionally to subjective task difficulty when success is possible (Brehm and Self 1989; Wright and Kirby 2001). Evidence for this effect is apparent when measuring physiological correlates of effort in cardiovascular reactivity (changes in pre-ejection period and blood pressure governed by the sympathetic nervous system) which suggest that energy mobilization and active coping is expressed through beta-adrenergic effects on heart (Richter et al. 2008). These theories and observations also endorse the notion of mental effort as an affective process with experiential, behavioural and physiological dimensions tied to value judgments and reward seeking. Within this context, it is noteworthy that both mood state and affective primes impact on level of perceived effort intensity (Gendolla and Silvestrini 2011; Silvestrini and Gendolla 2011) in a manner that is also related to the degree of cardiovascular response. Sadness states or implicit processing of sad stimuli diminish the capacity for mental effort, in contrast to anger or happiness primes (Brinkmann et al. 2009; Freydefont et al. 2012). With the advent and maturation of functional neuroimaging in humans, attention has been drawn to the neural substrates that underlie the different dimensions of mental effort and how these potentially inform our understanding of the mechanisms that facilitate the mobilization of extra cognitive resources.

16.3 Mental Effort and Regional Brain Activity

Functional neuroimaging studies in humans, as applied to cognitive and affective processes, extend the knowledge about the working anatomy of the human brain gained from clinical neurological observations and animal studies. Early studies (e.g. using Xenon clearance x-ray) provided evidence in humans for the coupling of mental effort to changes in regional cerebral blood flow (Ingvar and Risberg 1967). In healthy participants and in patients with discreet brain lesions, ‘suprasylvian’ frontoparietal (rather than temporal lobe) regions were more active when participants performed a difficult backward digit span (working memory) task. It was noted that task performance itself did not predict the individual differences in the magnitude of the regional blood flow change. Hence, the authors’ postulated that objective effort, and its impact on arousal levels, provided a better account of this activation pattern. Subsequent positron emission tomography (PET) methods using radio-labelled water to quantify changes in regional blood flow evoked by local neural activity provided a means of relating thoughts, feelings and perceptions to the dynamic processes within the living human brain. It became apparent that the same brain regions were consistently emerging as being activated by task performance across a variety of studies, notably the dorsal anterior mid-cingulate cortex. A review of 107 PET blood flow studies (Paus et al. 1998) highlighted this observation, and interpreted anterior mid-cingulate cortex activity as a signature of task difficulty: At that time, functional neuroimaging experiments generally used a standard ‘subtraction’ design that compared performance of an active task with a typically less-demanding control task (which lacked the component process of interest) to identify the extra activity associated with the target process. However, the intended specificity of the experimental subtraction design is confounded to a degree by non-specific aspects of cognitive demand and accompanying engagement of arousal and attentional resources. Thus, the procedure also identifies regions generally associated with resource allocation during the more demanding cognitive task. Activity in anterior mid-cingulate cortex reflects these demands on cognitive resources. Dorsal anterior cingulate activity was also implicated as the critical hub of a midline attentional system, and as the neural substrate for a range of executive functions including response-selection, error-monitoring and the initiation of behavioural corrections (Bush et al. 2000; Carter et al. 1999). This broad supragenual cingulate region extends rostrally to include cortex above and around the cingulate sulcus into medial prefrontal/paracingulate cortex (implicated in mentalization and representing thoughts of others), and caudally into motor regions (pre-supplementary motor area). Surprisingly, the neuropsychometric impact of lesions to this broad swath of cortex appears more constrained than might first be suggested by a large set of related studies implicating this region in a range of ‘core’ (executive and attentional) cognitive processes. A number of accounts suggest why this may be the case, including that the region is more closely involved in coordinating the bodily response to cognitive processes than primarily supporting the same cognitive processes themselves (Critchley et al. 2003).

While the dorsal anterior mid-cingulate cortex is implicated in cognitive and executive processes, a distinction was made with respect to pregenual and perigenual cingulate regions, which are more directly implicated in affective processing (Bush et al. 2000). The evidence came in part from neuroimaging of emotional Stroop tasks, in which the salience of emotional stimuli provides a competing demand on cognitive resources. Most inferiorly, ventromedial prefrontal cortex and subgenual cingulate appear to have an even greater association with affective processing and the representation and learning of reward and valence (Critchley 2004; Grabenhorst and Rolls 2011). An important observation was that the metabolic and functional activity within these ventral regions is often greater when participants were disengaged from effortful cognitive or behaviourally engaging tasks. The same is true of the posterior cingulate cortex. The term 'default mode network' was proposed to encompass this set of regions where activity is 'switched-off' by goal-directed cognitive processing associated with mental effort (Gusnard and Raichle 2001; Raichle et al. 2001).

Mental fatigue can be considered as the brain signal of increasing difficulty in sustaining demanding cognitive functions. However, this symptom has a more complex relationship with mental effort: The experience of mental fatigue undermines the ability to sustain task- and goal-directed cognitive processes and action; yet in such circumstances, mental effort is evoked and increased to maintain performance. Decreased fronto-parietal cortical activity is associated with fatigue-induced performance deficits on divided attention tasks. Increased task demand during fatigue putatively increases the level of compensatory mental effort, an effect that is associated with deactivation of midbrain centres (Nakagawa et al. 2013). This may indicate that effort is associated with the active suppression of a 'negative feedback system that normally triggers recuperative rest'. This suggestion highlights both a role for midbrain in the representation of fatigue and the expression of effort, through action-ready physiological states that plausibly mediate cancellation of fatigue signals.

Together, the above neuroimaging studies highlight the engagement of fronto-parietal cortices with increased cognitive demand, alongside anterior cingulate regions (anatomically coupled to subcortical centres) whose function appears to relate to non-specific, task-independent aspects of effort from low-level representation (and bodily engagement—see below) to high-level computations of goal attainability and metabolic costs. This understanding of neural substrates of effort also suggests an interface at the midbrain level between the representation and suppression of effort. Nevertheless, this modular view of information flow within the brain is complemented by alternative models of integrated and distributed brain processes.

16.4 Brain Networks in Mental Effort

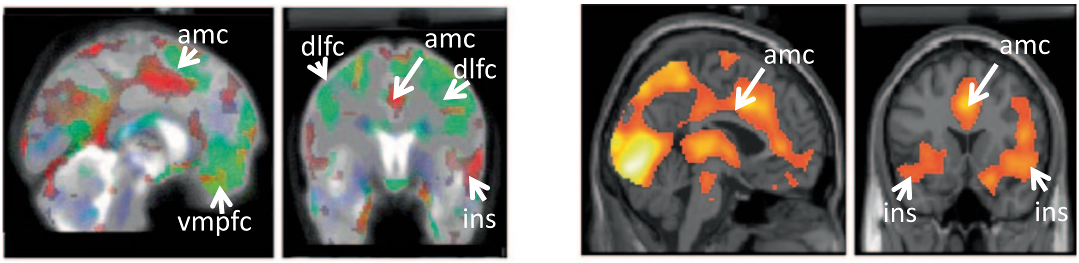
Increasingly, the understanding of brain processes is being framed within the context of large-scale brain networks identified through synchronised activity. Such networks are apparent as replicable patterns of regional brain activity driven by cognitive work and experimental tasks, but they are also manifest as predictable fluctuations in the correlated activity of anatomically separate regions in the absence of specific tasks (e.g. Bressler and Menon 2010; Greicius et al. 2003). Three major networks are associated with particular types of cognition (rather than sensory processing): (1) the default mode network (Greicius et al. 2003; involving ventromedial prefrontal and posterior cingulate regions) is more active at rest when an individual is not engaged in externally directed cognitive work. In addition, it is associated with sleep, self-referential cognitive processes and parasympathetic/antisympathetic (diminished) states of physiological arousal. (2) The salience network is associated with attentional orienting, affective arousal and goal-directed action and comprises regions including (anterior and mid) insula, dorsal anterior mid-cingulate cortices and also includes amygdala and hypothalamus (Seeley et al. 2007). As noted below, the salience network appears strongly coupled to the generation (medial visceromotor anterior cingulate cortex) and representation (insular cortex) of states of visceral arousal, particularly those mediated by enhanced sympathetic drive and shifts in sympathetic/parasympathetic balance. (3) The central executive network principally involves dorsolateral prefrontal cortex and posterior lateral parietal cortex. It is implicated in higher-order cognitive and attentional control, drawing on abstracted working memory, temporal and spatial representations (Seeley et al. 2007).

There is functional and structural overlap across the three networks: The anterior insular cortex is implicated in dynamic interaction and shifts between these networks (Sridharan et al. 2008). Together, these networks are likely to support not only performance of high-demand cognitive tasks but also the accompanying physiological expression of these in peripheral autonomic response. In addition, a 'directed effort network' has been postulated and encompasses the dorsal anterior cingulate cortex, posterior cingulate cortex, auditory cortex and hippocampus (Williamson and Allman 2012). At present, there is a need for empirical evidence to support this proposal, which was motivated by an attempt to relate structural neuroanatomical findings to certain negative symptoms experienced by patients with schizophrenia.

16.5 Neural Substrates of Physiological Arousal During Mental Effort

The coupling of mental processes to physiological arousal states is well recognised within psychophysiology (e.g. Kahneman et al. 1969). The physiological arousal associated with both responses to task demand and the application of mental effort is expressed typically as sympathetic enhancement and parasympathetic withdrawal. Within the cardiovascular system, there is suppression of the baroreflex such that heart rate and blood pressure rise together (e.g. Gianaros et al. 2012). Parasympathetic withdrawal contributes to cardiac acceleration. Changes in sympathetic/parasympathetic balance are also manifest across different organ systems (e.g. electrodermal response, pupillary dilatation, increased blood flow to limb muscles, patterned changes in skin perfusion and alteration of gastrointestinal motility, secretion and perfusion; Cacioppo et al. 2007).

Neuroimaging studies of evoked autonomic arousal largely implicate dorsal anterior cingulate cortex and bilateral insula cortices alongside (more variably) subcortical structures notably amygdala and dorsal brainstem. In a 'water-PET' study, healthy young participants performed easy and effortful versions of a cognitive task (mental arithmetic) and an exercise task (isometric handgrip; Critchley et al. 2000). Heart rate and blood pressure responses were recorded; analyses focused on identifying brain regions where activity correlated with these physiological measures during both mental and physical tasks. Thus, irrespective of task modality, activity, in particular within right anterior cingulate cortex, correlated with effort-evoked blood pressure increases. Extension of this study approach to a clinical 'lesion-deficit model' (patients with peripheral autonomic failure; Critchley et al. 2001) and to the measurement of heart rate variability in functional magnetic resonance imaging (Critchley et al. 2003) reinforced a notion that the dorsal cingulate cortex was involved in the generation of cardiac autonomic arousal during volitional effort (Fig. 16.1a). Correspondingly, perturbations in autonomic arousal during mental effort were observed in three patients with dorsal cingulate lesions (Critchley et al. 2003). These studies also fitted with a general notion of the anterior cingulate as visceromotor cortex (contrasting with the notion of insula as viscerosensory cortex) for which there is now a corpus of supporting neuroimaging and clinical evidence in humans (Critchley 2009). Nevertheless, a conjoint activation of dorsal anterior cingulate and insula cortex is observed in situations of mental effort and task engagement associated with (autonomic) bodily arousal, during the processing of motivationally important environmental (exteroceptive) stimuli

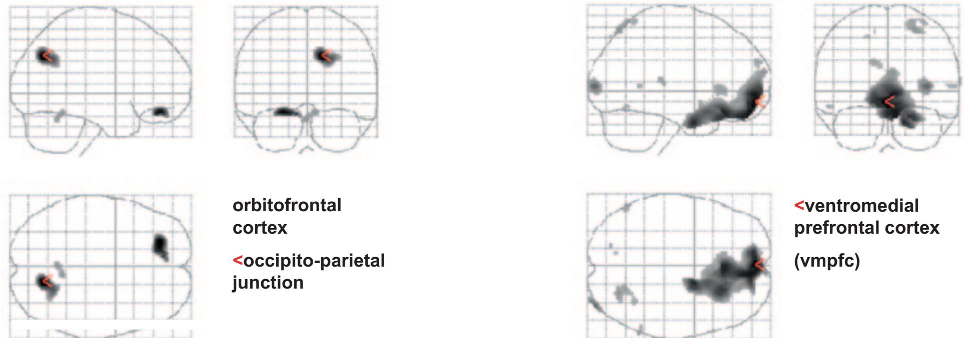


Activity related to autonomic influences on heart (red), effortful working memory (green), and exercise (blue)

a

Activity positively related to transient sympathetic electrodermal responses during biofeedback tasks

b



Activity related to achieving goals on arousal & relaxation biofeedback tasks

c

Activity negatively related to tonic sympathetic electrodermal level

d

Fig. 16.1 Brain correlates of effort and autonomic arousal. New figures (copyright of authors). (**a** Regional brain activity during performance of high and low effort mental work (shown as *green*-coloured voxels, working memory n-back task), isometric handgrip exercise at different brief time durations (*blue*) and associated with changes in heart rate variability (*red*). The figure is derived from the data reported in Critchley et al. (2003). F-tests were used to show significant changes corresponding to both increases and decreases in activity associated with high vs. low effortful performance of the interleaved tasks and increases and decreases in heart rate variability, subsequent analyses associated the anterior mid-cingulate (amc) and insula (ins) activity particularly with low-frequency heart rate variability (linked to sympathetic arousal) and ventromedial prefrontal activity (vmpfc) with increasing high-frequency (parasympathetic) change. The mental effort that generated these bodily responses was associated with enhanced activity within dorsolateral prefrontal (dlpfc) and parietal cortices (central executive/attentional network) with vmpfc decreases). Group statistical (F-value) data are presented on parasagittal and coronal slices of normalized template brain. **b** Brain activity associated with transient changes in electrodermal sympathetic arousal during performance of biofeedback arousal and relaxation tasks. Figure derived from Nagai et al. (2004). Sympathetic transients in these tasks represent deviations from the task goal and arguably a failure in sustained attention and the effortful biofeedback. This pattern of cingulate (amc) bilateral insula (ins) with thalamus and dorsal brainstem is consistent with activity within a central autonomic network also engaged by effortful mental effort. These data suggest the same system is employed in short-term orienting responses and the dynamic embodiment of fluctuations in task performance during tasks that require sustained attention. Group statistical (t-value) data are presented on parasagittal and coronal slices of a normalized template brain. **c** Data also from the Nagai et al. (2004) biofeedback arousal/relaxation study. In this study the same task, and equivalent demands on cognitive resources are coupled with opposite arousal states. The goal of the biofeedback arousal task is to increase sympathetic electrodermal tone in contrast to the relaxation biofeedback task (to decrease sympathetic electrodermal tone). When participants achieved success in either of these tasks, there is activity enhancement in mid-orbitofrontal cortex and occipitoparietal cortex (indicated on sagittal, coronal and axial 'glass brain' projections of suprathreshold group activity). **d** Figure representing data presented in the Nagai et al. (2004) biofeedback arousal/relaxation study. Decreases in sympathetic electrodermal tone were associated, independent of task, with enhanced activity within ventromedial prefrontal cortex, extending to contiguous regions of subgenual cingulate and orbital and polar cortex (indicated on sagittal, coronal and axial 'glass brain' projections of suprathreshold group activity) and in situations of reactive processing of pain or visceral (interoceptive) stimulation. In each of these situations, there is enhanced interchange between mental and visceral state (Medford and Critchley 2010).

Ventromedial prefrontal and subgenual cingulate cortices appear to have an inverse relationship with sympathetic cardiovascular arousal: activity within these regions is inversely correlated with electrodermal sympathetic tone (Nagai et al. 2004) and is positively correlated with heart rate variability measures of parasympathetic influences on the cardiovascular system (e.g. Matthews et al. 2004). During a 'social evaluative stress' task, increases in heart rate were evoked when participants were told to prepare a difficult speech that would be rated later by others (Wager et al. 2009). The effort and emotional stress associated with speech preparation was 'translated' into increased heart rate through increases in activity of dorsal cingulate cortex and decreases in activity of ventromedial prefrontal cortex (via thalamus and dorsal brainstem). Thus, task-evoked autonomic arousal is evidently mediated by two complementary systems, engagement of dorsal anterior mid-cingulate systems, plausibly driving sympathetic effects and withdrawal/disengagement of a ventromedial prefrontal system linked to withdrawal of the parasympathetic brake on heart rate (Critchley et al. 2011).

With increasing emphasis on network interactions within the brain, there is a noteworthy correspondence between the dorsal anterior mid-cingulate/insula activation associated with increasing autonomic arousal and what is termed the 'salience network' implicated in processing motivationally salient stimuli (Seeley et al. 2007). Correspondence is also observed between the ventromedial prefrontal cortex as an antisympathetic/parasympathetic hub and its role within the default mode network (Gusnard and Raichle 2001; Nagai et al. 2004). One conclusion is that both mental effort and emotional challenge evoke changes in bodily response through these two systems. However, the majority of neuroimaging studies described above assume that performance reflects effort, or that a manipulation of task demand evokes parametric changes in mental effort. Few studies have actually measured effort directly, and in fact even the titrating of task demand to performance measures has been variable across studies. The work of Gianaros and colleagues is an exception to this: By using adaptations of the (high cognitive demand) colour-word Stroop task and a multi-source interference task, the neural and autonomic responses of individual participants could be compared at equivalent levels of performance (e.g. Gianaros et al. 2009; Sheu et al. 2012). A series of studies undertaken by this team examined how individual differences in autonomic reactivity predict future cardiovascular disease. It is noteworthy that the degree of engagement of the dorsal anterior cingulate cortex and insula cortex (i.e. activity changes within these regions), and even resting state activity within these regions, predicted the autonomic reactivity (e.g. systolic blood pressure) rise evoked by performing effortful mental stress tasks (Gianaros et al. 2009; Sheu et al. 2012).

A similar approach was taken with a focus on neural mechanisms underlying suppression of the baroreflex. Normally, via the baroreflex, an increase in blood pressure evokes a decrease in heart rate. This effect is achieved by a well-defined set of interactions between the afferent neural information from stretch receptors in the great vessels (the baroreceptors) and, via medullary circuits, heightened vagus parasympathetic effect on heart. Suppression of this reflex occurs with effort and stress and can be measured from the dynamic relationship between beat-to-beat blood pressure and interbeat interval: During the difficult multisource interference task, baroreflex suppression was associated with the influence of pregenual anterior cingulate and amygdala on insula cortex (Gianaros et al. 2012). This observation, while constrained by the temporal resolution of functional neuroimaging (and limitations of undertaking the imaging separately from the physiological assessment), nevertheless suggests active interaction between cortical generators of autonomic response and areas involved in the sensory representation of the bodily arousal, such as insula (Critchley et al. 2003, 2004). Interaction between the processing of salient stimuli and the afferent feedback of internal visceral state is observed in many contexts (Medford and Critchley 2010): Experimentally, this can reach a level of detail such that neural processing of pain and autonomic reactions to pain (electrocutaneous shock) or emotional faces can be shown to depend not only on expectation but also on the afferent feedback from individual heartbeats (Gray et al. 2009, 2010, 2012).

Although a number of researchers highlight the coupling of a particular cardiovascular response (pre-ejection period) to mental effort (e.g. Richter et al. 2008), there have been very few attempts to examine the brain correlates of this specific autonomically mediated change. One study that came close to achieving this examined reactive threat processing (rather than mental effort) and used cardiac magnetic resonance imaging to measure the contractility of the heart during in a threat-processing task that was then repeated during functional brain imaging (Dalton et al. 2005). Activity within regions of amygdala, middle frontal cortex and insula showed a dependent relationship to the responses of the heart during threat, suggesting dynamic coupling of affective and physiological processes through these brain regions.

The central mapping of internal bodily state in insular cortex and related interoceptive centres (including amygdala) is implicated in the generation of affective feeling states. The bodily origin of emotions, formalised by James (1894) and Lange (1885) originates in Aristotelian thoughts (Gross 1995). Feeling states, or at least the arousal/intensity components of emotions, are argued to arise from the integration of information from the body with concurrent perceptions and cognitions. The notion of attributed arousal is important since it suggests that if a non-emotional source of the bodily arousal is recognised, then the affective impact of the arousal state is diminished (Barrett 2006; Cantril and Hunt 1932; Schachter and Singer 1962). On the other hand, states of anxiety might arise from unexpected arousal, and/or the heightened subjective perception of minor changes in bodily state. Both increase 'interoceptive prediction error signalling'. Predictive coding models view the brain as a 'Bayesian machine' that makes continuous predictions regarding the sources of sensory data (e.g. Friston and Kiebel 2009). When applied to internal states of bodily arousal, predictions regarding the state of the body interact with afferent viscerosensory information give rise to feeling states that include anxiety, risk, empathy and perceived mental effort and fatigue. Layers of such top-down and feedback interactions can plausibly account for both basic and higher-order emotions and also for more fundamental feeling states such as the sense of presence, agency and selfhood (Seth and Critchley 2013; Seth et al. 2011; Singer et al. 2009; see Fig. 16.2).

16.6 Arousal, Attentional Capacity and Resource Allocation

As alluded to in the previous section, mental effort is associated with on-task attention. This observation was theoretically and empirically elaborated by Kahneman (Kahneman 1973). Sustaining attention on a task is effortful (Warm et al. 2008) and requires the suppression of orienting responses to external stimuli and of internal tendencies towards mind-wandering. As noted above, such cognitive effort is accompanied by disengagement of the default mode network (associated with off-task effortless thinking including mind-wandering; Gruberger et al. 2011; Gusnard and Raichle 2001) and engagement of lateral frontal and parietal regions implicated within the 'dorsal attentional network' (which overlaps considerably with the executive network; Seeley et al. 2007; Sridharan et al. 2008). Sustained attention is however subject to momentary fluctuations which reflect interaction between these networks (Esterman et al. 2012) and the temporal relationship between the allocation of cognitive resources and task performance. Attentional effort can be dissociated from other aspects of task demands: Arousal can reflect the cognitive processing demands of the task, and such that fluctuations in arousal level follow within-task variation in cognitive demands. Objective measures of arousal such as pupillary dilatation

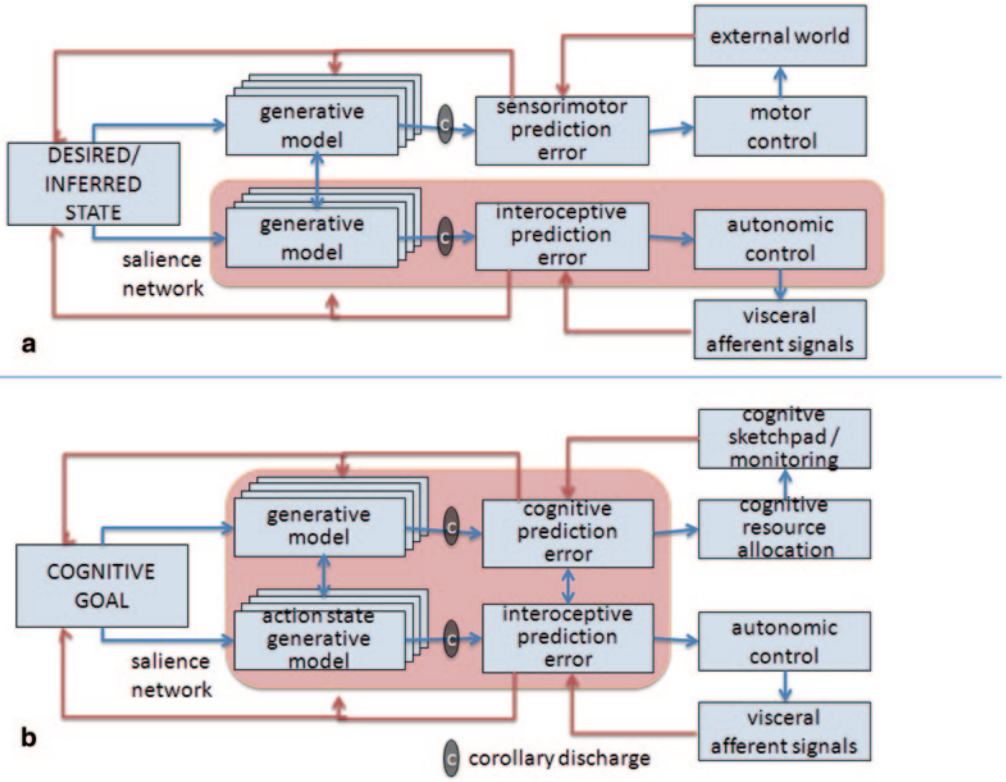


Fig. 16.2 Predictive coding model of effort as feeling state. (Figure adapted from Seth (2013) with permission from the author. The notion of predictive coding and active inference is extended from sensory motor literature to include the notion of interoceptive predictive coding. Generative models in the motor or central autonomic nervous system are tested against afferent information, leaning to prediction errors that drive learning. The representation of these efference models and predictive mismatch is proposed to underlie feelings of agency and control upon which selfhood is based. Moreover, specifically to interoceptive predictive coding, the hierarchy of generative models and predictions errors within homeostatic and allostatic regulation give rise to emotional feelings. This model, which is convergent with recent understanding of physical effort, arguably can be extended to mental effort. Generative models underpinned by motivation investment are expressed in bodily arousal states and feelings derived from motivation-related changes in internal arousal which add to the currency available to judge effort investment against goal attainment (extension of Seth (2013) model))

are also proposed to reflect mental effort allocation (e.g. Takeuchi et al. 2011). At the same time, pupillary arousal responses are also linked to aspects of self-monitoring and error detection that represent the momentary allocation of attentional resources. These occur at a different timescale to the immediate sensory processing and motor requirements of behavioural performance. Here, a link to salience and emotion is also suggested by the engagement of the same regions of dorsal cingulate cortex in association with both pupillary measures of arousal and the monitoring of behavioural errors (Critchley et al. 2005).

In this context, the performance of autonomic biofeedback tasks is of interest. Whereas equivalent attentional and motivational demands can be contrasted in different states of bodily arousal, Nagai and colleagues (Nagai et al. 2004) scanned healthy participants performing electrodermal biofeedback tasks to increase, and to decrease, their level of skin sympathetic tone, facilitated by direct visual feedback. The tasks themselves were broadly of equal cognitive demand, but distinct in the direction of sympathetic arousal state. This study observed dissociation between neural correlates of short-term 'momentary' fluctuations in autonomic arousal and tonic changes in sympathetic tone: The short-term changes typically reflected transient electrodermal arousal responses. Moreover, these transients confounded task performance; particularly in the relaxation condition (i.e. intended decreased electrodermal tone). Here, activity within dorsal anterior mid-cingulate, insula, thalamus and dorsal brainstem indicated the engagement of the salience, visceromotor-interoceptive, network. Also there were increases within dorsolateral prefrontal, parietal and early visual cortices, highlighting the engagement of the dorsal attentional network during these transient variations in task-coupled autonomic state (Fig. 16.1b). In contrast, the ventromedial prefrontal cortex extending to the medial orbitofrontal and subgenual cingulate regions demonstrated an inverse relationship with tonic level of sympathetic electrodermal arousal, irrespective of whether the participant was performing arousal or relaxation biofeedback (Fig. 16.1c, d). This was interpreted as an indication of the strong coupling of ventromedial prefrontal cortex (and the default mode network) to physiological arousal. Interestingly, mid-orbitofrontal cortex predicted task success irrespective of the nature of the task. The findings suggest a difference between reactive and active cognitive control.

The notion of effortless control has been proposed as a contrast to executive attention, the latter evoking the typical sympathetic autonomic arousal and conscious feeling of effort associated with demanding tasks (Naccache et al. 2005). However, patients with anterior cingulate damage can maintain executive task performance in the absence of subjective effort and sympathetic arousal, suggesting a basic dissociation of the embodied effort and associated feeling states from these immediate executive processes. Furthermore, motivation is an important consideration here: reward-based motivation may set up particular attentional sets associated with embodied effort. Time pressure also contributes to this motivational state. During a neuroimaging study of motivational decision-making, perceived time pressure influenced the processing speed for risky decisions and associated autonomic arousal. These interactions were reflected by changes in the neural activity of insula and ventral striatum (Jones et al. 2011).

16.7 Disturbances in Mental Effort

Insight into the processes underlying mental effort may be gained from observing clinical disorders in which mental effort is compromised. When considering clinical deficits in the mobilization of mental effort, the concept of *abulia* is particularly relevant. *Abulia* describes a decrease in motivational drive, associated with passivity and a failure to initiate action. This represents a failure in self-initiated action and drive and hence can be distinguished from apathy where there is indifference to behavioural challenge and a (potentially selective) failure to engage with external stimuli. Nevertheless, both *abulia* and apathy share impaired motivational behaviour, plausibly representing a failure to translate incentive into action. Lesions of striatum and prefrontal cortex are associated with both abulia and apathy, implicating reward incentive representation and working memory reserve to the application of goal oriented mental effort (Ghoshal et al. 2011).

Likewise, negative mood and clinical depression compromise the mobilization of mental effort through a discrete set of mechanisms. Abnormalities in ventromedial prefrontal and subgenual cingulate cortical activity are associated with rumination (Cooney et al. 2010), anhedonia (Keedwell et al. 2005), unipolar depression (Drevets 2007) and sickness behaviours (Harrison et al. 2009a). These observations suggest that disengagement of default mode network regions compromise the capacity for cognitive work and the effective mobilization of attentional and cognitive resources. There is also an accompanying decreased motivation and apathy to incentives. Attenuated cardiovascular responses to rewarding stimuli are observable in dysphoric individuals, indicating deficits in effort mobilization (Brinkmann et al. 2009).

On the other hand, patients with diffuse traumatic brain injury report much higher subjective mental effort than controls when performing high-demand dual tasks associated with divided attention (Azouvi et al. 2004). This effect was related to fatigue, and effort correlated poorly with task performance. Fatigue can be described as a 'failure to initiate and/or sustain attentional tasks and physical activities requiring self motivation' (Chaudhuri and Behan 2000). Fatigue is arguably a signal 'of necessary rest' (Nakagawa et al. 2013) and has an indirect relationship to effort. Mental fatigue is a feeling state, associated with impaired maintenance of performance and a reduced capacity to initiate subsequent effortful mental behaviours. It affects sustained attention, concentration, sequential cognitive tasks (e.g. puzzles or mathematics) and executive processes such as planning. The core feeling of mental fatigue is an amplified sense of effort (consistent with the notion of mental effort as a perceptual rather than action state; Damasio 1999). Fatigue is often accompanied by a constellation of other feelings including tiredness, sensory sensitivity, mental heaviness and 'brain fog'. Mental fatigue compromises cognitive performance at much lower demand levels than one might expect. However, some cognitive functions, e.g. memory recollection, are perhaps less affected than others. Neuroimaging studies of cognitive fatigue indicate the hyperactivation and enhanced recruitment of brain areas, indirectly suggesting inefficient information processing. This usually increases over the course of an effortful task (Chaudhuri and Behan 2000). Brain regions implicated in cognitive fatigue encompass executive centres such as dorsolateral and superior parietal cortices and, notably, both the dorsal anterior mid-cingulate cortex and neostriatum. It has been proposed that the physiological changes associated with mental effort are the cause of cognitive fatigue, which by extension may be an active coping response (Kohl et al. 2009). Mental fatigue is also prominent among a set of 'sickness symptoms' that can be evoked by peripheral inflammation and accompanies a range of rheumatological and neurological conditions. Clinical depression and chronic fatigue syndrome also share this symptom. Experimental models of sickness argue for a cortical basis to mental fatigue symptoms within anterior cingulate and insular cortices (Harrison et al. 2009b). However, behavioural manifestations such as psychomotor retardation are more directly linked to changes in the substantia nigra (Brydon et al. 2008). Interestingly, focal damage to basal ganglia can engender heightened mental fatigability, and thus the striatum is implicated in the 'central fatigue' that arises in the context of multiple sclerosis and Parkinson's disease (Chaudhuri and Behan 2000).

A different clinical expression of disordered mental effort is observed in the context of ADHD. This is a neurodevelopmental condition associated with distractibility, impulsivity and behavioural hyperactivity. One symptomatic feature of the condition is impaired inhibitory control (e.g. Gaultney et al. 1999) and the capacity to engage in tasks and activities that require delayed gratification, sustained attention or repetitive action. While fatigability is seen, it is commonly overshadowed by difficulties in applying 'top-down' voluntary mental effort. Autonomic correlates of ADHD are often attributable to responses associated with motor hyperactivity. However, there is also increasing evidence of a failure to generate states of sympathetic autonomic arousal, though heart rate increases can be brought about by withdrawal of parasympathetic tone (Crowell et al. 2006). The most reliably effective pharmacological treatments of ADHD are stimulant drugs (methylphenidate and amfetamines). These act on central noradrenergic and dopaminergic pathways and indicate a role of central monoamine action in supporting mental alertness and arguably mental effort. Stimulant medicines can normalize the attenuated sympathetic tone of ADHD patients (Negrao et al. 2011). Neuroimaging studies of ADHD suggest abnormalities in the engagement of the striatum, and prefrontal and parietal cortices, at rest and during employment of inhibitory control (Cubillo et al. 2010; Di Martino et al. 2013). These neuroimaging findings fit with putative involvement of motivational, executive and attentional brain systems underlying to the effortful mobilization of attentional and cognitive resources.

16.8 Mental Effort and the Negative Syndrome in Schizophrenia

Schizophrenia is one of a set of mental disorders that manifest a marked impairment in mobilizing and sustaining goal-oriented mental effort. This is particularly the case with the 'deficit' subtype of schizophrenia (with 'negative syndrome') which is characterised by a severe lack of cognitive resource allocation towards purposeful activities. Like ADHD, schizophrenia is a disorder arising from aberrant development of cognitive perceptual and motivational neural systems. Cognitive and behavioural deficits in schizophrenia include well-documented impairments in mental effort. These are among the core features of the 'negative syndrome', which refers to a collection of symptoms that including affective flattening, alogia, attentional deficit, avolition, *abulia,* apathy, anhedonia and asociality. The individual contribution of each negative symptom to the expression of deficits in mental effort is not clear. Neuropsychological studies show that schizophrenic patients with higher levels of negative symptoms manifest reduced performance of effortful tests (e.g. Word Memory Test) compared to controls and other psychiatric patients (Gorissen et al. 2005). Alternative explanations for the lack of mental effort mobilization are through the concurrent deficits in the motivation system or in executive function (including a failure in performance monitoring). The effect of reduced effort allocation is also an important consideration in neuropsychometric studies of schizophrenia. To address this, van Beilen and colleagues (van Beilen et al. 2005) developed the Cognitive Effort Test, which includes the measurement of effort voluntarily invested in the task execution. Intriguingly, the results of this test suggest deficits in 'planning' and 'workload' in schizophrenic individuals compared to controls. Surprisingly, these did not appear strongly related to negative symptoms, which indicated a complex non-linear relationship between negative symptoms and mental effort deficit. In addition, this study highlights the importance of evaluating and correcting for the reduced effort during task performance in schizophrenia.

One model of mental effort, the 'resource limitations vulnerability model' (Nuechterlein 1987) links the reduced availability of processing resources to deficits in early sensory information processing. Such a conjunction is documented in schizophrenic patients and correlated with the severity of negative symptoms (Butler et al. 2008). In the latter study, it was shown that effort-related autonomic arousal (measured by pupil dilation) increased with cognitive load in both schizophrenic patients and controls. Patients nevertheless showed performance deficits in early visual information processing, and a subgroup of patients with poor pupil reactivity exhibited more severe negative symptoms. These findings partially support the proposed 'resource limitation vulnerability' model (Granholm et al. 2007). In fact, this relationship between negative symptoms and (correlates of) mental effort consistently leads to the question whether performance deficits reflect primary cognitive deficits (intrinsic to the negative syndrome) or an inefficient engagement and allocation of resources.

Another avenue for studying the relationship between mental effort and schizophrenia is represented by the studies of decision-making. These suggest a pattern of impaired decision-making by patients with negative symptoms, which appears to represent an abnormality in effort–cost calculations when deciding between different response options (Gold et al. 2013). Patients with higher negative symptoms are biased towards attributing low values to rewarding cues, yet this also suggests a deficit in motivation where increased effort is perceived as more aversive. Correspondingly, effort–cost abnormalities correlate with the total score of negative symptoms, rather than just with avolition and apathy, suggesting that performance deficits arise from concurrent abnormalities within hedonic, affective, top-down attentional control systems which may share a common dependence on motivational drive (Gold et al. 2013). This more general affective model can account for the observed correlation in schizophrenic patients between effort–cost computations within the task and reduced emotional expressiveness.

A potential confound in interpreting the presence and impact of mental effort deficits in patients with schizophrenia and prominent negative symptoms is the presence of comorbid depression. Depressive mood symptoms, including anhedonia, are often comorbid with schizophrenia and are difficult to distinguish from core negative symptoms. One cognitive model of schizophrenia proposes that the presence of distorted beliefs about personal costs (i.e. effort/energy investment) underlies the development of passive behaviours and avoidance of effortful activities (Rector et al. 2005). This model leads to the prediction that the anticipation of failure and dysfunctional expectations about poor performance drive the disengagement of effort (alongside social and emotional withdrawal). Correspondingly, in schizophrenia, moderate correlations are observed between depression and all the negative symptoms (Avery et al. 2009). Specifically, dysfunctional expectancy appears to predict the severity of negative symptoms in a manner mediated by affective flattening and anhedonia (Avery et al. 2009).

Neurobiological correlates of negative symptoms and effort impairments in schizophrenia are broadly consistent with likely brain substrates implicated from studies of healthy participants. Thus, mental effort deficits in schizophrenia are putatively related to dorsal mid-anterior cingulate networks and subcortical regions influenced by reward/motivational-related dopaminergic projections (Gold et al. 2013). However, explaining how much of variance in brain activation in schizophrenia during effortful tasks is attributable to negative symptoms, and how much by deficits in effort allocation, presents problems. Early studies of regional cerebral flow observed deficits in the engagement of prefrontal cortex by increased mental effort in patients with chronic schizophrenia (Berman et al. 1986). However, it is difficult to link directly observed hypofrontality to deficits in the mobilization of mental effort. Similarly, more recent studies also show abnormal activation within the task-positive networks in schizophrenic patients, again consistent with deficient effort mobilization (Nygård et al. 2012). However, these studies remain correlational and the direct relationship between the disinvestment of mental effort and downregulation of the default mode networks is yet to be firmly established. Nevertheless, these data in schizophrenia corroborate models of mental effort emerging from studies of healthy individuals by showing compromised function in attentional and motivational systems linked to the embodied affective representations.

Conclusions

Neuroscientific studies of mental effort focus on descriptions of its affective and cognitive components, and the phsyiological correlates in bodily state (both as an objective index and as an account of the feeling state itself). Knowledge gained from neuroimaging and related techniques broadly endorse the notion that effort represents more than the allocation of attentional and information processing resources for enhanced task performance. In this context, effort has intrinsic value, visceral salience and its own sensory representation. Its dependent relationship to motivational drive is important for attaining immediate task goals, yet also weights future investment into effortful behaviour and adjusts the value of future outcomes. The experience of effort mirrors that of other feeling states including agency, achievement and emotion. Increasingly, predictive coding models are providing robust accounts of how the brain handles perception, experience and behaviour. There is an emphasis on the primacy of higher-order representations of external and internal environments, which in turn are tested against a stream of changing sensory data, including internal bodily signals (Friston and Keibel 2009; Seth et al. 2011; Seth and Critchley 2013; Seth 2013; Fig. 16.2). In this context, mental effort has a relationship to the notion of active inference, whereby sensory predictions are validated through the consequences of self-initiated behaviour. For effort, this includes the generation of internal bodily arousal states. The application of mental effort can thus be used to gauge the investment value of types of cognitive work and to tune both general and specific cognitive processes in anticipation of informational demand. The physiological embodiment of effort grounds its cognitive impact in action tendencies and motivational states. The enhanced understanding of mental effort and its underlying neurobiology has direct relevance to the expression of clinical symptoms across a range of psychiatric and neurological disorders including chronic fatigue, brain trauma, depression, Parkinson's disease, ADHD and schizophrenia.

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Psychobiology of Perceived Effort During Physical Tasks

17

Helma M. de Morree and Samuele M. Marcora

17.1 Perception of Effort

17.1.1 Definition

In the study of motivation and self-regulation, effort is usually defined in energetic terms as the mobilization of resources required for instrumental behavior (see other chapters in this book). This conceptualization is theoretically important and it provides the rationale for cardiovascular measures of effort. In fact, energy mobilization is assumed to require activation of the cardiovascular system to deliver oxygen and energy substrates to the brain and skeletal muscles (Gendolla et al. 2012). In this chapter, however, we focus on a different conceptualization of effort as "a general feeling of labour and personal strength common to all deliberate activity" (Preston and Wegner 2009, p. 573). People experience a general feeling of effort during tasks that require physical exertion, mental concentration, or self-restraint. Because in this chapter we mainly present studies from our field of exercise physiology, we focus specifically on what we call perception of effort, sense of effort, or perceived exertion during physical tasks.

Perception of effort during physical tasks is defined as "the conscious sensation of how hard, heavy, and strenuous the task is" (Marcora 2010b, p. 380). Sometimes, perceived exertion is defined in much broader terms, as "the subjective intensity of effort, strain, discomfort, and/or fatigue that is experienced during physical exercise" (Robertson and Noble 1997, p. 407). However, it has been shown that people are able to differentiate their perception of effort from other exercise-related sensations, such as pain and discomfort (Hamilton et al. 1996) and perception of effort and pain are based on different neurophysiological pathways (Marcora 2009; Smirmaul 2012). The latter definition is therefore too broad.

17.1.2 Measurement

Perception of effort is commonly measured with one of two psychophysical scales: the Borg rating of perceived exertion (RPE) scale (Borg 1970) or the category-ratio (CR10) scale (Borg 1982). The 15-point Borg RPE scale is an equidistant interval scale that was designed in such a way that ratings grow linearly with exercise intensity, heart rate, and oxygen uptake to achieve an easy comparison with objective measurements of exercise intensity (Borg 1998). The Borg CR10 scale is a category-ratio scale that was designed to enable direct estimation of intensity levels for interindividual comparisons. The responses

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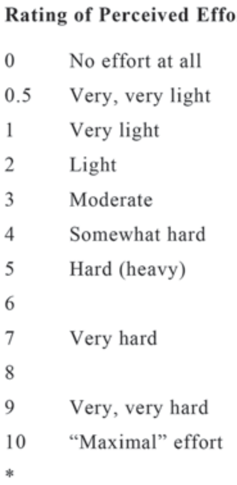


Rating of Perceived Effort

0	No effort at all
0.5	Very, very light
1	Very light
2	Light
3	Moderate
4	Somewhat hard
5	Hard (heavy)
6	
7	Very hard
8	
9	Very, very hard
10	"Maximal" effort
*	

Fig. 17.1 Example of the category-ratio (CR10) scale for rating of perceived effort

to this scale grow in a nonlinear and positively accelerating manner (Borg 1998). A black dot is placed at the bottom of the scale to provide the possibility to rate higher than ten, to avoid the "ceiling effect" that exists when a fixed endpoint is used. An example of the CR10 scale is presented in Fig. 17.1. Both the 15-point RPE scale and the CR10 scale have been shown to be valid and reliable, provided that the standardized procedures are followed during instruction and administration (Borg 1998).

17.1.3 Significance

Voluntary actions are accompanied by specific subjective experiences. The sense of effort is one of them (Lafargue and Franck 2009). Others are the experience of intention (planning to do something) and the experience of agency (the feeling that a particular external event was caused by one's own actions; Haggard 2008). It is thought that perception of effort has important benefits. It provides information about task difficulty, it is involved in the adaptive expenditure of energy, and it contributes to the feeling of conscious will (Preston and Wegner 2009). Moreover, effort has an important role in the self-regulation of behavior. According to Brehm's motivational intensity theory (Brehm and Self 1989; Gendolla et al. 2012; Wright 2008), effort is proportional to task difficulty until the maximum level of effort one is willing to invest (the so-called potential motivation) is reached. When this upper limit of effort is reached, or when success seems impossible, people reduce the level of effort they are exerting or they disengage from the task. This theory has been validated by several psychophysiological studies using a variety of mental tasks and experimental manipulations (Wright 1996, 2008).

The motivational intensity theory has formed the basis for the so-called psychobiological model of exercise performance, in which perception of effort plays a crucial role. Indeed, there is evidence that the increase in perception of effort occurring during prolonged exercise determines performance in time to exhaustion tasks (Marcora and Staiano 2010; Marcora et al. 2008, 2009). The psychobiological model of exercise performance predicts that exhaustion (task disengagement) during physical tasks occurs when (1) the perceived effort required by the task reaches the maximal effort one is willing to exert or (2) the participant believes to have exerted a true maximal effort, and continuation of the task is perceived as impossible (Marcora 2008).

The psychobiological model described above explains performance during physical tasks where the only possible form of self-regulation is to disengage from the task or to keep going. In fact, in these "time to exhaustion tasks," workload is fixed and cannot be self-regulated by the participant. In physical tasks where the workload is not fixed (time trials), a higher level of self-regulation (pacing) is possible. Pacing refers to the self-regulation of workload during time trials, which enables the participant to complete the task with the best possible performance. According to the psychobiological model of exercise performance, pacing is based on five psychological factors: (1) perception of effort, (2) potential motivation, (3) knowledge of the distance/duration to cover, (4) knowledge of the distance/duration covered/remaining, and (5) previous experience of perceived exertion during exercise of varying intensity and duration (Marcora 2010a). An example of how perception of effort influences pacing and performance during time

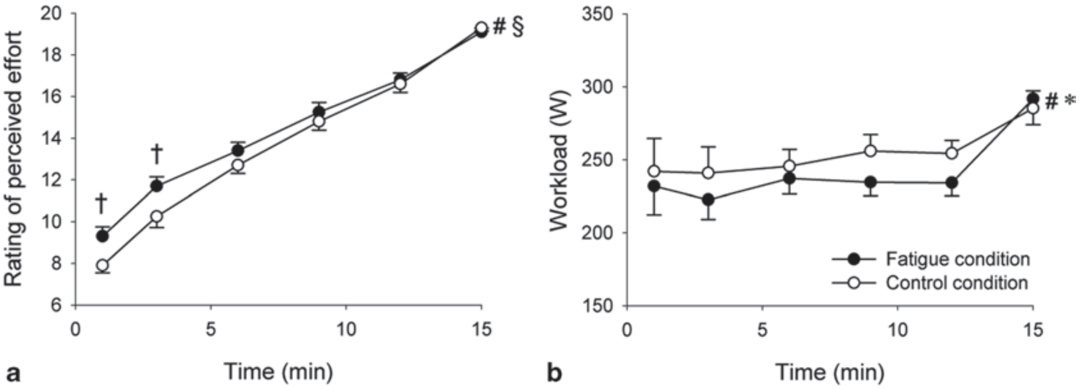


Fig. 17.2 Perception of effort and self-selected workload during a 15-min cycling time trial under conditions of leg muscle fatigue and control ($N=10$). # significant main effect of condition ($p<0.05$), * significant main effect of time ($p<0.05$), § significant condition × time interaction ($p<0.05$), † significant simple main effect of condition based on Holm–Bonferroni corrected α-levels. Data are presented as mean ± standard error of the mean. (Adapted from: de Morree and Marcora 2013, Copyright (2013), reproduced with permission from Springer)

trials is shown in Fig. 17.2. In our recent study on the effects of muscle fatigue on pacing and time trial performance (de Morree and Marcora 2013), we asked participants to complete as much work as possible while cycling on a cycle ergometer for 15 min in two different conditions: fatigue (preliminary exercise to fatigue the leg muscles) and control (no preliminary exercise). When cycling with fatigued leg muscles, participants kept perception of effort roughly the same as during the control condition, by reducing their workload. The slower pace is a behavioral response that compensates for the higher perception of effort induced by leg muscle fatigue. If workload would not have been reduced, perception of effort would have caused premature exhaustion in the fatigue condition, and the task would not have been completed.

Perception of effort is not only important for endurance athletes. There is evidence that perceived exertion is an important negative determinant of physical activity and exercise in the general population (Dishman et al. 1985). In fact, perception of effort seems to be one of the barriers preventing sedentary individuals from adopting an active lifestyle (Bauman et al. 2012; Trost et al. 2002). In other words, sensations of effort and strain experienced during exercise have a negative impact on health behaviors. Reducing perception of effort may therefore be an important target for interventions intended to promote an active lifestyle.

17.1.4 Physiological and Psychosocial Determinants

Many physiological factors can affect perception of effort during physical tasks (Noble and Robertson 1996). One of the most important factors is the (relative) intensity at which someone is exercising. Perception of effort increases with workload. It does, for example, require more effort to lift a heavy weight than to lift a light weight, and it is harder to cycle uphill than to cycle downhill. However, across individuals, the relationship between absolute workload and perception of effort is poor because perception of effort reflects relative exercise intensity. Relative exercise intensity depends not only on the actual workload (such as weight lifted or power output during cycling) but also on an individual's physical fitness. What is heavy/hard for a sedentary person can be light/easy for an athlete.

Muscle fatigue, defined as an "exercise-induced reduction in the ability to exert muscle force or power, regardless of whether or not the task can be sustained" (Gandevia 2001, p. 1732), is another important determinant of perception of effort (Enoka and Stuart 1992). When our muscles get fatigued, we do not directly sense that our ability to produce force or power is decreased. Instead, we feel that we are fatigued because we perceive the higher effort required to produce the same submaximal force or power. In our studies, we have shown experimentally that perception of effort is indeed higher when performing the same physical task with fatigued muscles (de Morree and Marcora 2010; Marcora et al. 2008).

Perception of effort also increases with time-on-task when a fixed workload is sustained for a prolonged period of time (Smith et al. 2007; Søgaard et al. 2006). This increase in effort with time-on-task is often considered a sign of muscle fatigue. However, there are several other factors that might underlie the increase in perception of effort over time. A mismatch has been found between the increase in perception of effort and the degree of muscle fatigue that occurs during sustained low-force contractions (Smith et al. 2007; Søgaard et al. 2006). In fact, the increase in perception of effort is much higher than the increase expected from the loss of muscle strength induced by prolonged exercise. One possible explanation for this mismatch is that the increase in perception of effort over time might have a cognitive component. This would fit with recent findings that mental fatigue causes higher perception of effort during constant-workload cycling in the absence of physiological changes (Marcora et al. 2009).

The subjective nature of RPE means that it can also be affected by psychological and social factors, although it has been pointed out that these factors might be more salient at light and moderate exercise intensities than at high exercise intensities (Noble and Robertson 1996). Psychological factors that have been shown to influence RPE include personality, mood, self-efficacy, and locus of control (Morgan 1994; Robertson and Noble 1997). That social factors can influence RPE is shown, for example, by a study where participants rated lower effort when exercising together with a coactor than when exercising alone (Hardy et al. 1986). Moreover, It has been shown that male participants report significantly lower perceived effort during cycling when the experimenter is female than when the experimenter is male (Boutcher et al. 1988).

17.2 Theories About the Neurophysiological Basis of Perception of Effort

In the nineteenth century, when physiologists first became interested in the "muscle sense" (Ross 1995), two main theories arose about the neurophysiological basis of perception of effort. The peripheralists believed that the sense of effort arises from afferent feedback from the muscles, whilst the centralists believed that the sense of effort arises from central motor commands to the muscles (Lafargue and Sirigu 2006). The Scottish philosopher Alexander Bain was one of the first advocates of the centralist view. He stated that "the mind appreciates the motor influence as it proceeds from the brain to the muscles, without depending on a returning sensibility through the proper sensory fibers" (Bain 1868, p. 78). One of the first devotees of the peripheralist theory was the (also Scottish) surgeon Sir Charles Bell. He stated that "a motor nerve is not a conductor towards the brain, and…it cannot perform the office of a sensitive nerve" (Bell 1826, pp. 167–168). The scientific debate between the "centralists" and the "peripheralists" is still ongoing today (Marcora 2009).

17.2.1 Afferent Feedback Model

The afferent feedback model entails that afferent feedback from the skeletal muscles, the heart, and/or the lungs provides the sensory signals processed by the brain to generate perception of effort (Hampson et al. 2001). However, experimental evidence does not support an important role for afferent feedback in the generation of perception of effort. Initially, it was thought that sensory signals from the heart might have a role in perception of effort. The positive correlations between heart rate and perceived exertion even led to the format of the original 6–20 Borg scale, which was designed to reflect the range of heart rates of young and fit individuals, from 60 beats min^{-1} at rest up to 200 beats min^{-1} during maximal exercise (Borg 1982). However, experimental studies have shown repeatedly that heart rate and RPE can be dissociated (Pandolf 1983; Robertson 1982). RPE is unchanged or even increased when heart rate is reduced by calcium channel and β-adrenergic blockade (Myers et al. 1987). Further evidence against a role for afferent feedback from the heart in perception of effort comes from a study showing that cardiac transplant patients (who have a denervated heart) report normal perception of effort during incremental exercise (Braith et al. 1992).

Afferent feedback from chemo- and mechanoreceptors in the lungs, airways, and chest wall is important in generating feelings of air hunger, chest tightness, and unsatisfied inspiration (O'Donnell et al. 2007). However, the feeling of respiratory effort experienced by healthy individuals during exercise is a different sensation (Grazzini et al. 2005), which seems to be independent of these afferent inputs. In fact, patients with double lung transplantation are still able to estimate the magnitude of inspiratory resistive loads based on a normal perception of respiratory effort (Zhao et al. 2003) and similar results have been obtained in healthy participants with anesthetized airways (Burki et al. 1983).

Group III and IV fibers in skeletal muscles provide afferent feedback related to metabolic, thermal, and mechanical stress to the central nervous system. Metabolic stress, temperature, and mechanical stress are all known to increase during intense exercise (Kaufman et al. 2002). However, the fact that afferent feedback and perception of effort both increase during exercise does not necessarily mean that the two are causally related. In fact, several experimental studies have found dissociations between perception of effort and afferent feedback from the active muscles. For example, studies employing partial blockade of sensory signals from skeletal muscle afferents with epidural anesthesia show that RPE is unchanged or even augmented during exercise with partial sensory blockade (Fernandes et al. 1990; Kjaer et al. 1999; Smith et al. 2003). If afferent feedback from the active muscles was an important sensory signal for perception of effort, RPE should be reduced during exercise with epidural anesthesia. The increase in RPE is probably due to muscle weakness induced by the epidural anesthesia, which causes a compensatory increase in central motor command to the muscles (see Sect. 17.2.2 on the corollary discharge model).

Mitchell et al. (1989) designed a study in which the reduction in muscle strength induced by epidural anesthesia was controlled for by keeping relative exercise intensity constant. Participants performed static leg extensions with and without epidural anesthesia. The epidural anesthesia induced a large strength loss (on average 62 %) in the leg extensors. At the same time, the epidural partially blocked the afferent feedback from the muscles. Importantly, participants performed the leg extensions under epidural anesthesia not only at the same absolute force as before the epidural but also at the same relative force (30 % of maximum immediately prior to exercise). In both conditions, the blockade of afferent feedback was the same, but central motor command was different. The results show that RPE was significantly higher than control in the condition where afferent feedback was blocked and where central motor command was increased (same absolute force). However, when the confounding effect of central motor command was removed (same relative force), there was no change in RPE compared to the control condition. This is compelling evidence against an important role for afferent feedback from skeletal muscles in the generation of perception of effort.

17.2.2 Corollary Discharge Model

According to the corollary discharge model, perception of effort arises from corollary discharges of the central motor command to the working muscles (including the respiratory muscles). The term "corollary discharge" was introduced by Roger Sperry in 1950 to describe "internal signals that arise from centrifugal motor commands and that influence perception" (McCloskey 1981, p. 1415), and central motor command can be defined as "a discharge or pattern of discharge that is generated within the central nervous system and that leads to the excitation of spinal α-motor neurons" (McCloskey 1981, p. 1421). Corollary discharges are thought to have perceptual consequences in two distinct ways. On the one hand, they are thought to modify the processing of incoming sensory information, for example, to enable the discrimination between self-generated and external stimuli (McCloskey 1981). Several corollary discharge circuits of this type have now been uncovered across the animal kingdom (Crapse and Sommer 2008; Poulet and Hedwig 2007). On the other hand, corollary discharges may give rise to sensations of various kinds in their own right (McCloskey 1981). This is the type of corollary discharge pathway that is thought to be involved in perception of effort.

Evidence for an important role of corollary discharges in perception of effort comes from experiments that were based on the prediction that conditions in which the central motor command necessary to achieve a given muscular performance is increased should lead to increased perception of effort. On the contrary, conditions in which central motor command is decreased should lead to decreased perception of effort (McCloskey et al. 1983). For example, during muscle fatigue a higher than usual central motor command is necessary to produce a certain force. This has been shown to lead to an increase in perception of effort (McCloskey et al. 1974). The same effect was found during partial paralysis induced by injection of a paralyzing agent (D-tubocurarine or decamethonium) into the forearm (Gandevia and McCloskey 1977a, 1977b), and in patients with hemiparesis (Gandevia and McCloskey 1977b).

In whole-body exercise, similar results have been found. When whole-body skeletal muscle weakness was induced by venous administration of Norcuron (curare), which partially blocks the neuromuscular junction without affecting afferent pathways, RPE during subsequent static knee extensions and dynamic cycling exercise was significantly increased on average by 2.8 points on the 6–20 RPE scale for the static exercise and by an average of 5.5 points during the cycling exercise (Gallagher et al. 2001). Moreover, we have shown a significant increase in perception of effort during constant-workload cycling exercise to exhaustion after we induced eccentric muscle fatigue in the leg muscles, without affecting afferent feedback from the muscles (Marcora et al. 2008).

During aerobic exercise, the sensation of respiratory effort partly contributes to overall perception of effort. This sensation is generated by corollary discharges of the central motor command to the respiratory muscles (Grazzini et al. 2005; O'Donnell et al. 2007). As discussed earlier, the sensation of respiratory effort is independent of feedback from pulmonary afferents. In fact, respiratory effort and motor effort (referring to the exercising muscles) seem to share a common neurophysiological mechanism. Corollary discharges of the central motor command to the exercising muscles give rise to the sense of motor effort, whereas corollary discharges of central motor command to the respiratory muscles give rise to the sense of respiratory effort (Fig. 17.3).

17.3 The Cortical Substrates of Perception of Effort

17.3.1 Neuroimaging Studies

Williamson and colleagues have used hypnosis to experimentally manipulate perception of effort while measuring regional cerebral blood flow (rCBF) distribution in several cortical areas (Williamson et al. 2001, 2002). They showed that, compared to a control condition, participants rate their effort significantly higher for constant-workload cycling under the hypnotic suggestion that they are cycling uphill, and they are rating their effort significantly lower when under the hypnotic suggestion that they are cycling downhill (Williamson et al. 2001). The uphill condition elicited a significant increase in rCBF distribution to the right thalamic region and right insular cortex, whereas the downhill condition elicited a significant decrease in rCBF distribution to the anterior cingulate cortex and the left insular cortex. The second study compared RPE

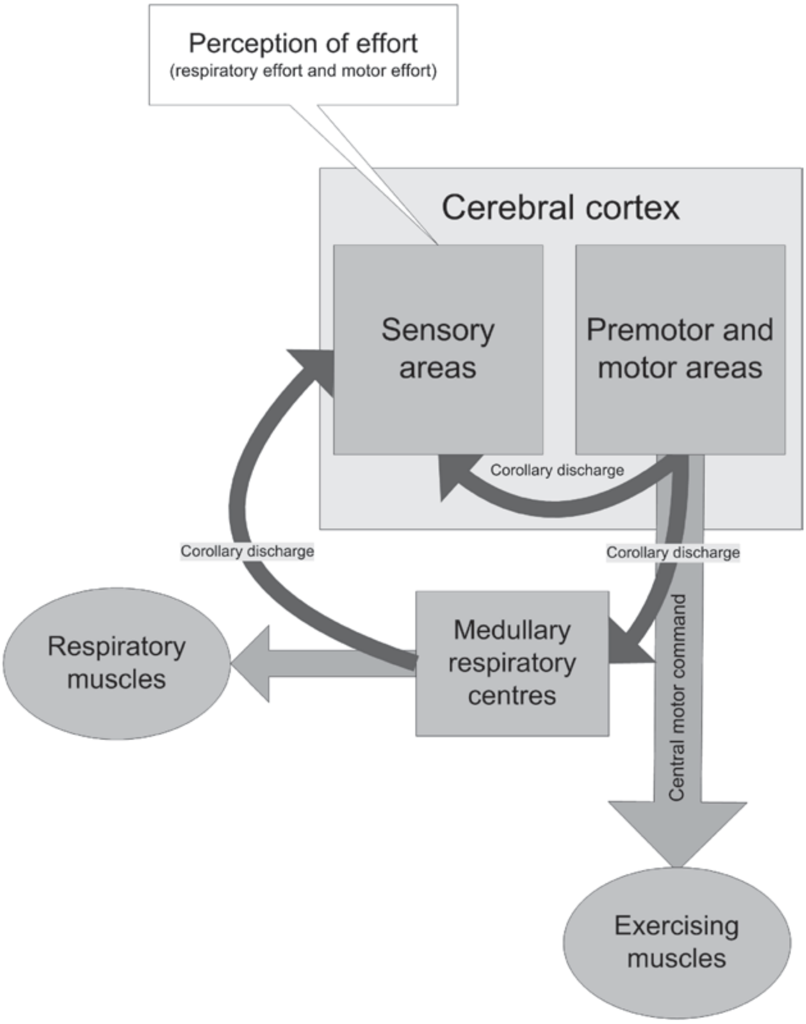


Fig. 17.3 Schematic representation of the neurophysiological pathways underlying the corollary discharge model of perception of effort

and rCBF during actual and imagined (by hypnotic suggestion) handgrip exercise (Williamson et al. 2002). In this case, a group of participants with high hypnotizability was compared with a group of participants with low hypnotizability. It appeared that, during the imagined exercise condition, the high hypnotizability group gave significantly higher RPE compared to the low hypnotizability group. There was no significant increase in RPE in the low hypnotizability group during the course of the imagined handgrip exercise. Significant between-group differences were found in rCBF distribution change scores between actual and imagined exercise conditions in the anterior cingulate cortex, the right inferior insular cortex, and the left inferior insular cortex.

Recently, Fontes et al. (2013) have assessed which brain areas are activated during effortful cycling exercise, by using functional magnetic resonance imaging (fMRI) during cycling on an MRI-compatible cycle ergometer. They compared cycling that was perceived as “hard” (RPE > 15 on 6–20 scale) with cycling that was perceived as less than “hard” (RPE ≤ 15), and found significant differences in the activity of the posterior cingulate cortex and the precuneus. However, contrary to the studies by Williamson and colleagues (Williamson et al. 2001, 2002), the confounding effects of other exercise-intensity-related responses were poorly controlled for by the study design. Therefore, it is too early to conclude that these cortical areas are involved in the generation of perceived exertion. Better-controlled experimental studies using fMRI are necessary to investigate the cortical substrates of perception of effort.

17.3.2 Electrophysiological Studies

To study motor-related brain activity with a high temporal resolution, electroencephalogram (EEG) is one of the best techniques available (Kutas and Federmeier 1998). By averaging several EEG signals time-locked to movement onset, the so-called movement (or motor)-related cortical potential (MRCP) can be extracted from the EEG during simple motor tasks. The MRCP is a slow negative going potential that appears over the scalp 1–2 s before the onset of voluntary movement. It is thought to represent excitatory postsynaptic potentials in the apical dendrites of cortical pyramidal neurons (Ikeda and Shibasaki 2003; Jahanshahi and Hallett 2003).

From several source localization studies using EEG (both scalp and intracranial recordings), magnetoencephalography, fMRI, and positron emission tomography, a consensus has been reached that the MRCP starts in the bilateral supplementary motor areas (pre-supplementary motor area, SMA; SMA proper; and cingulate motor area) and shortly thereafter in the bilateral lateral premotor cortices. Later (about 400 ms before movement onset), the MRCP is generated mainly by the contralateral lateral premotor cortex and primary motor cortex (Shibasaki and Hallett 2006). The MRCP after movement onset (during movement execution) has received less attention in the literature than the MRCP during movement preparation. The MRCP after movement onset is probably related to activity not only in the primary motor cortex and in the primary sensory cortex (Ikeda and Shibasaki 2003) but also in the SMA (Milliken et al. 1999), the premotor cortex, the cingulate cortex, and the parietal cortex (Rektor et al. 1998). It is thought that this activity is related not only to movement generation and afferent processes but also to more cognitive processes (Rektor et al. 1998).

MRCP amplitude provides an indication of the magnitude of the central motor command. Indeed, MRCP amplitude increases in situations where central motor command is expected to be augmented. For example, MRCP amplitude increases with exercise intensity during isometric elbow exercise (Siemionow et al. 2000), and with artificially induced muscle weakness during finger abductions (Jankelowitz and Colebatch 2005). It has also been shown that MRCP amplitude is decreased during leg extensions after resistance training (Falvo et al. 2010).

We have recently completed two studies with a total of four experimental manipulations to investigate whether central motor command (represented by MRCP amplitude) correlates with perception of effort during physical tasks. In our first study, we have measured perception of effort and MRCP amplitude during unilateral dynamic elbow flexions in 16 healthy male volunteers (de Morree et al. 2012). We experimentally manipulated perception of effort by inducing muscle fatigue in one randomly selected arm and comparing this with the nonfatigued arm. Muscle fatigue was induced by an eccentric fatiguing protocol, which caused a 35 % reduction in elbow flexor strength, without affecting afferent feedback from the muscles (Nielsen et al. 2005; Skurvydas et al. 2000). As a second manipulation, we compared lifting a light weight (20 % of one-repetition maximum) with lifting a heavier weight (35 % one-repetition maximum). Participants repeatedly lifted a handheld dumbbell in a set rhythm, each time touching a flexible ruler placed 2 cm above the dumbbell (for experimental setup, see Fig. 17.4). Participants were required to lift the same two absolute weights with the fatigued arm and the nonfatigued arm, giving a total of four blocks: light fatigued, heavy fatigued, light nonfatigued, and heavy nonfatigued. The blocks were presented in a random order. Each block consisted of 50 trials. After every set of ten lifts, participants rated the average effort experienced during those ten lifts.

As expected, RPE increased significantly with weight and with muscle fatigue (Fig. 17.5a and 17.5b). Moreover, we found significant effects of both manipulations on MRCP amplitude during

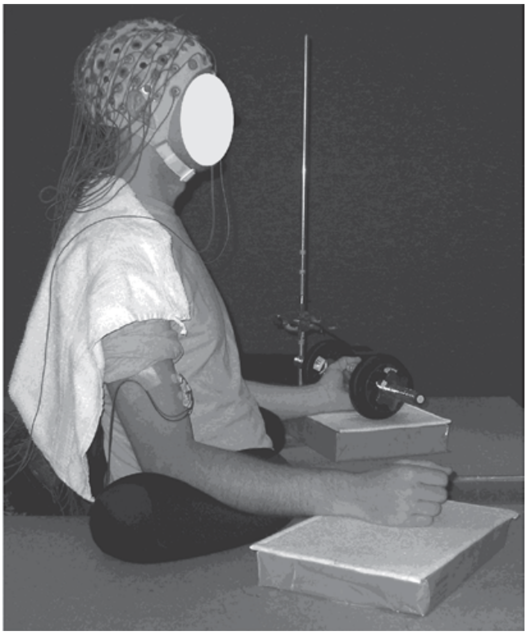


Fig. 17.4 Experimental setup for dynamic unilateral elbow flexion protocol

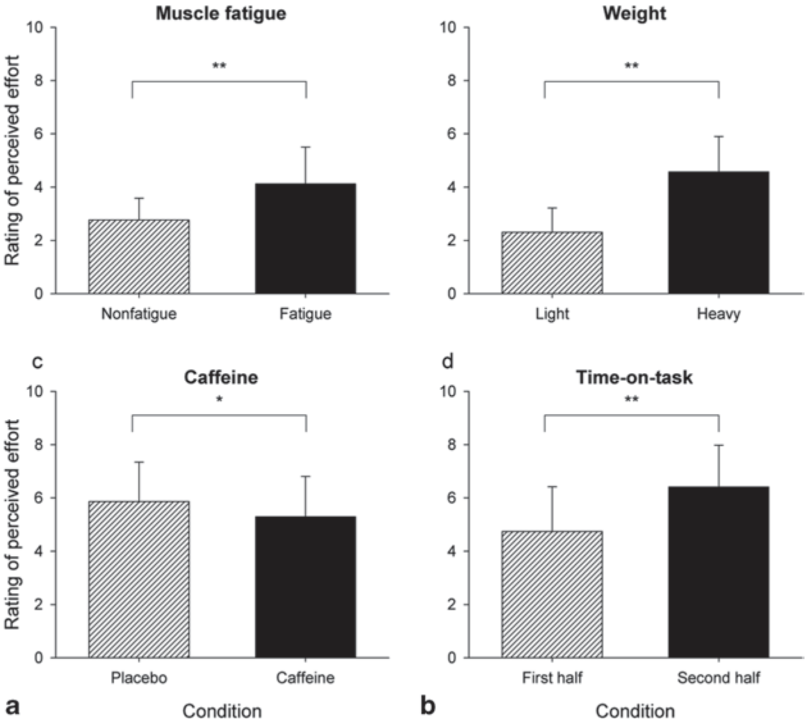
the weight-raising epoch at the vertex electrode Cz (Fig. 17.6a and 17.6b). Electromyogram (EMG) amplitude of the biceps brachii muscles increased in parallel with MRCP amplitude and perception of effort. Correlational analysis confirmed statistically that MRCP amplitude during weight raising at electrode Cz correlated significantly with RPE across both our experimental manipulations ($r(14) = -0.64$, $p < 0.001$). These results suggest that MRCP amplitude during movement execution is a neural correlate of perception of effort. This study was the first to provide direct neurophysiological evidence that MRCP amplitude during movement execution correlates with perception of effort, which supports the corollary discharge theory of perception of effort.

In our second study, we measured perception of effort and MRCP amplitude during repeated isometric leg extensions in 12 healthy female volunteers (de Morree et al. 2013). We manipulated perception of effort by administering caffeine (6 mg kg^{-1} body weight) in one condition and comparing this with a placebo condition, because caffeine is known to reduce perception of effort during subsequent exercise (Davis and Green 2009; Doherty and Smith 2005). Moreover, we looked at the effects of time-on-task because it had previously been shown that perception of effort increases over time during prolonged constant-workload exercise (Smith et al. 2007; Søgaard et al. 2006). The design of the experiment was double-blind, placebo controlled, and randomly counterbalanced. Participants sat on a custom-built isometric leg-extension table with their right leg in an aluminum modular brace that was fixed to the table (for experimental setup, see Fig. 17.7). A target line representing 61 ± 5 % of the individual maximum torque was presented on a feedback screen. Participants received instant feedback about the torque they were producing by means of a red bar moving towards the target line. After every ten muscle contractions, participants rated their perception of effort. They completed a total of 100 muscle contractions.

We found that perception of effort during the submaximal isometric leg-extension protocol was significantly reduced by caffeine ingestion compared to placebo and that perception of effort was significantly higher during the second half of the protocol compared to the first half (Fig. 17.5c and 17.5d). MRCP amplitude at electrode Cz during the contraction was significantly decreased with caffeine compared to placebo and significantly increased with time-on-task (Fig. 17.6c and 17.6d). EMG amplitude of the vastus lateralis muscle and force output were unaffected by either manipulation. The findings of this study not only support the findings of our first study that perception of effort correlates with central motor command but also provide direct neurophysiological evidence that changes in central motor command during submaximal exercise can occur in the absence of changes in motoneuron output and force output.

Taken together, all manipulations affected perception of effort in the expected direction and they all significantly affected MRCP amplitude at electrode Cz during the initial phase of muscle contraction in the same direction as perception of effort. It is encouraging that our four manipulations have led to very consistent findings despite differences in the active muscles (elbow flexors and leg extensors), the type of exercise (dynamic

Fig. 17.5 Rating of perceived effort for **a** muscle fatigue ($N=16$), **b** weight ($N=16$), **c** caffeine ($N=12$), and **d** time-on-task ($N=12$) manipulations. ** significant main effect of condition ($p<0.01$), * significant main effect of condition ($p<0.05$). Data are presented as mean ± standard deviation



and isometric), the direction of the effects (increase and reduction), and the target location of the manipulations (peripheral and central).

Although we did not find correlations between MRCP amplitude before movement onset and perception of effort in our laboratory, Slobounov et al. (2004) have found some evidence that MRCP during movement preparation might reflect perception of effort. However, they did not find the expected correlations between MRCP amplitude and perceived effort during isometric index finger contractions. Contractions at 30 and 70 % were perceived as more effortful than contractions at 50 % of maximal voluntary force. The cognitive demands related to the production of low force levels based on visual feedback (Freude and Ullsperger 1987) and anticipated effort (Slobounov et al. 2004) might have confounded the effects of force production on MRCP amplitude and perception of effort.

More recently, Berchicci et al. (2013) have found that MRCP amplitude during movement preparation correlated significantly with perception of effort during isometric leg-extension exercise. The fact that we have not found significant effects of our manipulations on MRCP amplitude during movement preparation and other authors have might be explained by methodological differences in experimental setup and experimental manipulations. More research is needed to investigate the relationship between MRCP amplitude during movement preparation and perception of effort. Importantly, however, all current electrophysiological evidence supports the corollary discharge model of perception of effort, as all these studies show significant correlations between motor-related brain activity and perception of effort.

17.4 Directions for Future Research

Future research is required to further investigate which brain areas and pathways, and which neurotransmitters, are involved in perception of effort and in what way. This could eventually lead to interventions that reduce perception of effort during exercise. Moreover, future studies should

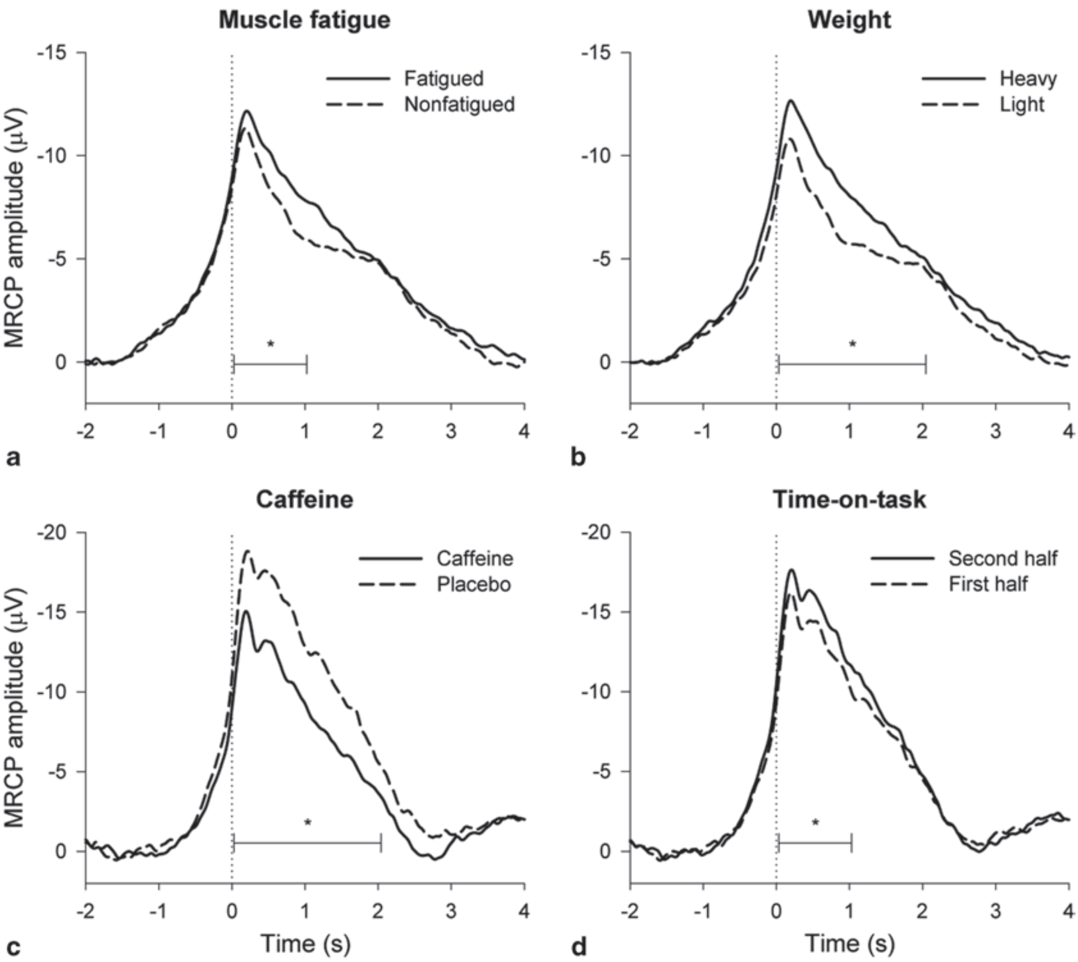


Fig. 17.6 Grand averages of the movement/motor-related cortical potential (*MRCP*) at electrode Cz (vertex) for **a** muscle fatigue ($N=16$), **b** weight ($N=16$), **c** caffeine ($N=12$), and **d** time-on-task ($N=12$) manipulations. Time 0 m electromyogram onset. * Significant simple main effect of condition based on Holm-Bonferroni corrected α-levels

try to dissociate completely the effects of perception of effort from the effects of afferent feedback on MRCP amplitude and perception of effort. One way would be to block afferent feedback from the muscles, without affecting motor nerve activity, by epidural anesthesia with fentanyl (Amann et al. 2009). Another way would be by blockade of large-diameter afferent fibers with ischemic nerve block (Christensen et al. 2007).

Other interesting techniques that could be used to further investigate the neurophysiology of perception of effort are repetitive transcranial magnetic stimulation (rTMS) and transcranial direct current stimulation. Both these methods can be used to induce relatively long-lasting (positive as well as negative) changes in cortical excitability (Priori et al. 2009). Interestingly, a study by Rossi et al. (2000) has shown that low-frequency rTMS of the primary motor cortex causes a reduction in MRCP amplitude without affecting overt motor performance during thumb oppositions. It would be very interesting to investigate the effects of this type of stimulation over different brain areas on perception of effort.

Fig. 17.7 Experimental setup for repeated isometric leg-extension protocol

17.5 Clinical Applications

There is evidence that perception of effort is disturbed in patients with chronic fatigue syndrome (CFS). These patients experience an increased perception of effort, without signs of muscle weakness (Lawrie et al. 1997; Wallman and Sacco 2007). Now that it has been demonstrated that MRCP amplitude reflects central motor command, and that it is correlated with perception of effort, this technique could be employed to study the causes of the altered perception of effort in CFS patients. MRCP amplitude has been measured previously during exercise in CFS patients, and it was shown that the peak amplitude of the MRCP is significantly higher in CFS patients than in healthy controls (Siemionow et al. 2004). It would be interesting to investigate whether these differences in MRCP amplitude correlate with RPE, and whether similar effects can be found in other patient groups suffering from fatigue, such as cancer patients (Ryan et al. 2007).

Conclusion

Despite the long history of research on the sense of effort and the widespread application of RPE in exercise and sport settings, we have only recently begun to understand the psychobiology of perception of effort, based on neurophysiological evidence from EEG and neuroimaging studies. Further research in this area should focus on possible targets for interventions aimed at reducing perception of effort. These might benefit endurance athletes, patients with CFS, and other patient populations suffering from fatigue (such as cancer patients). Moreover, interventions that reduce perception of effort might affect self-regulation of physical activity behavior and could lead to increased physical activity and improved health in sedentary individuals.

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Bounded Effort Automaticity: A Drama in Four Parts

18

Guido H.E. Gendolla and Nicolas Silvestrini

18.1 Introduction

As all behavior, the preparation and execution of self-regulated actions need resources, which can be biochemical (e.g., adenosine triphosphate—ATP), psychological (e.g., attention), or physical (e.g., time) in nature. Thus, understanding the principles underlying resource mobilization and allocation is central for understanding self-regulation and human behavior in general. Nevertheless, most research on human action has been concerned with *what* people do rather than with *how* they do it (see Geen 1995; Heckhausen and Heckhausen 2008; Weiner 1992). Likewise, research on self-regulation has revealed important insights on how the self influences the direction of behavior (see Leary 2007)—e.g., *what* people do to maintain positive self-esteem. But still little is known about *how* people do this. The self's impact on the energetic aspect of behavior—the mobilization of resources to prepare and execute action, which is *effort*—is not well understood. This chapter aims at contributing to close this gap. We suggest a bounded effort automaticity approach that considers and integrates two important principles of resource mobilization in self-regulation: resource conservation and automaticity. To achieve this, we have divided this chapter into four parts that mirror the structure of a classical drama.

In the first part, we set the stage, by discussing research on motivational intensity and cardiovascular adjustments. Central to this work has been the notion that behavior is guided by a resource conservation principle—people prefer to minimize effort to attain their goals. In the second part, the plot thickens when we discuss some problems that arise when the resource conservation principle is confronted with research on automaticity. In the third part, our hero enters the scene, in the shape of our proposal for a theoretical integration of two basic principles of effort mobilization, leading to a bounded effort automaticity approach. Finally, in the fourth part, our hero saves the day, when we present studies that have tested and supported our bounded effort automaticity approach and discuss their implications. The core idea of our analysis is that the resource conservation principle moderates and limits automaticity effects on resource mobilization.

18.2 Part I: The Stage Is Set—The Principle of Resource Conservation

An early and well-supported idea about resource mobilization is that organisms are basically lazy—for good reasons. Organisms try to avoid wasting resources and thus do not more

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than necessary for attaining their goals. This resource conservation principle has been of high (evolutionary) value because it permitted goal accomplishment without losing behavioral flexibility (see Gendolla and Richter 2010, for a more complete discussion). According to this principle, people mobilize enough resources to cope with obstacles in the goal attainment process, facilitating goal pursuit and accomplishment. But importantly, resource conservation reduces the probability of depletion and exhaustion and thus permits flexibility in responding to both urgent environmental demands and accomplishing long-term goals. If organisms would always respond with the mobilization of maximal resources, success would also be most likely. However, the price would be depletion and—in extreme cases of exhaustion—an inability to act at all. If, on the other hand, organisms would always only mobilize low effort, they could conserve a lot of resource. But given that low effort is frequently insufficient to cope with big obstacles during goal pursuit, mobilizing low resources would actually be a waste of energy in those cases, because the invested resources would not bring return. Thus, mobilizing *just sufficient* resources should be most adaptive for goal attainment without risking depletion—it would be "motivationally most intelligent."

Pioneers in psychology have called this basic principle of behavior—which was borrowed from mechanical science—the "principle of least action," postulating that individuals invest only the effort that is minimally required to perform a task (Gibson 1900). Different schools of motivation research have adopted and shared this idea. Hull (1943)—a classical behaviorist—suggested a "principle of strongest habit," meaning that organisms always prefer the best learned (i.e., the easiest) behavior to attain a reinforcer. Tolman (1932)—a cognitively colored behaviorist—posited a "principle of minimal effort," meaning that organisms choose the easiest way to attain their goals. Cognitive will psychologists postulated in the "difficulty law of motivation" that effort is mobilized proportionally to the magnitude of obstacles in the goal pursuit process (i.e., volition), once a person has intentionally committed to a goal (Ach 1935; Hillgruber 1912).

Apparently, early scholars of human and animal behavior had little doubt that organisms' tendency to conserve resources is a fundamental principle of behavior. However, maybe due to Skinner's (too) simple approach to merely describe behavior in terms of "stimulus–response–stimulus–response" chains (e.g., Skinner 1938, 1976), which has dominated mainstream behavior research for long, academic psychology started to focus on reinforcement and punishment, and later on positive and negative incentive, as the significant variables for understanding behavior (Atkinson 1964, Chaps. 4–6). But even classical behaviorism has not always neglected energetic processes. Drive reduction theory (Hull 1943) regarded them as necessary for understanding how and when organisms behave and learn. However, energetic processes lost appeal. As one of the consequences, the principle of resource conservation was also forgotten in the psychological study of behavior, although the idea that people try to get what they need by investing only the minimal necessary input has always been accepted as a basic principle of action in other disciplines, such as economy.

In line with psychology's long neglect of the importance to consider energetic processes to understand behavior, also social psychology—the home discipline of self-regulation research—has just recently started to highlight the process of resource mobilization, investment, and its consequences (e.g., Baumeister et al. 2003; Gendolla and Richter 2010; Higgins 2006; Kruglanski et al. 2012; Chap. 20, this volume; Wright and Kirby 2001). By contrast, in physiology and psychophysiology, energetic processes have been intensely studied for more than a century (see Berntson and Cacioppo 2000)—which has been largely ignored in social psychological research on self-regulation. One exception, which has revealed important insights into the process of resource mobilization, is Brehm's theory of motivational intensity (Brehm et al. 1983; Brehm and Self 1989).

In the middle of the 1970s, Brehm rediscovered the principle of resource conservation for psychology, and inspired a research program on the antecedents and consequences of effort mo-

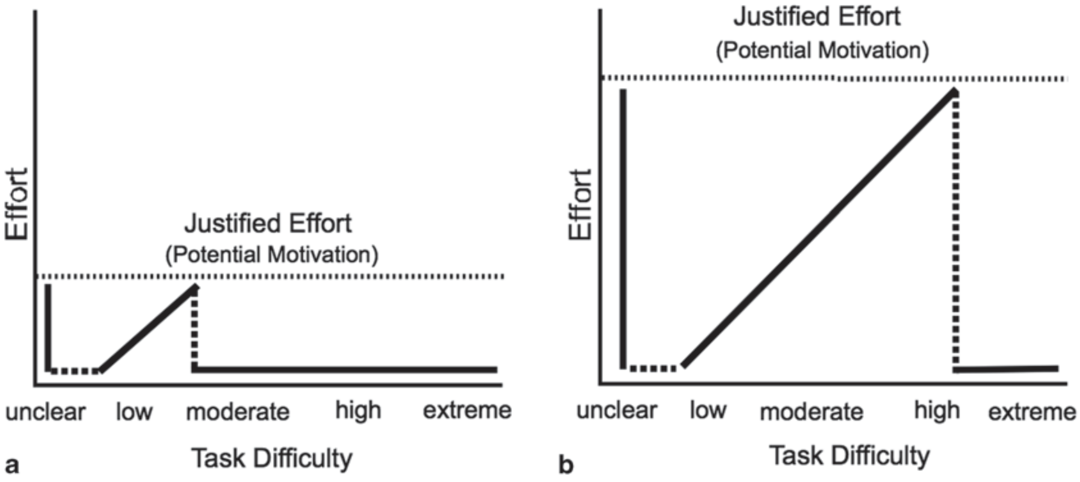

Fig. 18.1 The joint impact of subjective task difficulty and importance of success on effort mobilization according to motivational intensity theory (Brehm and Self 1989). *Panel* **a** shows the condition of low importance of success. *Panel* **b** shows the condition of high importance of success. (Printed with permission. Copyright: Oxford University Press)

bilization that lasts until today (Brehm 1975). Originated as a social psychological theory of the factors determining effort mobilization and its consequences for experienced goal valence, it has been early integrated with insights from psychophysiology (Wright 1996) and elaborated in different contexts of resource mobilization (see Gendolla et al. 2012a for a review; see also the Chaps. 19, 20, and 22, in this volume).

18.2.1 Motivational Intensity Theory

Motivational intensity theory (Brehm et al. 1983; Brehm and Self 1989) departs from the idea that effort mobilization follows the resource conservation principle. The theory posits that given that people try to avoid wasting resources, subjective task difficulty—the extent of experienced obstacles during goal pursuit—is the key variable determining effort. Thus, basically, effort increases with subjective demand. However, the relation between demand and effort is not monotonic; the theory posits two limits of the difficulty–effort relationship. One limit is defined by persons' ability. That is, effort rises proportionally with the extent of subjective difficulty until demand exceeds a person's abilities—i.e., when a task is too difficult. The second limit is the level of maximally justified effort, which refers to the importance of success or, in terms of motivational intensity theory, "potential motivation." If more effort is needed than justified by a goals' importance, people withdraw effort. Thus, put into one sentence, motivational intensity theory posits that *effort rises with subjective difficulty as long as success is possible and the necessary effort is justified*. In order to prevent senseless energy investment that would not bring return, people disengage (i.e., do not mobilize any effort) when one of these limits is attained. Figure 18.1 depicts the predictions of motivational intensity theory for conditions of low (Panel a) and high (Panel b) importance of success.

Complying with the resource conservation principle requires that people who are facing a challenge have an idea about the level of actual demand. Whenever individuals confront tasks with a fixed performance standard (e.g., "memorize these 6 items within 2 minutes"), difficulty is relatively clear and the necessary resources can be adjusted to the level of experienced task demand. But sometimes task difficulty is unspecified, e.g., because no clear fixed performance standard is provided (e.g., "memorize items until somebody says stop"). For this case, motivational intensity theory predicts that people will strive for the highest possible performance level that is justified to be accomplished in order to assure goal attainment. Consequently, only when persons have no idea about task demand, effort intensity should be determined by the value of success (i.e., the level of potential motivation).

Numerous published studies have brought empirical support for the principles of motivational intensity theory (see Gendolla et al. 2012; Wright and Kirby 2001 for reviews). The vast majority of these studies have operationalized effort mobilization physiologically, in terms of responses in the activity of the cardiovascular system, as we discuss below.

18.2.2 Measuring Effort

As stated at the beginning of this chapter, effort is defined as the mobilization of resources for carrying out instrumental behavior and refers to the intensity aspect of motivation (Gendolla and Wright 2009). Researchers have applied several operationalizations to assess this variable. Examples are performance, persistence, or self-report, which—unfortunately—all have several disadvantages (see Gendolla and Richter 2010; Gendolla et al. 2012 for discussions). Alternatively, researchers with an interest in energetic processes started to focus on physiological measures of resource mobilization. Given that the function of the sympathetic branch of the autonomic nervous system is the activation of the body (see Richter and Wright 2013), parameters of sympathetic activation have early been used as measures of effort. Examples are skin conductance (e.g., Stennett 1957) or pupil dilation (e.g., Kahneman 1973). However, due to physiological reasons and psychological processes, these measures have also been topic of debate (e.g., Fowles 1983). More promising have been measures of sympathetically mediated responses in the cardiovascular system, i.e., changes in cardiac and vascular activity in the context of action.

18.2.2.1 Effort-Related Cardiovascular Response

One of the main reasons why effort researchers started to focus on cardiovascular activity has been that the cardiovascular system is necessary for carrying out behavior (Papillo and Shapiro 1990)—it is the body's transport system for bringing oxygen and nutrients to the body's cells and to dispose metabolic waste from there. To use a metaphor, similar to the traffic intensity in a country increasing with the amount of resources needed by its industries, the activity of the cardiovascular system increases when the body needs more resources because of increased behavior intensity. For physical tasks, this has been long known. However, particularly interesting for psychologists, pioneering research by Paul Obrist and colleagues has revealed that sympathetically mediated responses in the cardiovascular system also sensitively respond to variations in cognitive task demand (see Obrist 1976, 1981)—maybe even independently of the brain's metabolic needs.

Research in psychophysiology has revealed many links between motivation and responses of the cardiovascular system (see Wright and Gendolla 2012). Most relevant for effort research, Obrist and colleagues discovered that sympathetically mediated activity of the cardiovascular system responds proportionally to experienced task demand whenever organisms have control over a performance outcome—a setting that was called *active coping*. In short, Obrist found that especially the sympathetic impact on the heart via beta-adrenergic receptors is proportional to task engagement (i.e., effort) during active coping. Noninvasively assessed, this beta-adrenergic impact becomes especially evident in shortened cardiac pre-ejection period (PEP)—a cardiac contractility index defined as the time interval between the onset of left ventricular excitation and the opening of the aortic valve (Berntson et al. 2004). PEP has been suggested to be the "gold standard" of noninvasive measures of cardiac contractility and thus as a very suitable measure of effort mobilization (Obrist 1981; Kelsey 2012; Wright 1996). In healthy young adults, PEP takes around 90–100 ms during rest and becomes shorter with increased beta-adrenergic impact.

Wright (1996) has integrated Obrist's active coping research with Brehm's motivational intensity theory. According to this integrative approach, beta-adrenergic impact on the heart is proportional to experienced task demand as long as success is possible and justified. This integration has been an important breakthrough in effort research. It offers a precise prediction about effort mobilization that integrates psychological theorizing on the principle of resource conservation and its elaboration with a specific operationalization of the dependent variable based on physiological research—with a level of precision that is otherwise rare in psychology.

As outlined so far, PEP should be a highly reliable measure of effort mobilization. However, beta-adrenergic sympathetic nervous system impact on the heart can also influence other indices of cardiovascular activity, like systolic blood pressure (SBP)—the maximal arterial pressure after a heartbeat (Brownley et al. 2000). Systolic pressure is systematically influenced by cardiac contractility due to its impact on cardiac output. Consequently, several researchers have used SBP response as a measure of effort, which is easier to measure than PEP (see Gendolla et al. 2012a; Gendolla and Richter 2010; Wright and Kirby 2001 for reviews). But blood pressure is also influenced by peripheral vascular resistance, which is not systematically influenced by beta-adrenergic impact (Levick 2003). Consequently, PEP is the much purer measure of beta-adrenergic impact. The influence of peripheral resistance on diastolic blood pressure (DBP)—the minimal arterial pressure between two heartbeats—is still stronger than on SBP, making predictions for effort effects on DBP very difficult. Still other studies (e.g., Eubanks et al. 2002) have quantified effort as responses in heart rate (HR). However, HR is influenced by both beta-adrenergic sympathetic impact *and* parasympathetic impact and should thus only reflect effort mobilization to the extent to which the sympathetic impact is stronger (Berntson et al. 2004), making predictions also difficult.

Summing up, PEP is the most reliable and valid indicator of effort intensity among these parameters of cardiovascular activity (Kelsey 2012), and SBP can, but does not have to, bear effort effects. Predictions for effort effects on DBP and HR are difficult. Nevertheless, PEP should always be assessed together with blood pressure and HR to control for possible preload (ventricular filling) or afterload (arterial pressure) effects, which can influence PEP beside beta-adrenergic impact (Sherwood et al. 1990). These effects are, however, most unlikely if decreases in PEP that reflect stronger contractility are accompanied by simultaneous increases in HR and DBP.

18.2.3 Task Demand Effects on Effort

Research on the resource conservation principle in terms of its elaboration in motivational intensity theory (Brehm and Self 1989) has focused on several variables influencing experienced task demand. Examples are fixed performance standards (e.g., Wright et al. 1986), ability beliefs (see Wright 1998), fatigue (see Wright and Stewart 2012), mood (see Gendolla et al. 2012b), depressive symptoms (Brinkmann and Gendolla 2008), and extraversion (Kemper et al. 2008). All of these variables have been found to systematically influence the experience of task demand and the intensity of cardiovascular response during task performance, as long as success was possible and the necessary effort was justified. By contrast, variables defining potential motivation, which is the level of maximally justified effort, are monetary incentive (e.g., Eubanks et al. 2002; Richter and Gendolla 2009), instrumentality of success for obtaining a desired outcome (e.g., Silvestrini and Gendolla 2009; Wright and Gregorich 1989), or the extent to which performance has consequences for performers' self-definition, personal interest, or self-esteem (Gendolla and Richter 2010)—for example, because performance is observed (Gendolla and Richter 2006a) or evaluated by others (e.g., Wright et al. 1998) or oneself (Gendolla et al. 2008).

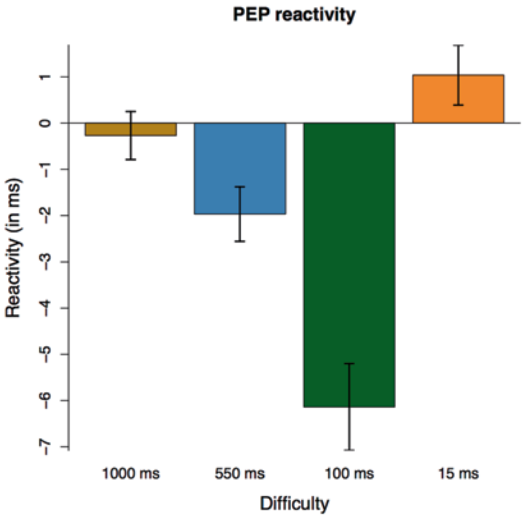

Fig. 18.2 Cell means and standard errors of cardiac pre-ejection period reactivity during task performance in the experiment by Richter et al. (2008). *PEP* pre-ejection period. (Printed with permission. Copyright: Wiley-Blackwell)

One of the clearest illustrations for the strong and systematic impact of task demand on cardiac response during a cognitive task is provided by an experiment by Richter et al. (2008) that included measures of PEP, blood pressure, and HR. After assessment of cardiovascular baseline activity during rest, the study presented participants a recognition memory task that required them to indicate repeatedly whether a target letter had appeared in a preceding string of four letters (see Sternberg 1966). Difficulty was manipulated by displaying the initial string for 1000 ms (easy), 550 ms (moderately difficult), 100 ms (highly difficult), or 15 ms (extremely difficult). Predictions were derived from Wright's (1996) integration of motivational intensity theory (Brehm and Self 1989) with the active coping approach (Obrist 1981) we have discussed above. Results are depicted in Fig. 18.2. As expected, PEP responses assessed during performance with reference to baseline values became progressively stronger from the low- to the moderate- to the high-difficulty condition, and then dropped on the extremely difficulty level. Overall, SBP reactivity revealed a similar pattern (see Chap. 19, this volume), but differences between the easy-, moderate-, and high-difficulty levels were less pronounced—which is in line with the above discussion of PEP as the much purer index of beta-adrenergic impact on the heart.

18.3 Part II: Problems Arise—Automatic Effort Mobilization

As discussed so far, the resource conservation principle and its elaboration in terms of motivational intensity theory (Brehm and Self 1989) have provided a powerful explanation of and clear predictions for effort mobilization. Evidence for the critical role of experienced task demand and the importance of success as key variables in effort mobilization is ample and clear (see Gendolla et al. 2012; Wright and Kirby 2001, for reviews). However, recent evidence for automatic and "direct" effort mobilization poses some problems for the idea that resource conservation is really the fundamental principle of resource mobilization.

Research on automaticity or behavior priming has revealed ample evidence that implicitly processed stimuli can systematically influence human behavior (see Bargh 2006; Bargh and Chartrand 1999; Custers and Aarts 2005; Dijksterhuis and Aarts 2010; Kruglanski et al. 2002, for reviews). Besides attitudes and stereotypes, also mental representations of goals or emotions can be implicitly activated and automatically influence behavior (see Bargh 1997; Gendolla 2012; Greenwald and Banaji 1995). Contributing to this evidence, a recent line of research found that priming the concepts of general "action" or "inaction" has nonspecific effects on both cognitive and motor performance (Albarracín et al. 2011): Activation of the general "action" concept led to higher performance than activation of the general "inaction" concept.

Albarracín et al. (2008) used a goal-priming procedure. That is, the researchers first activated either the concept of action or inaction using different priming procedures. Then, after the activation of the action or inaction concepts, participants performed different types of cognitive or physical tasks. As already mentioned above, the

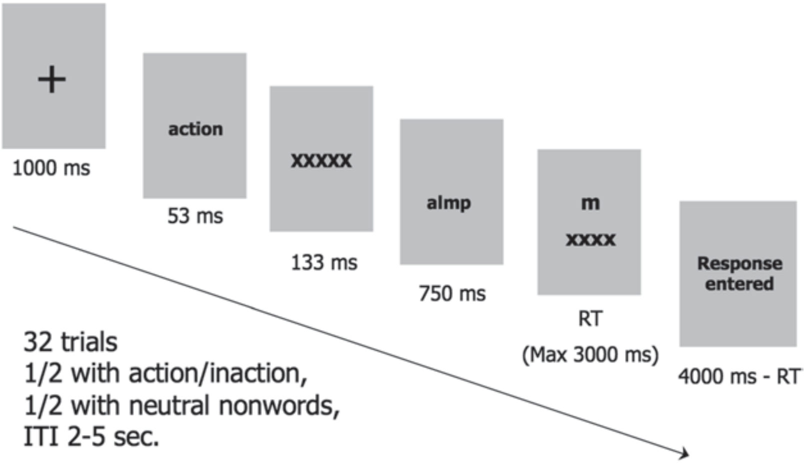

Fig. 18.3 Trial structure of the recognition memory task in the experiment by Gendolla and Silvestrini (2010). Reaction Time (RT) and Inter Trial Interval (ITI)

studies revealed that the implicit activation of the action concept led to higher performance than the implicit activation of the inaction concept. These performance effects may be attributed to higher effort due to the activation of the action concept. However, as also discussed above, performance depends on more variables (e.g., ability or strategy) than effort alone (Locke and Latham 1990). Thus, performance measures alone give only limited insight into effort intensity. However, most relevant for the present analysis, there is evidence that priming the "action" concept leads to stronger cardiac PEP response than activation of the "inaction" concept, which is a reliable measure of effort, as discussed above.

18.3.1 Evidence for Automatic Effort

An experiment by Gendolla and Silvestrini (2010) tested the hypothesis that activating the concepts of action or inaction *during* task performance would "directly" lead to either mobilization (action) or withdrawal (inaction) of effort under "do-your-best" instructions. To achieve this, we applied a behavior-priming procedure and integrated action and inaction primes *into* a task to establish a so-called direct perception–behavior link rather than exposing participants first to the primes and assessing then if this has effects on a subsequent task—as usually done in goal-priming studies. On the basis of the research by Albarracín et al. (2008), we also anticipated corresponding effects on task performance, specifically, better performance in the action-prime condition than in the inaction-prime condition.

After a habituation period for physiological baseline assessment, participants were randomly assigned to an action-prime, inaction-prime, or control condition and performed a recognition memory task. The concepts of general action and inaction were activated using corresponding words (action: go, run, action, fast; inaction: sleep, slow, passive, stop) that were suboptimally presented during a Sternberg-type short-term memory task. The prime words were largely inspired by studies by Albarracín et al. (2008). To prevent fast habituation to the prime words, half of the trials presented nonwords, created by juggling the letters of the action and inaction primes. In the control condition, only nonwords were presented. As depicted in Fig. 18.3, trials of the memory recognition task started with a fixation cross (1000 ms) followed by a prime word (53 ms) and then a backward mask (XXXXXXX, 133 ms). The mask was followed by a string of four letters (750 ms) and then again a backward mask with a target letter appearing above the mask. At this moment, participants had to indicate by pressing a "yes" or a "no" key if the target letter was part of the previously presented string or not. Effort intensity was operationalized as responses in cardiac PEP during task performance.

As expected, exposure to backward-masked action words resulted in significantly stronger PEP reactivity than exposure to masked inaction words. Reactivity in the control group fell in between these two conditions, indicating that the action primes led to “real” effort mobilization, while the inaction primes resulted in “real” effort withdrawal. Moreover, task performance revealed a corresponding pattern and was correlated with PEP: Reaction times rose from the action via the control to the inaction-prime condition. Thus, performance corresponded to effort-related cardiac response: When effort was low, performance was weaker than when effort was high. These results provide the first evidence that the implicit activation of action and inaction cues can directly influence effort mobilization and performance in a cognitive task.

18.3.2 An Explanation: Event Coding

We have interpreted the action/inaction-priming effects on effort mobilization (Gendolla and Silvestrini 2010) as further evidence for an automatic—i.e., implicit and unintentional—link between perception and behavior (see Bargh and Chartrand 1999; Dijksterhuis and Bargh 2001). More specifically, we have elaborated on basic assumptions of the theory of event coding (Hommel et al. 2001) to explain how action and inaction primes that are processed online *during* the performance of cognitive tasks can influence effort mobilization. This approach holds that planned actions (e.g., executing a given task) and simultaneously perceived events (e.g., primes) share a common representational domain. Consequently, features that are activated in the perception domain can influence the action domain correspondingly. As we have outlined earlier (Gendolla and Silvestrini 2010), the concept of action (in contrast to inaction) involves—as its fundamental feature—the mobilization of resources, because all actions need resources to be executed. In a task context, the action concept feature “effort” and the specific task-related activity—which also involves the feature “effort” because it needs resources to be carried out—share a common representational domain. Consequently, activating the general action concept *during* task performance should result in increased effort invested into the task, while activation of the inaction concept should lead to effort withdrawal.

In contrast to the goal-priming approach by Albarracín et al. (2008, 2011), this is an interpretation in terms of an ideomotor principle in behavior priming (cf. Förster and Liberman 2007). As we spell out in more detail below, we do not doubt that it is possible to activate action and inaction goals, as suggested by Albarracín and colleagues. However, we posit that it is also possible to prime effort directly online during task performance according to an ideomotor principle.

18.4 Part III: Integration—Resource Conservation Moderates Automaticity

Evidence for automatic effort mobilization through action/inaction priming and the significant role of the resource conservation principle have existed in parallel, proposing apparently diverging mechanisms and key variables determining effort. To overcome this conceptual gap in understanding the processes underlying resource mobilization, we have recently suggested a conceptual integration of both principles of resource mobilization (Silvestrini and Gendolla 2013). This conceptual integration—which we call here a *bounded effort automaticity approach*—has been guided by the idea that the resource conservation principle moderates and limits automaticity effects on effort. Accordingly, priming action and inaction during task performance should have an automaticity effect on effort mobilization, but—importantly—only as long as success is possible and justified. That is, we posit that the resource conservation principle sets limits to effort automaticity.

In a broader theoretical perspective, our conceptual integration aims at advancing the understanding of the moderating and limiting conditions of priming effects on behavior, supporting the relatively new idea of *situated automaticity* (e.g., Loersch and Payne 2011; Wheeler and DeMarree 2009). Referring to the “situated” aspect, our bounded effort automaticity approach posits that task context, in terms of objective task difficulty and incentives for success, moderates and limits automaticity effects on effort mobilization according to the resource conservation principle.

18.4.1 Bounded Effort Automaticity

If the resource conservation principle indeed sets limits to the automaticity effect on effort mobilization, then automatic effort mobilization due to the above-discussed principles of event coding (Hommel et al. 2001) should only occur as long as success is possible and justified. Consequently, implicitly activating the action concept during task performance should result in higher effort than priming inaction on all task difficulty levels on which success is possible—e.g., on easy, moderate, and difficult performance levels—but not when success is obviously impossible. In the latter condition, effort should be low in general because people disengage in order to avoid resource mobilization that would have no effect, because this would violate the principle for resource conservation (e.g., Gendolla and Richter 2006b). That is, the automaticity effect of the action/inaction cues should not occur because the person's construal of the situation moderates and limits automaticity. Or in short, one cannot prime the impossible.

Besides the moderating effects of task difficulty, incentives should also have a boundary effect on automatic effort mobilization if one takes the resource conservation principle into account. The reason is that incentive determines the amount of *justified* effort, or potential motivation, as discussed above (Brehm and Self 1989). Consequently, low incentives should limit automatic effort mobilization, because low incentives only justify low effort (see Silvestrini and Gendolla 2011; Richter and Gendolla 2009; Wright et al. 1990). The implicit activation of the action concept during task performance may potentially stimulate the mobilization of high resources, but actual effort should only be mobilized to the degree to which it is justified. Or in short, one cannot prime the unjustified.

In summary, our integrative bounded effort automaticity approach suggests the following: Implicit activation of the action concept during task performance increases effort mobilization "automatically," but only as long as success is possible and the necessary effort is justified. That is, automatic effort mobilization is situated in—and thus moderated and bounded by—task context. Two experiments tested this idea.

18.4.2 Evidence for Bounded Effort Automaticity

To test the hypothesis that effort can only be mobilized automatically as long as success is possible, Experiment 1 by Silvestrini and Gendolla (2013) manipulated the objective difficulty of a memory recognition task—participants worked on an easy, difficult, or extremely difficult task—and were simultaneously exposed to suboptimally presented (i.e., masked) action versus inaction primes. According to our bounded effort automaticity approach, action primes should lead to higher effort-related cardiac response than inaction primes as long as success is possible, but they should have no effect in the extremely difficult condition, where success is impossible. Task difficulty was manipulated by presenting series of three (easy) versus seven (difficult) versus fourteen (extremely difficult) digits for 750 ms. In half the trials, the letter strings were preceded by a backward-masked action versus inaction word, respectively. In the other half of the trials, nonwords were presented to prevent fast habituation to the primes. After the task, participants rated experienced task difficulty, subjective ability, and success importance and were interviewed in a funnel debriefing procedure about the study's purpose and what they had seen during the trials (Chartrand and Bargh 1996). Effort intensity was operationalized as responses in cardiac PEP during task performance.

The error rates and the subjective task difficulty manipulation check both reflected a highly efficient task difficulty manipulation with significant differences between all three difficulty levels. That is, task difficulty was clear for participants. Thus, if effort mobilization would have only been piloted by the resource conservation principle, a difficulty main effect should have emerged on PEP, with weak reactivity in the easy condition (low demand), strong reactivity in the difficult condition (high demand), and weak reactivity in the extremely difficult, actually impossible condition (disengagement). However, in support of our bounded effort automaticity approach, task difficulty interacted with the action/inaction primes, as depicted in the top panel of Fig. 18.4.

As predicted by our bounded effort automaticity approach, effort intensity was stronger in the action-prime than in the inaction-prime condition as long as success was possible, i.e., in both the easy and the difficult conditions. But when it was impossible to succeed on the task, the primes lost their effect and participants disengaged. Moreover, PEP reactivity was correlated with participants' reaction times, and effort was especially linked to performance in the difficult condition. Here, correct responses were faster in the action-prime condition than in the inaction-prime condition, as presented in the bottom panel of Fig. 18.4. Apparently, effort had no strong impact in the easy and extremely difficult conditions, which makes sense because in both conditions performance should have been highly ability-dependent. In the easy condition, all participants had far enough ability to succeed, while no participant's ability was sufficient to succeed in the extremely difficult condition. Consequently, effort could not contribute much to performance on these two difficulty levels. However, effort had a stronger impact on performance in the difficult condition, where performance was less strongly determined by ability, leaving more variance to be explained by effort.

Finally, in the funnel debriefing procedure, only four participants could guess the content of the primes suggesting that 94 % of the participants processed the primes without awareness of their meaning. In summary, this study revealed that the resource conservation principle limited the automaticity effect on effort mobilization. Or in other words, due to the resource conservation principle it was not possible to prime the impossible.

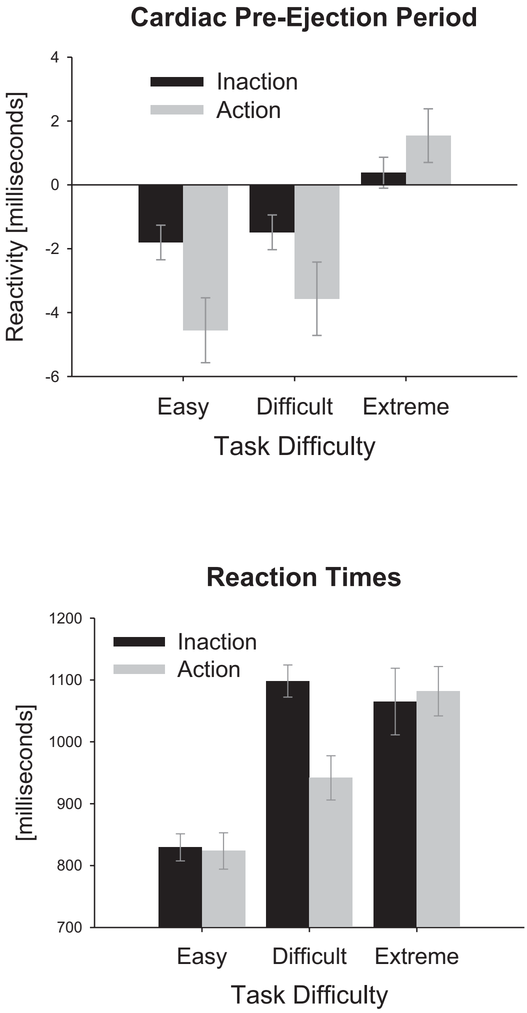

Fig. 18.4 Cell means and standard errors of cardiac pre-ejection period (*top panel*) and reaction times (*bottom panel*) in Experiment 1 by Silvestrini and Gendolla (2013). (Printed with permission. Copyright: American Psychological Association)

Experiment 2 by Silvestrini and Gendolla (2013) tested the second limit that the resource conservation principle should be set to automatic effort mobilization—success incentive determining the level of justified effort. Therefore, participants expected low versus high monetary incentive for success on an arithmetic task that took about 5 min. According to our bounded effort automaticity approach, action primes should "automatically" lead to higher effort than inaction primes, but only if success incentive is sufficiently high to justify the high effort in the action-prime condition. This was only warranted in the high-incentive condition.

After completing measures of cardiovascular baseline values, participants worked on a moderately difficult arithmetic task, adapted from Bijleveld et al. (2010), with integrated action versus inaction primes. The priming procedure was similar to our above-discussed experiments. In each trial, an arithmetic equation appeared after the backward mask of the primes. The equations consisted of three single digits adding up to a sum. Participants had to indicate by pressing respective response keys within a response time window of 3.75 s whether the equation was correct (e.g., 4+5+9=18) or incorrect (e.g., 7+2+6=14). Before the task, participants learned that they could win either 1 Swiss franc (about US$ 1, low incentive) or 15 Swiss francs (about US$ 16, high incentive) if they responded correctly in at least 90 % of the trials. Effort intensity was again operationalized as responses in cardiac PEP during task performance.

As depicted in the top panel of Fig. 18.5, results were as expected: PEP reactivity in the action-prime/high-incentive condition was significantly stronger than in the other three conditions. That is, action primes led only to higher effort than inaction primes when high incentive also justified the mobilization of relatively high resources. When success incentive was low, also priming action resulted in only low effort, because the high effort potentially activated by the action primes was not justified. The reactivity patterns of SBP and DBP corresponded with that of PEP (i.e., stronger blood pressure responses when PEP response was strong). Moreover, as presented in the bottom panel of Fig. 18.5, task performance in terms of error rates corresponded to PEP. Participants committed significantly fewer errors in the action-prime/high-incentive condition, where PEP response was strong, than in the other three conditions, where PEP response was weak. This indicates again a significant link between effort and performance.

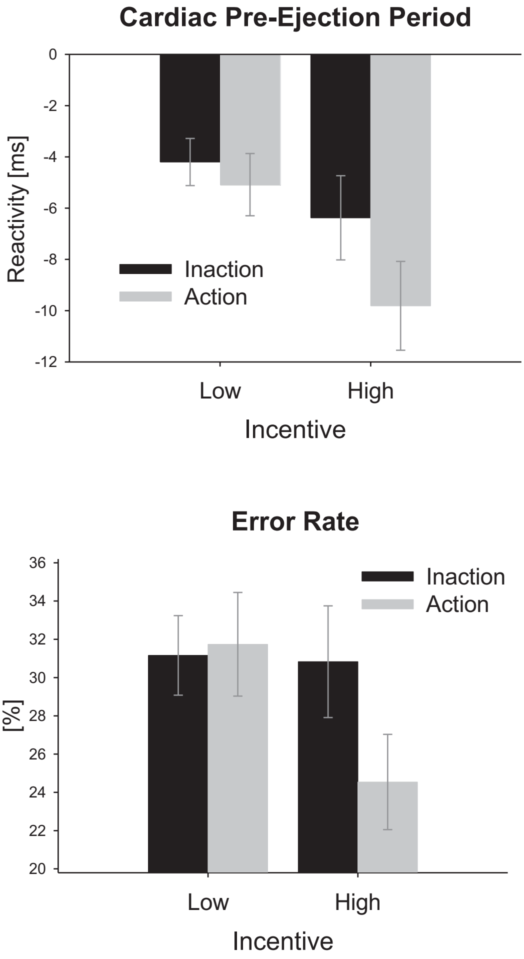

Fig. 18.5 Cell means and standard errors of cardiac pre-ejection period (*top panel*) and error rates (*bottom panel*) in Experiment 2 by Silvestrini and Gendolla (2013). (Printed with permission. Copyright: American Psychological Association)

18.5 Part IV: Conclusions—All's Well That Ends Well

As discussed at the beginning of this chapter, the resource conservation principle and its elaboration in terms of motivational intensity (Brehm and Self 1989) has provided clear and strong predictions for resource mobilization, which have found ample support in studies on effort-related cardiovascular response (see Gendolla et al. 2012;

Wright and Kirby 2001 for reviews). However, research on automaticity has suggested that effort mobilization can also be stimulated directly, i.e., without considering task demand as the key variable (Gendolla and Silvestrini 2010). The present chapter has provided an attempt to integrate these two empirically supported, though apparently incompatible, principles of effort mobilization in terms of a bounded effort automaticity approach. Our basic idea is that implicit activation of the general action versus inaction concepts can influence effort mobilization "automatically" through an event coding principle (Hommel et al. 2001), but that the energy conservation principle sets limits to this. Accordingly, automatic effort mobilization should occur only as long as success is possible and the necessary effort is justified. We interpret the results of the two experiments by Silvestrini and Gendolla (2013) as support for our bounded effort automaticity approach. That is, task context in terms of objective task difficulty and success incentive moderated and limited the automaticity effect on effort mobilization. Or in other words, we could only prime the possible and justified.

Other researchers have similarly found that implicitly processed motivational stimuli can influence physiological reactions referring to resource mobilization (e.g., Bijleveld et al. 2009; Capa et al. 2011; Pessiglione et al. 2007; Silvia 2012). However, the effects on PEP in our studies (Gendolla and Silvestrini 2010; Silvestrini and Gendolla 2013) are among the clearest evidence to date that effort mobilization can be influenced automatically, because action versus inaction primes were processed online during performance and PEP is a highly reliable and valid indicator of effort mobilization (Kelsey 2012; Wright 1996). Moreover, adding to the predicted effects on effort in terms of PEP reactivity, our studies found significant effects on performance. Implicitly activating the action concept did not only result in increased resource mobilization but also brought return. This is not always the case, because in addition to effort, performance is at least also determined by ability and strategy (Locke and Latham 1990). Moreover, the effort–performance link may depend on the type of task. In inhibitory tasks, action primes may also lead to higher effort, but simultaneously to worse performance, as suggested by recent evidence for an inaction-prime advantage in inhibitory tasks (Hepler and Albarracín 2013; Hepler et al. 2012).

Our findings also suggest that action and inaction primes' impact on behavior is not limited to goal-priming procedures (cf. Albarracín et al. 2011). In our experimental paradigm, action and inaction primes were processed online during task performance rather than before a task. Processing the primes had an immediate effect on effort that even overrode the information about objective task difficulty on feasible difficulty levels. However, this does not contradict the idea that action and inaction primes *can* also induce implicit action and inaction goals in a goal-priming paradigm, in which participants perform tasks *after* instead of while action and inaction have been primed (e.g., Albarracín et al. 2008). In our priming procedure, participants are already engaged in a task and their goal is already set. Consequently, action and inaction primes in our paradigm are expected to influence effort mobilization according to an event coding process (Hommel et al. 2001)—but only as long as success is perceived as possible and justified.

In a broader conceptual perspective, we hope that our analysis encourages more attempts to specify the boundary conditions of already identified general psychological principles. Concerning automaticity, researchers have recently started to investigate such conditions in terms of a situated automaticity approach (e.g., Loersch and Payne 2011; Wheeler and DeMarree 2009). To date, that research has primarily studied how persons' evaluations of administered primes moderate their effects—for example, the difference between the effects of primes that are regarded as valid or trustworthy versus those that are regarded as invalid or untrustworthy (e.g., DeMarree et al. 2012; Loersch and Payne 2012). Other research has shown that primes only influence thoughts and behaviors when these environmental stimuli are relevant in a given situation (e.g., Cesario et al. 2010), contributing to a better understanding of applicability as a boundary condition for the effects of implicitly activated concepts. Extending the basic idea that automaticity effects are context-dependent, we have here proposed that also a person's construal of a given task situation in terms of what is possible and justified moderates automaticity effects on behavior. We think that identifying more of such boundary conditions that specify *when* and *how* automaticity is moderated is more fruitful for advancing our understanding of human action than endlessly discussing if behavior is primarily piloted by conscious *or* unconscious processes. According to our present bounded effort automaticity approach, both processes can work together very well—and we are sure that this is only one example for that.

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The Intensity of Behavioral Restraint: Determinants and Cardiovascular Correlates

19

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19.1 Behavioral Restraint: Fighting the Urge

Effective functioning sometimes requires behavioral restraint, that is, resistance against an urge to act in a way that could yield an undesired consequence or set of consequences. Consider, for example, an alcoholic experiencing an urge to drink or a soldier experiencing an urge to flee. Processes involved in behavioral restraint commonly are referred to as *self-regulatory* or *inhibitory control* processes. They are thought to be multifaceted and to engage multiple bodily systems, including the cognitive, affective, and behavioral systems (Baumeister 1998; Molden et al. 2012).

19.2 Restraint Intensity

In this chapter, we examine restraint from the perspective of an integrative analysis that has guided research in our laboratory for over two decades. The analysis offers an understanding of restraint *intensity*—that is, the degree of restraint at a point in time —and makes suggestions about cardiovascular (CV) responses that might be associated with it. An understanding of restraint intensity is important in part because restraint outcomes—i.e., self-regulatory successes and failures—should at least sometimes depend on it (Harkins 2006). An understanding also is important because there is reason to believe that restraint could sometimes impact health. Thus, for example, Pennebaker and colleagues (Pennebaker 1989, 1995; Pennebaker et al. 1988) have argued that personal trauma can produce urges to disclose and that resistance against these can yield adverse health consequences, including hypertension and compromised immune system function (see also Polivy 1998). A common assumption is that health risk increases the more frequently and forcefully people resist, which highlights the need for a conceptual framework that allows anticipation of the presence and power of resistance.

Suggestions about CV responses that might be associated with restraint intensity are noteworthy because they draw attention to pathological pathways through which restraint could lead to some adverse health outcomes (Bongard et al. 2012; Contrada 2011; Kamarck et al. 1997). The suggestions also present the possibility that the CV system could provide a covert means of assessing degrees of resistance, something that could be of practical value in laboratory, clinical, and other settings.

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19.3 Integrative Analysis

The integrative analysis begins with the idea that a particular class of CV adjustments—those associated with beta-adrenergic sympathetic nervous system (SNS) activity—vary with effort, that is, the degree to which people work intensively in a performance situation (Kahneman 1973; Higgins 2006). The greater the level of effort, the more pronounced the adjustments are expected to be. This is a simple adaptation of the well-known "active coping" hypothesis proffered by Obrist (1976, 1981; Light 1981).

Beta-adrenergic activation increases the frequency and force of ventricular (heart) contractions (Brownley et al. 2000; Kelsey 2012). However, frequency effects can be masked by coincidental parasympathetic nervous system activity, which works to slow heart rate. Accordingly, heart contraction force is considered to be the preferred, "gold standard" beta-adrenergic index.

A secondary "downstream" indicator of beta activation is systolic blood pressure (SBP), defined as the peak arterial pressure following a heartbeat. SBP is determined by the force of its preceding beat in combination with vascular resistance—vascular constriction affecting space in the vascular network. Holding constant or increasing vascular resistance (i.e., holding constant or decreasing vascular space), SBP should rise with heart contraction force and, thus, beta-adrenergic activation. SBP could rise with contraction force in the presence of a decrease in vascular resistance (i.e., an increase in vascular space), although this would depend on the balance—or relative strength—of the relevant changes in force and resistance. Thus, for example, a sharp increase in contraction force might cause SBP to rise in the presence of a modest resistance decrease, whereas a blunted increase in contraction force might not. The reason would be because the augmenting effect of the sharp increase on SBP might more than offset the dampening effect of the modest resistance decrease, whereas the augmenting effect of the blunted increase might not. Measures of SBP are easier to obtain than measures of heart contractility. Consequently, effort investigators have been especially likely to employ them despite their limitations and required cautious interpretation.

With Obrist's hypothesis in place, the integrative analysis applies Brehm's motivation intensity theory (MIT; Brehm and Self 1989; Richter 2013; Wright 1996, 2008) and an ability extension from it (Ford and Brehm 1987; Wright 1998; see also Kukla 1972) to identify conditions under which people should display more and less effort and associated CV responses when presented a performance challenge, i.e., a chance to alter some course of events by acting.

19.3.1 Motivation Intensity Theory

In brief, MIT asserts that effort is determined directly (proximally) not by factors associated with success importance (e.g., need, incentive value) but rather by what can, will, and must be done to achieve a purpose driving behavior. If the purpose can be achieved easily, then performers should exert little effort regardless of how important they perceive success to be. As the difficulty of achievement increases, so should effort up to one of two points (i.e., difficulty levels). The first is the point at which effort requirements are no longer justified by the significance (i.e., importance) of the driving purpose. The other is the point at which purpose achievement is viewed as impossible. In short, effort should comport with difficulty until success is viewed as excessively difficult—given the benefit that may be accrued—or impossible. So long as success is possible, its importance should moderate the relation between difficulty and effort. That is, its importance should determine whether the requirements of a challenge are justified and, thus, whether effort will be proportional to difficulty or low.

Fundamental relations among effort, difficulty, and success importance are depicted in Fig. 19.1a. This figure presents a case in which importance sets the upper limit of effort exertion. Presentation of a case in which impossibility sets the upper limit would show a drop in effort prior to the point (difficulty level) at which effort intersected with the horizontal importance line.

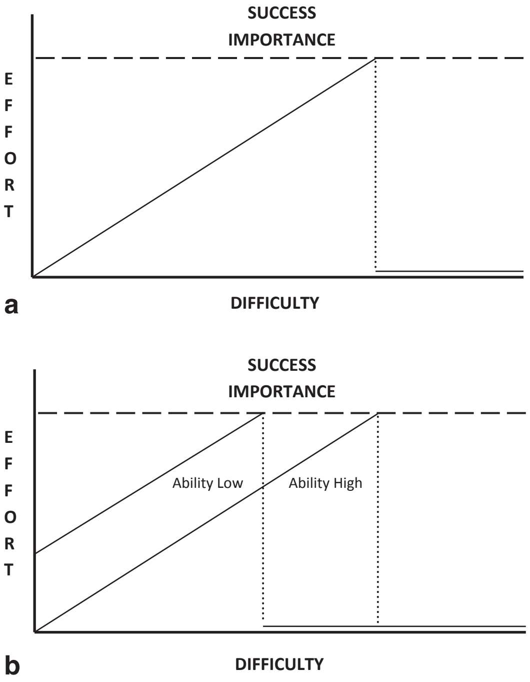

Fig. 19.1 Effort intensity as a function of difficulty and success importance (*Panel A*) and difficulty, success importance and ability (*Panel B*)

19.3.2 Ability Extension

Ability has been incorporated into the integrative analysis through the intuitive assumption that less capable (i.e., low-ability) performers view relevant performance challenges as more difficult than more capable (high-ability) performers (Hockey 1997; Kanfer 2011). This implies that low-ability performers should exert more effort than high-ability performers so long as they view success as possible and worthwhile (Fig. 19.1b). It also implies that low-ability performers should withhold effort at a lower difficulty level than should high-ability performers, because they should conclude more readily that success is either excessively difficult or impossible for them. Where both low- and high-ability performers view success as excessively difficult or impossible, ability should bear no relation to effort, being low for both groups. In theory, success importance should moderate the relation between ability and effort at a given difficulty level so long as success is perceived as possible. Thus, for example, ability might be inversely correspondent to effort at a modest difficulty level if importance is high (reflecting stronger striving where ability is low), but directly correspondent to effort at this difficulty level if importance is moderate (reflecting stronger striving where ability is high—see Fig. 19.2).

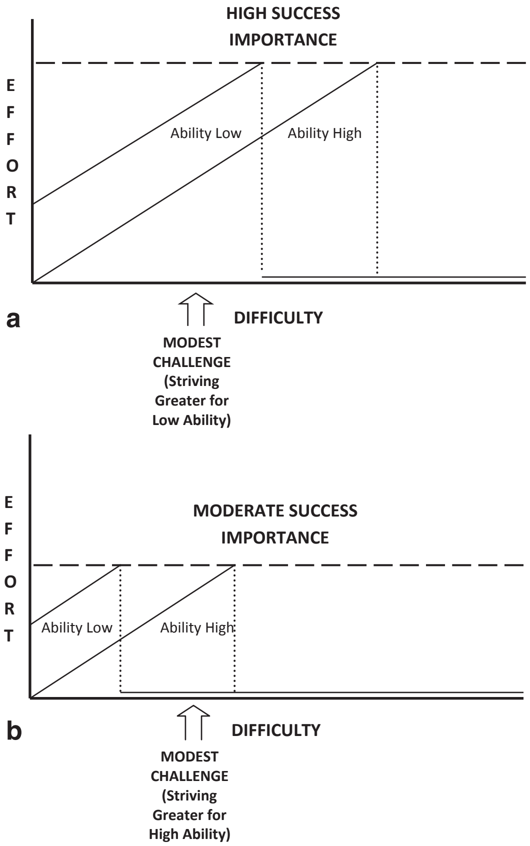

Fig. 19.2 Effort intensity for low- and high-ability performers at a modest difficulty level where success importance is high (*Panel A*) and moderate (*Panel B*)

19.4 Financial Investment Metaphor

Our effort thinking can be elaborated through use of a financial investment metaphor (Wright 1998, 2008; Wright and Kirby 2001; for a similar use, see Kruglanski et al. 2012). We envision effort as a finite currency invested following a principle of conservation. We see performers as having an upper limit on how hard they can try and being inclined to expend effort, (1) only to the degree it is needed and (2) only under conditions where it yields a return that exceeds its own value. Difficulty in this metaphor corresponds to the price of an item that might be purchased. As the price increases, so does the currency performers invest so long as the price is justified and the purchase is possible. If the price exceeds what performers can "pay" or are willing to pay, no investment will be made. Where a purchase is impossible, effort should be low because its expenditure will yield no benefit. Where a purchase is possible, but not justified, effort should be low because its expenditure will yield a return of insufficient value.

We connect ability in this context with the value—or purchase *power*—of the effort currency that is available. We see high-ability performers as having more valuable currency than low-ability performers. That is, we see them as being able to accomplish more at any given effort level than low-ability performers in the same way that travelers carrying a high-value currency can purchase more at any unit investment level than travelers carrying a low-value currency. Just as low-value travelers will have to expend more to meet a possible and worthwhile price, so will low-ability performers have to expend more to meet a possible and worthwhile performance challenge. Similarly, just as low-value travelers will disengage from the purchase process at a lower price point, so will low-ability performers disengage from goal pursuit at a lower difficulty level. Even high-value travelers can be confronted with a price that they cannot or will not meet. At and beyond this price point, these travelers should hold their cash in reserve in the same way that travelers with low-value currency should, rendering null the relation between purchase power and currency investment. In like fashion, high-ability performers can be confronted with challenges that they cannot or will not meet. At and beyond this difficulty level, the performers should hold their effort in reserve as low-ability performers should, rendering null the relation between performance capacity and effort investment.

We might note in discussing this metaphor that, insofar as we know, published depictions of MIT do not spell out our assumption that performers have an upper limit on how hard they can try. However, the assumption comports with MIT reasoning regarding the impossibility of success and has intuitive appeal. Further, it has been implicit in elaboration regarding the role ability should play in determining effort intensity. In context of the financial investment metaphor, the finite effort performers have available is analogous to finite cash travelers might have in their wallet or purse. For travelers, purchase will be impossible if the value of available cash is insufficient to meet a given price. For performers, success will be impossible if the performance product of maximum effort is insufficient to meet a given performance demand.

19.5 Fatigue as an Ability Factor

Before returning to behavioral restraint, we might note further that a number of recent experiments have examined effort correlates of fatigue construing fatigue as one factor that can determine performance ability (see Wright and Stewart 2012, for a review). In combination with the ability reasoning discussed above, this construal intimates that fatigue should not have a single effort influence, but rather a multifaceted one—sometimes augmenting effort, sometimes retarding it, and sometimes having no effect on it. Broadly, fatigue should combine interactively with difficulty and success importance to determine the extent to which performers apply themselves in meeting a performance challenge. Interactional relations among effort, difficulty, success importance, and fatigue can be seen in Fig. 19.1b, replacing the label "ability low" with "fatigue high" and the label "ability high" with "fatigue low." The recent fatigue experiments have conceived of fatigue in terms of resource depletion within a performance system and are strongly relevant to an influential limited resource analysis of self-regulatory control developed by Baumeister et al. (2007; Lopez et al., this volume; Muraven and Baumeister 2000;

Vohs et al. 2008). The limited resource analysis has a similar fatigue conception and is discussed in more detail below.

19.6 Intensity of Behavioral Restraint

So what might this integrative reasoning tell us about the intensity of behavioral restraint? Application begins with the understanding that urge resistance is a purpose that can be pursued more or less intensively, with pursuit (i.e., restraint) intensity arguably affected by at least three factors. One intensity factor is the *value* that people place on restraint, that is, how important they consider self-regulatory success to be. Another is the magnitude of the urge that must be resisted. A third is the ability of the individual experiencing the urge to resist. In the subsections that follow, we discuss these factors and the roles they should play in determining restraint intensity—taking the integrative analytic view.

19.6.1 Importance of Regulatory Success

The perceived importance of self-regulatory success should affect the intensity of resistance because it should determine people's willingness to work to resist an urge. Higher importance appraisals should be associated with greater willingness. This factor must be considered in models of resistance intensity because there is reason to believe that importance appraisals vary markedly across situations and people.

19.6.1.1 Situation Variation

It is more important to restrain in some situations than in others. Reasons can be related to social norms, as might be the case for an individual resisting the urge to cough at a concert hall as opposed to a doctor's office. But they will not necessarily, pertaining instead to nonnormative costs and benefits. Consider for example a soldier on the wrong side of enemy lines. She might refrain from crying out when she steps on a nail—not to abide by a norm, but rather to avoid capture. Some situations are broadly conducive to behavioral restraint, whereas others are conducive in a highly specific fashion. Specific conduciveness would apply to (1) particular urges, (2) particular people, and (3) particular urges in particular people. Consider in this regard a funeral, which can include norms that call for global respectful reserve in nonintimates of the deceased, but allow for overt expressions of grief (but not, say, erotic joy) among intimates.

19.6.1.2 Person Variation

Some people place greater value on restraint than do others. Once again, reasons can be variable, having to do with such things as culture, religious training, family background, and experience with outcomes that are believed to have followed from low or high self-control (Lu et al. 2012). People can place a broad premium on restraint or a premium that is more specific. Specific premiums would apply to (1) particular urges, (2) particular situations, and (3) particular urges in particular situations. Thus, for example, a Christian evangelical from the south of the USA might have a value system that calls for resistance against aggressive, but not devotional, urges in a Sunday worship service, but the reverse in a Saturday football game.

19.6.2 Urge Magnitude

Also affecting restraint intensity should be the power with which an urge is felt. Urge magnitude should be influential because it sets the external difficulty of the restraint challenge, with restraint being more difficult in the presence of a more powerful urge. By "external," we mean the difficulty of the restraint challenge not taking resistance ability into account. Once again, this factor must be considered in models of restraint intensity because there is reason to believe there are marked variations moving across situations and people.

Points of note regarding situational and personal variations in urge magnitude are similar to those pertaining to situational and personal variations in restraint importance. Some situations can be assumed to be more evocative of urges than others. Some are broadly evocative whereas others are specifically evocative, that is, evocative (1) in regard to a limited set of urges, (2) for a limited set of people, or (3) in regard to a limited set of urges for a limited set of people. Examples might be political conventions and family gatherings that include discordant members, respectively. Political conventions can evoke a range of (e.g., inspirational) urges in many attendees (broad evocativeness); by contrast, family gatherings with discordant members can evoke a narrow set of (e.g., hostile) urges in some, but not all, attendees (specific evocativeness).

Just as some situations are likely to be associated with stronger urges, so might be some people. That is, it is reasonable to assume that some people experience urges more intensively than others. They could do so broadly, as has been discussed in regard to personality dimensions such as impulsivity, extroversion, and sensation seeking (Eysenck et al. 1985; Revelle 1997; Zuckerman 2009). Alternatively, they could do so specifically, in regard to limited urges, in limited situations, or in regard to limited urges in limited situations. Thus, for example, teenagers as a group might feel some (e.g., erotic), but not other (e.g., nurturing), urges with special strength when presented some—but not all—relevant stimuli.

19.6.3 Ability to Resist

The third intensity factor identified, ability to resist, has been discussed widely, but not always with discussions including a clear articulation of what should make people more and less restraint-capable. The most developed and influential ability position is seen in the limited resource analysis mentioned earlier (Lopez et al. this volume; Muraven and Baumeister 2000). In its most familiar form, this analysis holds that self-regulatory (i.e., behavioral) restraint involves a special inhibition system that functions like a muscle. Comparable to a muscle, the proposed system can become resource depleted (i.e., fatigued) and thereby weakened in the short term through use. Also like a muscle, the system can be strengthened through extended use over time. The limited resource analysis implies that people can vary in restraint ability both in the short term and in the long term, with short-term variations reflecting degrees of fatigue and long-term variations reflecting degrees of strength. Ability discussed in this sense should affect restraint intensity because it should combine with the magnitude of an urge experienced to determine what must be done to resist. Holding urge magnitude constant, people with low restraint ability should have to do more to resist than people who have high restraint ability.

19.6.4 Roles of the Restraint Intensity Factors Taking the Integrative View

With the restraint intensity factors discussed in these terms, it is easy to see the roles they should play in determining restraint intensity taking the integrative analytic view. As illustrated in Fig. 19.3a, restraint value (i.e., regulatory success importance) appraisals should set the upper limit of what people would be willing to do to restrain, but not determine restraint intensity directly, as some might suppose. What should determine restraint intensity directly is the difficulty of the restraint challenge, which should be a function of the magnitude of the urge resisted. Where resistance is perceived as possible and worthwhile, its intensity should be proportional to difficulty. Where resistance is perceived as impossible or excessively difficult—given the importance of regulatory success—resistance should be low, with importance appraisals moderating the relation between effort and difficulty so long as success is perceived as possible.

Also contrary to what some might suppose, restraint ability should not exert a single influence on restraint, but rather a multifaceted influence dependent on the difficulty of the restraint challenge and the value placed on meeting it (Fig. 19.3b). Where both low- and high-ability restrainers view success as possible and worthwhile, restraint intensity should be (1) correspondent to difficulty

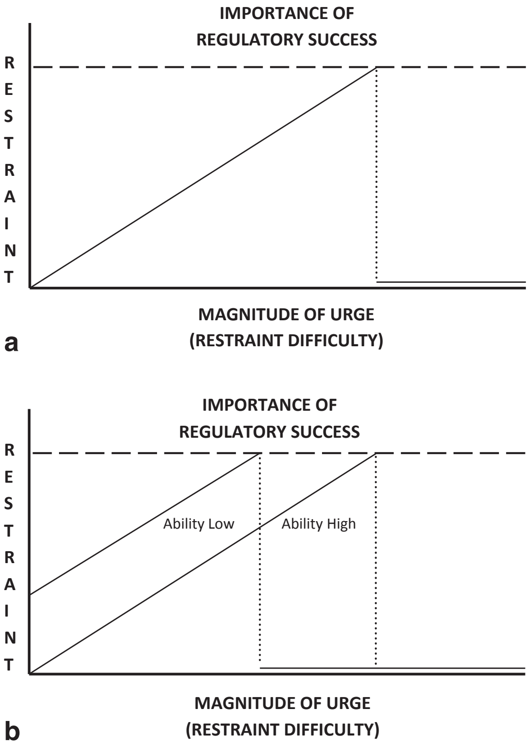

Fig. 19.3 Restraint intensity as a function of urge magnitude and value placed on success (*Panel A*) and urge magnitude, value placed on success and restraint capacity, including that associated with fatigue (*Panel B*)

for both groups and (2) greater for the low-ability group by a constant. Where high-ability restrainers view success as possible and worthwhile, but low-ability restrainers do not, restraint intensity should be (1) low for the low-ability group and (2) correspondent to difficulty for the high-ability group. Where difficulty and value appraisals are such that neither low- nor high-ability restrainers view success as possible and worthwhile, restraint intensity should be low for both groups.

19.7 CV Correlates

Of course, the integrative analysis addresses not only effort but also CV responses associated with it, assuming proportionality between effort intensity and beta-adrenergic SNS activation. The CV component suggests that the regulatory success importance, urge magnitude, and restraint ability factors discussed above might combine interactively to determine the intensity of this class of CV responses in the same way that they should combine to determine restraint intensity. Just as restraint intensity should first rise and then fall abruptly with the difficulty of a restraint challenge (i.e., the magnitude of an urge), so might the relevant CV responses—with the importance of regulatory success moderating the relation between difficulty and the responses so long as success is possible. Similarly, just as restraint intensity should bear different relations to restraint ability under different regulatory success importance and difficulty (urge magnitude) conditions, so might these CV responses. In short, all the relations indicated for restrain intensity in the panels of Fig. 19.3 might also hold for beta-adrenergic responsiveness.

19.8 Direct Evidence

Direct evidence for this application of the integrative analysis is undeniably thin. It consists chiefly of findings from two types of experiments, ones that show (1) elevated CV responses in participants directed to resist an impulse (Gross 1998; Gross and Levenson 1993; see also Wegner et al. 1997) and (2) elimination of self-regulatory performance deficits in "ego" (i.e., resource)-depleted participants under incentivized performance conditions (Muraven and Slessareva 2003). The findings comport with the notion that restraint requires work that can enhance CV activity and be promoted through the provision of incentives. However, they do not evaluate the nuanced implications of the application, such as the implication that resistance and associated CV responses should bear different relations to restraint ability under different success importance and difficulty (urge magnitude) conditions.

19.9 Indirect Evidence

On the other hand, indirect evidence for the application—from nonregulatory tests of the integrative analysis and its application—is abundant.

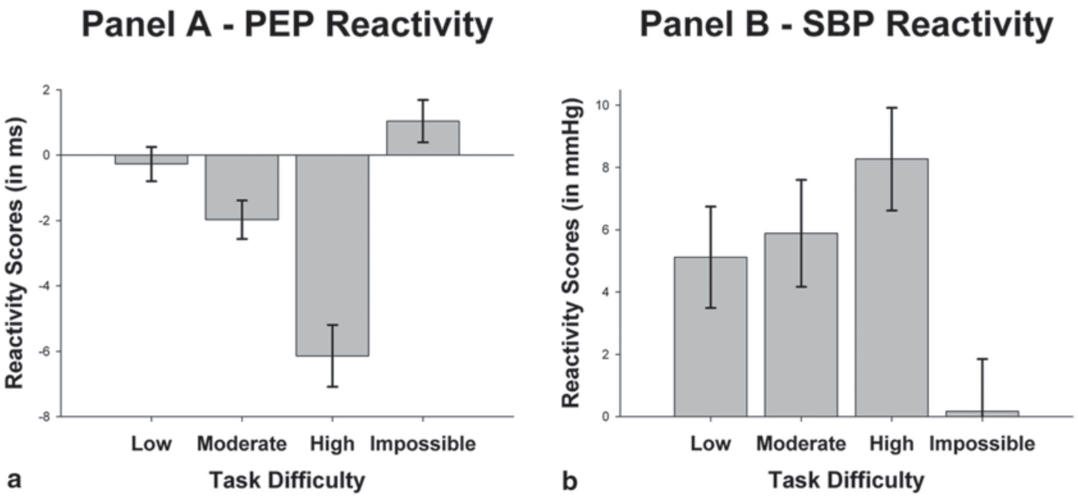

Fig. 19.4 Pre-ejection period (PEP—*Panel A*) and systolic blood pressure (SBP—*Panel B*) responsiveness at four levels of task difficulty. Bars indicate standard errors. Note that lower PEP values indicate increased heart contraction force. (From Richter et al. 2008—reprinted with permission from John Wiley and Sons, also seen in Fig. 24.2 in Gendolla et al. 2012)

Early reviews of the relevant literature considered data from studies that involved a variety of protocols and effort intensity indices (e.g., Brehm and Self 2001). Later reviews focused on CV studies, which emerged as the largest component of the full body of evidence (Gendolla and Richter 2010; Gendolla and Wright 2005; Gendolla et al. 2012). Collectively, the reviews revealed remarkable support.

19.9.1 Simple Examples

To provide a flavor, consider a simple CV response study by Richter et al. (2008). Expanding on work by Obrist et al. (1978), Smith et al. (1990), Wright et al. (1986), and others, the investigators presented participants trials of a character recognition task whose difficulty varied across four levels, ranging from low to impossibly high. For some participants (mild challenge), the initial character string was displayed for 1000 ms; for others (moderate challenge), the string was displayed for 550 ms; for a third group (strong challenge), the string was displayed for 100 ms; for a final group (impossible challenge), the string was displayed for 15 ms. As expected, SBP and heart contraction (pre-ejection period, or PEP) responses assessed during performance rose steadily across the first three difficulty conditions and then fell (Fig. 19.4).

Also consider an experiment by Silvia et al. (2010) that examined interaction implications in an objective self-awareness (OSA) theoretical context (see Silvia, this volume). OSA theory (Duval and Wicklund 1972) asserts that self-focus draws attention to where one stands in regard to performance standards, elevating the importance of meeting them. Applying the integrative analysis, an implication is that self-focus should moderate the relation between difficulty, on the one hand, and effort and associated CV responses, on the other, so long as task success is possible. Investigators presented participants a more or less difficult scanning task (d2; Brickenkamp 1981) under conditions more or less conducive to self-focus, using a mirror focus manipulation. Easy participants had 3000 ms to scan; difficult participants had 650 ms to do so. Analysis of SBP data collected during performance showed the expected 3 versus 1 response pattern. Responsiveness was correspondent to difficulty when self-focus was

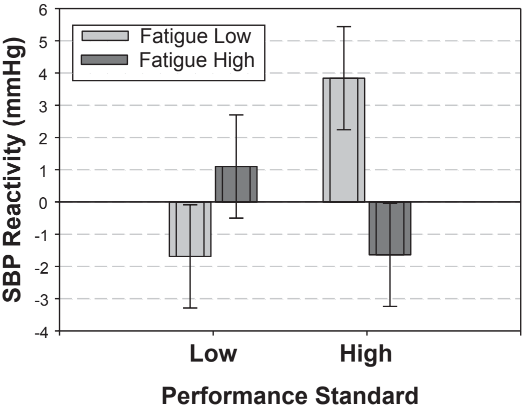

Fig. 19.5 Systolic blood pressure (SBP) responsiveness as a function of difficulty for low- and high-fatigued participants. Bars indicate standard errors. (Based on data from Wright et al. 2003—also seen in Fig. 24.4 of Gendolla et al. 2012)

high, but low irrespective of difficulty when self-focus was low.

19.9.2 Ability Construed as Fatigue

Illustrative of studies that evaluated more complex influences are two CV experiments that crossed difficulty and ability factors operationalizing ability in terms of fatigue, assuming lower ability among more fatigued participants. These are especially relevant to the restraint application because so much attention has been devoted to the Baumeister limited resource model of self-control. One experiment (Wright et al. 2003) examined the idea that mental fatigue should augment or retard effort and associated CV responses depending on whether it causes success to be perceived as excessively difficult or impossible. Participants performed an easy (fatigue low) or difficult (fatigue high) counting task for 5 min. They then were presented mental arithmetic problems with the chance to earn a prize if they attained a low (30th percentile) or high (80th percentile) performance standard. Analysis of second period SBP responses revealed a fatigue × standard (difficulty) interaction, with means in a crossover pattern (Fig. 19.5). Analysis of diastolic blood pressure (DBP—the trough pressure following a heartbeat) and mean arterial pressure (MAP—average pressure across a heart cycle) data revealed the same interactions and mean configurations.

The other experiment (Stewart et al. 2009) evaluated the implication that success importance should moderate the relation between mental fatigue, on the one hand, effort and associated CV responses, on the other, at a given difficulty level so long as success is possible. It first manipulated fatigue by requiring participants to perform an easy (fatigue low) or difficult (fatigue high) paced scanning task (version of the d2) and then presented the participants mental arithmetic problems with instructions that they would earn a high or low chance of winning a prize if they did as well as 50 % of those who had performed previously. Investigators assumed that extra demand associated with fatigue would be justified when the chance (i.e., success importance) was high, but not when it was low (Bandura 1982; Vroom 1964). Consequently, they anticipated fatigue augmentation of effort and associated CV responses under high-, but not low-, chance conditions. Analysis of task period CV responses confirmed the prediction for SBP and revealed similar DBP and MAP response patterns.

19.10 Summary and Concluding Comments

We have sketched here an understanding of behavioral restraint intensity and CV responses that may accompany it. The understanding represents an application of an integrative analysis that has guided research in our laboratory and has distinctive implications relative to traditional self-regulation perspectives. One core idea is that restraint intensity varies proximally with the magnitude of the urge resisted—first rising and then falling, with the fall occurring where regulatory success appears impossible or excessively difficult given its importance. Another is that restraint ability factors have different influences on restraint intensity depending on the magnitude of an urge and the importance of resisting it. This second idea has special relevance to the Baumeister limited strength model of self-regulation, which articulates how people can become more and less restraint-capable through short- and long-term efforts to maintain behavioral control. CV responses accompanying restraint intensity may be those associated with beta-adrenergic SNS activation, most often assessed in terms of heart contraction force and SBP. Direct evidence for this understanding is limited, but indirect evidence—from nonregulatory tests of the integrative analysis and its application—is abundant.

The sketched understanding is noteworthy in part because it has potential for improving prediction of regulatory successes and failures, which can—but will not necessarily—correspond to how hard restrainers try. It suggests for example that where the effort-to-performance relation is favorable, success importance factors should tend to predict performance if those factors determine whether the effort required to meet a possible restraint challenge is justified, but not if they do not determine this. If the factors determine whether the required effort is justified, restraint intensity should be greater and regulatory success should be more likely under high-importance conditions. If the factors do not determine whether the required effort is justified—in other words, if the effort is or is not justified at all levels of the factors—restrain intensity and success likelihood should be dissociated with success importance (see Fig. 19.3a). The understanding is noteworthy as well because it has potential for improving prediction of adverse health outcomes that might follow from restraint. It identifies conditions under which possibly health-toxic restraint efforts should occur in different degrees and suggests for example that chronic regulatory system fatigue might (1) be associated with health risk when it does not alter the perception that regulatory success is possible and worthwhile, but (2) not be associated with health risk when it does (Fig. 19.3b).

The suggested link between restraint intensity and the magnitude of certain CV responses draws attention to pathways through which restraint might negatively impact health. In particular, it draws attention to the so-called reactivity hypothesis, which delineates (e.g., mechanical) outcomes that can accompany persistently exaggerated CV responses and lead to pathological endpoints (Kamarck et al. 1997). This hypothesis cannot account for all adverse health outcomes that have been linked to resistance, but it can reasonably be supposed to account for some, such as hypertension. The suggested link also presents the possibility that resistance might be assessed covertly via careful tracking of beta-adrenergic SNS adjustments.

We feel comfortable with this understanding as a model of restraint intensity, but recognize that it is not a final product. There is much empirical work to be done to establish the validity of the core ideas. There also is conceptual work to be done, for example, regarding additional factors that might be incorporated. Concerning additional factors, special thought might be devoted to the value that performers place on restraint resources. There is reason to believe this can vary and have an impact on the willingness to work (Kruglanski et al. 2012; Muraven et al. 2006).

A question relevant to this and all other discussions of behavioral restraint is what determines the presence and intensity of behavioral urges (Frijda 1986). The answer is critical because it tells us when resistance in different measures can occur. Investigators commonly assume that urges are evoked by salient outcomes and vary to the degree that those outcomes have personal significance (“relevance”). However, this almost certainly represents an oversimplification. It is beyond our scope here to delve into this issue, but we can conclude by referring readers to a sister theory of MIT—Brehm’s emotion intensity theory (EIT)—for possible direction. EIT has received modest attention since it was proposed, but represents one of the most sophisticated treatments of behavioral urges to date. Central presentations (e.g., Brehm 1999) should be required reading for all serious students of regulatory control.

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Self-Striving: How Self-Focused Attention Affects Effort-Related Cardiovascular Activity

20

Paul J. Silvia

20.1 Introduction

Unlike most animals, humans can mentally represent themselves and their actions. We can think about ourselves, reflect on our pasts, consider what we are doing, and envision what we might do instead. As a result, human action is flexible: People can intervene in the flow of behavior and direct their actions. Many streams of social thought have addressed the consequences of our capacity for self-reflection, from theories of personality concerned with how people judge themselves (e.g., Freud 1923) to sociological theories of how people internalize and experience social norms (e.g., Shibutani 1961).

In social-personality psychology, the first modern theory of self-regulation was probably Duval and Wicklund's (1972) theory of objective self-awareness. Duval and Wicklund proposed that reflecting on the self causes self-evaluation: People judge themselves against salient standards and become motivated to meet them. The theory has been unusually fertile since then, sparking a family of related theories (e.g., Carver and Scheier 1998; Duval and Silvia 2001; Gibbons 1990; Hull and Levy 1979) and applications to many clinical and applied problems. The present chapter digs into one of the theory's fundamental problems: How does self-awareness influence effort? When people reflect on the self, why do they strive harder for goals or decide that the goal is not worth the effort? How do beliefs about goal attainment, such as self-efficacy and positive expectancies, influence effort?

This chapter reviews a line of psychophysiological research that takes a novel perspective on the classic problem of self-awareness, self-regulation, and effort. Using motivational intensity theory as a model of effort (Brehm and Self 1989), we show (1) how the self-regulatory dynamics presumed by self-awareness theory can be grounded in physiological processes, and (2) how the predictions made by self-awareness theory can be refined and extended. Intersecting self-awareness theory and motivational intensity theory thus offers a new look at some classic problems in self-regulation.

20.2 Objective Self-Awareness Theory

Objective self-awareness theory, first developed by Duval and Wicklund (1972), proposed that people could experience the self subjectively or objectively. Subjective awareness of the self involves experiencing the self as the agent of action. In this mode, people are absorbed in what they are doing, whether it is thinking, behaving, feeling, or interacting with others. Objective awareness of the self, in contrast, involves experiencing the self as the object of thought. People

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reflect on themselves just as they would reflect on other people or on objects in the world. Objective self-awareness is typically prompted by reminders of the self as an observable object, such as seeing one's image in a mirror or video monitor (Duval 1976; Silvia and Phillips 2004; Wicklund and Duval 1971), being watched by other people (Carver and Scheier 1978), sticking out in the social context (Silvia and Eichstaedt 2004; Snow et al. 2004), or having self-knowledge activated via priming (Macrae et al. 1998; Silvia and Phillips 2013). Over the years, alternative terms for "objective self-awareness" have become more common, such as self-awareness, self-focused attention, self-focus, and self-consciousness.

When people hold the self as the object of attention, they can think about it and evaluate it. Duval and Wicklund (1972) proposed that objective self-awareness evokes an automatic process of self-evaluation, which consists of comparing the self to internalized standards of correctness. If people fall short of their standards, then heightened self-focus creates negative affect and motivates them to strive to meet the standard. The self-to-standard comparison process was thought to be the fundamental consequence of self-awareness. Thus, although the term *self-regulation* was not widely used in the early 1970s, it is clear that the original self-awareness theory was fundamentally a self-regulatory theory. The nature and dynamics of self-awareness have been expanded by many later models, some of which emphasized self-regulation (Carver and Scheier 1998), information processing (Hull and Levy 1979), and inner experience (Gibbons 1990). Readers interested in the contemporary state of self-awareness research can consult several recent reviews (Carver 2012; Duval and Silvia 2001; Silvia and Duval 2001a; Silvia and Eddington 2012).

Most of the evidence for the self-regulatory effects of self-awareness has used two classes of methods: self-reports and behavioral measures. The most diverse, self-report measures have examined a wide range of outcomes that reflect striving to meet standards. Some studies have examined how people's self-reported beliefs align with their standards. When self-focused, people are more likely to report attitudes and preferences that align with internalized standards and values (Baldwin and Holmes 1987; Gibbons 1978). Other studies have shown that increasing self-focus will change self-reported positive and negative affect (Phillips and Silvia 2005) and reduce state self-esteem (Ickes et al. 1973) when discrepancies from standards are made salient. Finally, self-awareness shifts the self-reported attributions people make for failing to meet standards. When self-focused people feel able to meet a standard, they attribute failure to themselves (Duval and Silvia 2002); when they feel unable to meet a standard, they attribute failure defensively to the standard (Dana et al. 1997; Duval and Lalwani 1999) or to other people (Silvia and Duval 2001b).

Behavioral measures have played a large role in self-awareness research, largely due to the emphasis on behavior in the early experiments. Some studies measured behavioral avoidance. When success is unlikely, people can reduce awareness of a self-standard discrepancy by avoiding self-focus, such as by leaving the situation (Greenberg and Musham 1981) or immersing oneself in distracting activities (Moskalenko and Heine 2003). Typically, however, studies have measured motivation to meet a standard. These studies explicitly seek to measure motivation, and they have done so using measures of *performance* (how well people do) and *persistence* (how long they spend).

Performance outcomes assess motivation to meet a standard based on how well people actually perform. For example, if the standard is to do well on a computer-based cognitive task, researchers can measure whether self-focus improves response times or accuracy (e.g., Eddington and Foxworth 2012; Silvia and Phillips 2013). Another approach is to measure how close people get to achieving a goal (Carver et al. 1979b) or to assess observers' ratings of how well people performed a task (Burgio et al. 1986; Silvia and Phillips 2004, Study 2). In all cases, motivation is presumably reflected in greater success. Persistence outcomes, in contrast, assess motivation to meet a standard based on the duration of activity. Persistence is usually measured in units of time. For example, researchers have used the time spent working on a task—often an unsolvable one—as a measure of motivation (e.g., Carver et al. 1979a). In other cases, persistence is measured as units of work. Several studies, for example, have asked people to copy foreign text and quantified motivation as the number of words copied (e.g., Duval and Lalwani 1999; Wicklund and Duval 1971).

One theme of the large self-awareness literature is that people's expectancies are critical moderators of the effects of self-awareness on motivation. When self-focused attention reveals a discrepancy between the self and a standard, people will vary in their perceived ability to reduce the discrepancy. Carver and Scheier (1981) proposed that people's expectancies moderated whether self-focus caused approach or avoidance. Most work has viewed expectancies as simply favorable or unfavorable, akin to self-efficacy for attaining the standard (Carver and Scheier 1998). In later work, Duval et al. (1992) suggested that perceived *rate of progress*—people's expectancies for attaining the standard in light of how far away they are—more accurately captures the nature of people's expectancies. In either case, many experiments have found interactions between self-focus and expectancies: People are most likely to strive to meet a standard when they are self-focused and feel they might be able to attain it (for reviews, see Carver 2012; Duval and Silvia 2001).

The self-awareness literature is deeply interested in self-regulation and motivation, but its measurement of motivation has conflated some important distinctions. In particular, it is essential to distinguish between *effort, performance,* and *persistence* as aspects of motivated action. Effort, the intensity aspect, reflects the intensity of motivation recruited during goal striving. Effort seems to be what most researchers intended to measure, but they assessed it obliquely using performance (the quality aspect) and persistence (the duration aspect). These three aspects can covary, of course, but they have important differences. For example, some tasks can be completed successfully in a short period of time, so high effort and high performance will entail low persistence. In other cases, high persistence can reflect a distracted and listless approach to a task—something familiar to professors who have heard students say they stayed up all night studying—so high persistence can involve low effort and low performance. And in other cases, high performance need not entail high effort. How well people perform is affected by many things—level of effort, cognitive abilities, and task-specific strategies and skills—so effort is but one of many factors. In many cases, high effort can be associated with poor performance. Compensatory effort—such as when people try harder to make up for stress or fatigue—is a classic example of high effort in the face of poor performance (Hockey 1997).

20.3 Motivational Intensity Theory

Understanding how self-awareness affects effort requires intersecting self-awareness theory with a theory of effort dynamics. Motivational intensity theory (Brehm and Self 1989), developed by Jack Brehm during the late 1970s, offers a graceful and productive model of why and when people mobilize and withdraw effort. It starts with the reasonable assumption that effort involves mobilizing energy for the purpose of attaining a goal. Because effort is not free—both in expending caloric energy and in creating wear and tear on the body due to gearing up—the intensity of effort is guided by rational principles aimed at conserving energy (Richter 2013).

Motivational intensity theory is reviewed in detail in several other chapters in this volume (see chapters by Brinkmann and Franzen; Richter; Wright; and Gendolla and Silvestrini) as well as in several recent reviews (Gendolla and Richter 2010; Richter 2013; Wright 2008; see also Wright and Gendolla 2012), so only the main ideas will be covered here. Unlike many models of motivation, which seek to encompass all possible variables with a morass of arrows and boxes, motivational intensity theory emphasizes two abstract variables that influence effort: the *importance* of the goal and the *difficulty* of achieving it. The joint effects of these factors are shown in Fig. 20.1. The importance of the goal determines *potential motivation,* the amount of effort people are willing to expend if needed. Importance thus establishes a ceiling on the level of effort. The difficulty of attaining the goal, in contrast, determines the actual amount of motivation expended. Motivation is low when difficulty is low and then increases as difficulty increases. Eventually, motivation will decline for one of two reasons. In some cases, people hit the ceiling of potential motivation—they could attain the goal with further effort, but the goal is not important enough to do so. In other cases, the goal seems impossible to attain—expending more effort for an impossible goal is fruitless, so motivation should decline for impossible tasks.

Tasks with a fixed level of difficulty are "all or none" tasks: People either perform at the required level and achieve the goal or they do not. Some tasks, however, do not have a level of difficulty. Such tasks are sometimes known as piece-rate tasks, do-your-best tasks, or unfixed-difficulty tasks; for simplicity, we will use *unfixed tasks* (Wright et al. 2002). In piece-rate work, for example, people receive a reward for each unit of work. In research, these tasks either offer a reward for each successful action or simply tell people to do their best and accomplish as much as they can during the task period. For such tasks, the theory predicts that the degree of effort should be a function of the value of the reward. Effort for unfixed tasks is thus defined by the level of potential motivation (Wright 2008).

Much of the power of motivational intensity theory comes from its links to physiological measures. Wright (1996; Wright and Kirby 2001) integrated motivational intensity theory with Obrist's (1981) psychophysiological research on autonomic activity during active coping. Wright highlighted the significance of the sympathetic branch of the autonomic nervous system as a marker of effort. Cardiovascular measures of sympathetic activity have been the most popular. One effect of increased sympathetic activity on the heart is increased contractility (Drew and Sinoway 2012; Mohrman and Heller 2010), the force of the heart muscle's contraction. Increased contractility increases cardiac output, the amount of blood pumped per minute, which (all else equal) increases systolic blood pressure (SBP; the peak pressure during a contraction period). SBP is thus an indirect marker of the influence of sympathetic activity on the heart. Although less direct and precise than metrics such as the cardiac pre-ejection period (PEP; the time in milliseconds between the onset of contraction and the opening of the aortic valve; Kelsey 2012), SBP has been more widely used, in part because of its methodological simplicity and its intuitive bridges to the study of stress and health.

20.4 Integrating Self-Focus and Motivational Intensity

Motivational intensity theory's two parameters—difficulty and importance—give it enormous breadth. The many influences on effort, from personality traits to transient states, can be understood as factors that shift difficulty or importance, not as singular causes of effort in their own right. Given the theory's scope and elegance, it is not surprising that it has emerged as a major perspective in modern motivational science (see Gendolla et al. 2012).

How might we intersect self-awareness theory with effort dynamics? The two key variables found in the self-awareness literature—expectancies and self-focused attention—align well with the difficulty and importance parameters in motivational intensity theory. People's expectancies regarding their ability to achieve a goal dovetail naturally with the difficulty parameter. Furthermore, self-focused attention probably influences the importance parameter. Theories of self-focus generally agree that self-focused attention brings about a self-evaluative state that can reveal unpleasant discrepancies between the self and its goals, values, and standards (Carver 2012; Duval and Silvia 2001). Other models have suggested that self-focus makes standards more salient (Gibbons 1990) or self-relevant (Hull and Levy 1979). In all cases, however, self-focus can be easily seen as a factor that increases the importance of meeting goals and standards (Gendolla and Richter 2010).

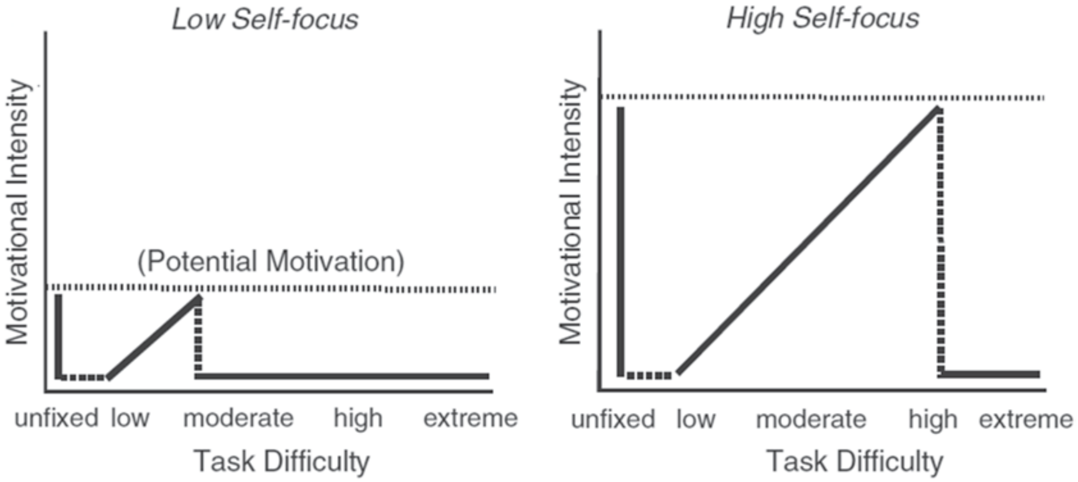

Fig. 20.1 The joint influence of potential motivation and task difficulty on the intensity of motivation. For unfixed tasks, motivation is a function of potential motivation; for fixed difficulty tasks, motivation rises until it hits the ceiling of potential motivation and then declines. (From Gendolla et al. 2008, Fig. 1. Reprinted with permission)

Motivational intensity theory does more than simply recast the literature on self-awareness; it can make nonintuitive and refined predictions concerning effort. Specifically, motivational intensity theory offers several new ideas for the study of self-awareness.

First, self-focus and task difficulty should jointly affect effort in a nonlinear function (see Fig. 20.1). When self-focus is low and success is thus less important, effort should be relatively low regardless of task difficulty. But when self-focus is high and success is thus more important, effort should be a nonlinear function of difficulty: low for easy tasks, higher for harder tasks, and low again for impossible tasks. This prediction is contrary to the prevailing predictions in the self-awareness literature, which presume that positive expectancies foster higher motivation. In Carver and Scheier's (1998) model, for example, self-focused people should try hardest when they have positive expectancies. According to the rational conservation of resources implicit in motivational intensity theory, however, it would be wasteful to gear up for an easy goal, regardless of how important it is.

Second, the type of task—unfixed or fixed in difficulty—should be an important moderator. Social-personality research on motivation has not generally appreciated this distinction, and it has tended to use unfixed tasks or tasks held constant at a challenging level. For unfixed tasks, effort should be solely due to self-focus, which affects the ceiling of potential motivation; for fixed tasks, effort should be a joint function of self-focus and task difficulty.

And third, we should expect dissociations between effort, measured physiologically, and behavioral performance, measured by how well people actually do on the task. The distinction between effort, performance, and persistence has not seeped into social-personality research, but it is critical. One would expect self-focus and task difficulty to have different effects on performance in some circumstances. When self-focused people face an easy goal, for instance, we would expect low effort but high performance.

The rest of this chapter reviews a series of experiments that examined the effect of self-focus on effort. Using motivational intensity theory as a framework, these studies assessed effort using changes in sympathetic cardiovascular activity. The general method involved assessing SBP, diastolic blood pressure (DBP), and heart rate (HR) during a baseline period and again during a task period. An increase in SBP—higher reactivity from baseline to task—can be interpreted as reflecting higher effort-related sympathetic activity. This chapter focuses solely on the effects for

SBP, but it is worth noting that DBP effects appeared in some studies and HR effects appeared in a few. Unlike SBP, DBP is less consistently affected by beta-adrenergic sympathetic influence on the heart and relatively more affected by alpha-adrenergic peripheral resistance, making it a less reliable marker of beta-adrenergic sympathetic activity than SBP. HR is strongly affected by both sympathetic and parasympathetic branches (Drew and Sinoway 2012), so changes in HR are not easily understood without concurrent assessment of parasympathetic activity.

The first block of studies used explicit manipulations of self-focus, such as mirrors and video cameras. These classic manipulations are "explicit" in that they use obvious stimuli in the environment to evoke strong, conscious feelings of self-awareness. The second block of studies, in contrast, used implicit manipulations, such as rapid masked priming of people's first names. Theories of self-awareness contend that self-focus has the same effects regardless of how it is evoked, so using subtle methods to activate self-knowledge outside of awareness can test the robustness of self-focus's effects on effort. Finally, our third block used individual differences, known as trait self-focus.

20.5 Effects of Explicit Manipulations of Self-Focus on Effort

The most common manipulations of self-awareness are explicit, such as placing people in front of large mirrors or having people view their image on a video monitor. People feel much more self-conscious and know that the stimulus is the cause, so there is both a conscious experience of self-focus and knowledge about its source. These are among the earliest and most popular manipulations (Carver and Scheier 1978; Wicklund and Duval 1971), so they were the natural first step for examining effort dynamics.

In our first experiment (Gendolla et al. 2008, Study 1), we used video recording to manipulate self-focused attention. In the high self-focus conditions, the experimenter used a video camera to record the participant, who could see the image on a small monitor placed on his or her desk. In the low self-focus conditions, no recording was conducted. After a baseline period, people worked on a cognitive task known as the d2 task (Brickenkamp and Zillmer 1998). This task presents *d*s and *p*s on the screen. Each letter has zero, one, or two apostrophes above and below it. People have to indicate whether the letter is a d2 (a *d* with two apostrophes above or below it, or a *d* with one above and one below it) versus any other item. The task is well suited for effort research because it has simple rules and is easily adapted to different difficulty levels and reward structures. In some conditions, people completed an unfixed version of the d2 task: They were told simply to do their best and to get as many correct in the 5-min task period. In other conditions, people completed an easy version of the d2 task: The item appeared on the screen for 3000 ms, and people were told that the standard was to respond correctly 90 % of the time. Responding early did not terminate the trial—the items stayed on the screen for the full 3000-ms response window—so people could not work at their own pace or accelerate the easy task.

Figure 20.2 shows the pattern of results. For the unfixed task, high self-focus increased SBP reactivity; for the fixed-easy task, SBP reactivity was low, regardless. A second experiment (Gendolla et al. 2008, Study 2) used three task levels: an unfixed condition, a difficult condition, and an impossible condition. The unfixed condition, like before, asked people to do their best and work at their own pace. In the fixed conditions, the goal was to get 90 % of the trials correct, and the response windows were 600 ms (difficult but feasible) and 350 ms (impossible). Figure 20.3 shows the results, which again supported our predictions. High self-focus increased SBP reactivity in the unfixed condition and in the difficult condition. In the impossible condition, effort was low. All told, the findings revealed that self-focus increases potential motivation: When the task demanded more effort, self-focused people tried harder. But when the task demanded little effort or was impossible, effort was low, regardless.

A later study examined the biggest difference between traditional self-awareness models and

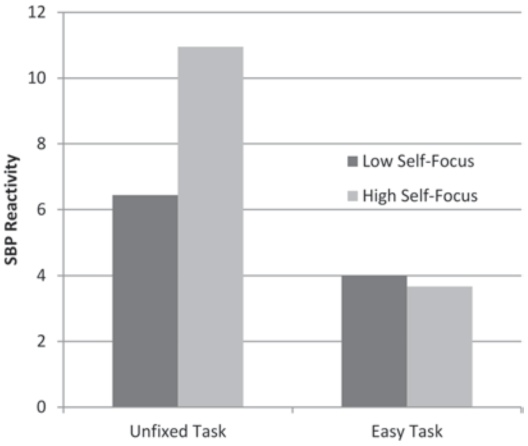

Fig. 20.2 Effects of self-focus on systolic blood pressure (*SBP*) reactivity for unfixed and easy tasks. (Data from Gendolla et al. 2008, Study 1)

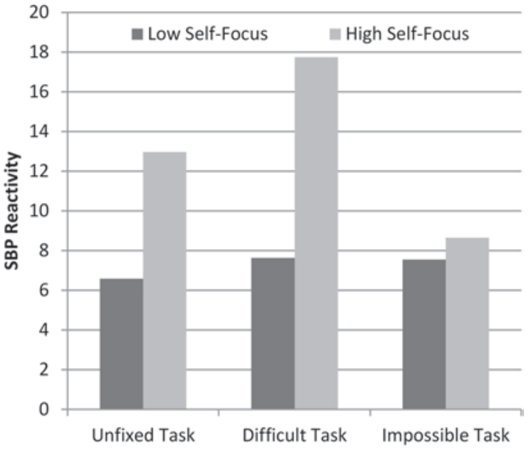

Fig. 20.3 Effects of self-focus on systolic blood pressure (*SBP*) reactivity for unfixed, difficult, and impossible tasks. (Data from Gendolla et al. 2008, Study 2)

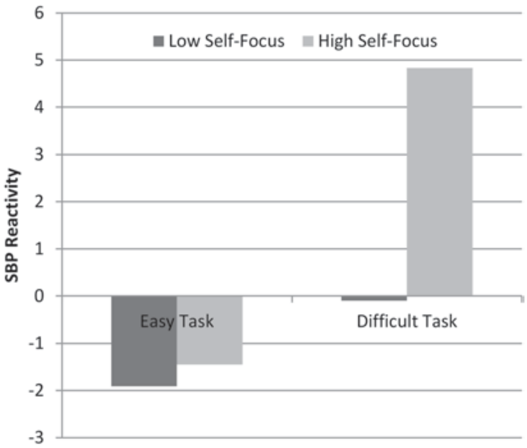

Fig. 20.4 Effects of self-focus on systolic blood pressure (*SBP*) reactivity for easy and difficult tasks. (Data from Silvia et al. 2010)

motivational intensity theory—effort for easy tasks. People have very favorable expectancies for such tasks, so self-awareness theories expect higher motivation (Carver and Scheier 1981). Motivational intensity theory, however, contends that easy goals demand little effort, regardless of how important they are, so effort should be low. In an experiment (Silvia et al. 2010), we varied self-awareness using a large mirror and had people work on a version of the d2 task that was either easy (a 3000-ms response window) or challenging (a 650-ms window). The results, shown in Fig. 20.4, supported our application of motivational intensity theory. When the task was easy, SBP reactivity was low regardless of self-focus; when the task was hard, however, SBP reactivity was high only in the high self-focus condition, consistent with our view that self-focus increases potential motivation. Self-report measures confirmed that people in the easy conditions had much more favorable expectancies regarding goal success, but people only put forth more effort when the goal required it (high difficulty) and merited it (high self-focus).

20.6 Effects of Implicit Manipulations of Self-Focus on Effort

After establishing that motivational intensity can illuminate how self-awareness affects effort, we tested the limits of these effects. Instead of manipulating self-focused attention using conscious methods, we used implicit priming to directly activate self-knowledge. A handful of past studies had found that masked priming of last names (Macrae et al. 1998) and first-person pronouns (Koole and Coenen 2007) were effective, and in our recent behavioral studies, we had found that masked first-name priming replicated mirror manipulations (Silvia and Phillips 2013).

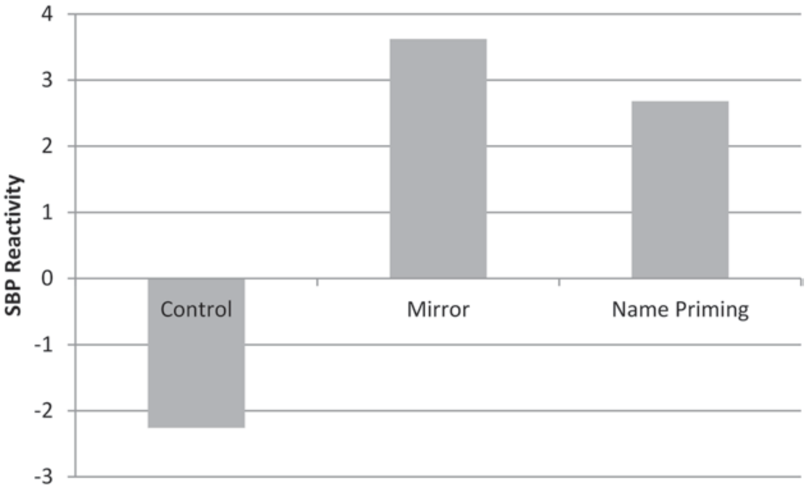

Fig. 20.5 Effects of explicit self-focus (a mirror) and implicit self-focus (first-name priming) on systolic blood pressure (*SBP*) reactivity for an unfixed task. (Data from Silvia 2012, Study 1)

Implicit manipulations are interesting for a few reasons. For one, they allow a test of the generality of self-awareness's effects on effort. Furthermore, they directly target an assumption of self-awareness theory—that self-evaluation is an automatic consequence of directing attention to the self (Carver 2012; Duval and Silvia 2001). The self-evaluative consequences of self-focus thus ought to be apparent when self-focus is sparked outside of conscious awareness. Finally, there is an emerging interest in implicit influences on effort (e.g., Gendolla 2012; Gendolla and Silvestrini 2010), so studying implicit name priming contributes to the broader problem of implicit aspects of effort regulation.

In our first study (Silvia et al. 2011a), we explored how first-name priming during an unfixed version of the d2 task affected SBP reactivity. Because some work had suggested that prime frequency—the percent of trials with a prime—could be important (Silvestrini and Gendolla 2011), we evaluated four conditions. In a control condition, 0 % of the trials had primes; in the other conditions, 33 %, 67 %, or 100 % of the trials started with the participant's first name, which was presented rapidly (27 ms) and masked. We found a significant 3 versus 1 effect of priming: All prime levels beyond 0 % increased SBP reactivity, so the specific frequency seemed less important. The remaining studies thus used either 67 % or 100 % frequencies. In a later study, implicit and explicit manipulations—first-name priming and a large mirror—had the same effects on SBP reactivity during an unfixed task (Silvia 2012, Study 1). As Fig. 20.5 shows, both the mirror and name-priming conditions had higher SBP reactivity than a control condition. These studies support the view that self-focused attention has the same self-evaluative effects regardless of how it is evoked (Duval and Silvia 2001).

We then turned to examining how implicit first-name priming influenced SBP reactivity for fixed-difficulty tasks. In a series of experiments (Silvia 2012, Studies 2 and 3; Silvia et al. 2014), we varied the task difficulty across a range of levels, from very easy to challenging to impossible. As expected, we found the predicted nonlinear functions for SBP reactivity. First-name priming increased the amount of effort people were willing to expend, as shown by increases in effort from easy-to-hard conditions (Silvia 2012). When the task seemed impossible, however, effort declined (Silvia et al. 2014). Most of these experiments manipulated both explicit and implicit self-focus and found that they had the same effects, further supporting the claim that different routes to self-focus have the same effects.

20.7 Effects of Individual Differences in Self-Focus on Effort

Thus far, we have considered experiments that manipulated self-focused attention. A few of our studies, however, have explored individual differences in self-focus. Early in self-awareness research, researchers speculated that people might differ in their habitual tendencies toward focusing on the self (Fenigstein et al. 1975). The early self-consciousness scales proposed dimensions of private self-consciousness, public self-consciousness, and social anxiety (Fenigstein et al. 1975). Over the years, private self-consciousness has attracted the most attention, largely because it is conceptually closest to manipulations of state self-awareness. Because the self-consciousness scales tend to have poor internal consistency, we measured trait self-focus using the self-reflection scale (Grant et al. 2002), either alone or in combination with the revised private self-consciousness scale (Scheier and Carver 1985). The self-reflection scale has a strong internal consistency and performs well (Silvia and Phillips 2011).

In one experiment (Silvia et al. 2011b), we found that trait self-focus had an analogous influence on potential motivation: People high in trait self-focus were more willing to put forth effort than people low in trait self-focus. After completing measures of individual differences, people worked on the d2 task, which was manipulated to be either easy (a 2500-ms window), difficult (a 1250-ms window), or very difficult (a 750-ms window). As shown in Fig. 20.6, people high in trait self-focus had higher potential motivation: They were still willing to expend effort at the highest level of difficulty, whereas people low in trait self-focus had already withdrawn effort. Additional support comes from the implicit priming experiment, reviewed earlier, that varied four levels of priming during an unfixed task (Silvia et al. 2011a). We had measured trait self-focus in that study as well, and we found a significant interaction between trait self-focus and implicit name priming. People high in trait self-focus had higher SBP reactivity regardless of priming, which suggests that they had higher potential motivation.

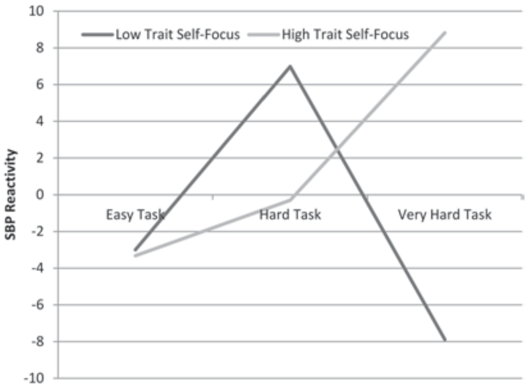

Fig. 20.6 Effects of individual differences in trait self-focus on systolic blood pressure (*SBP*) reactivity for an easy, difficult, or very difficult task. (Data from Silvia et al. 2011a)

But there is probably more to trait self-focus than making goals more important. A curious feature of trait self-focus is that it makes people more sensitive to influences in the environment. Hull's model of self-focused attention has emphasized that self-focus can make ideas and goals more self-relevant (Hull and Levy 1979; Hull et al. 1988). As a result, self-focused people might experience primes as more relevant, causing stronger priming effects. In fact, several studies have found that people high in trait self-focus are more influenced by priming (DeMarree and Loersch 2009; Hull et al. 2002; Wheeler et al. 2008). We thus explored whether trait self-focus amplified the effects of other implicit primes on effort. In an experiment (Silvia et al. 2013), we manipulated both importance and difficulty using rapid masked priming. Importance was varied using name priming (first names vs. no priming); difficulty was varied using words implying an easy task (e.g., *easy, simple*) versus a hard task (e.g., *hard, difficult*). These primes were presented sequentially, using multiple masks, prior to each trial of a d2 task. The task was held constant at a challenging level.

Figure 20.7 shows the results, which were estimated based on regression interactions. When trait self-focus was low, the importance and difficulty primes had minor effects at most on SBP reactivity. But when trait self-focus was high, SBP reactivity followed the pattern predicted by

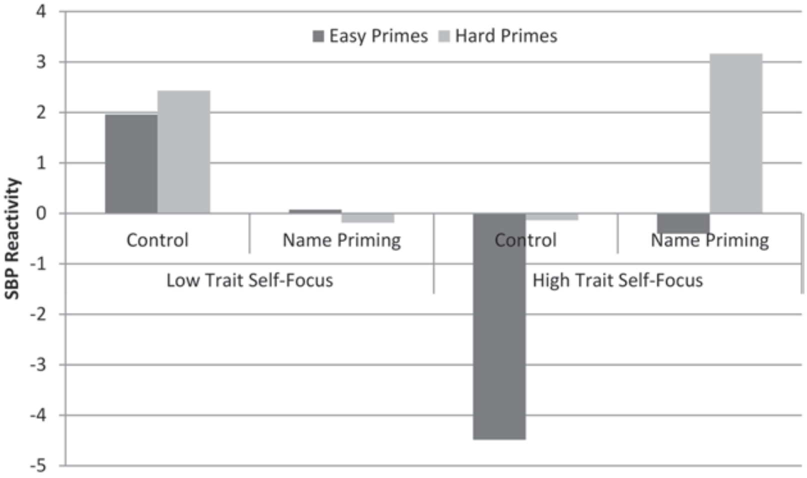

Fig. 20.7 Moderating effects of trait self-focus on the effects of implicit first-name primes and implicit difficulty primes. *SBP* systolic blood pressure. (Data from Silvia et al. 2013)

motivational intensity theory: Effort was highest when success was relatively more important (name priming) and difficult (difficulty priming). The findings thus reveal an additional role for trait self-focus in the regulation of effort. By making importance and difficulty information more self-relevant, trait self-focus amplified their effect on effort. People high in trait self-focus are more likely to capitalize on environmental information that is relevant to goal pursuit, which should make their self-regulatory processes more effective.

Conclusions

This chapter reviewed the interface of two major traditions in motivational science: objective self-awareness theory, a prominent model of self-regulation; and motivational intensity theory, a leading model of effort. Self-awareness research has emphasized the role of self-reflection in behavioral self-regulation; motivational intensity research has emphasized why and when people put forth effort. Together, the models offer new and insightful predictions about the biobehavioral regulation of effort when people are striving for goals.

Self-focused attention can be understood as a factor that makes achieving a goal more important. It is thus like other factors, such as self-relevance and monetary rewards (e.g., Gendolla and Richter 2010; Richter and Gendolla 2009), that affect effort via the importance parameter. People's goal expectancies, like factors such as fatigue and moods (e.g., Gendolla 2012; Wright and Stewart 2012), influence the difficulty parameter. With these assumptions, we can derive predictions about biological effort regulation from motivational intensity theory. As this chapter has shown, these predictions have received strong support.

First, the type of task—unfixed or fixed in difficulty—yields the expected effects. For unfixed tasks, effort is due solely to importance and hence to self-focused attention; for fixed tasks, effort is a joint function of both self-focused attention and task difficulty. Second, extensive support was found for the nonlinear effort functions predicted by the theory. In particular, several studies supported motivational intensity theory's most controversial prediction: that effort is low when expectancies are high, a view that conflicts with the notion that high self-efficacy and positive goal expectancies are themselves motivating (e.g., Bandura 1997; Carver and Scheier 1998). Several experiments found lower effort, measured with SBP reactivity, when tasks were easy than when they were hard (Gendolla et al. 2008; Silvia 2012; Silvia et al. 2010). Although counterintuitive, it follows logically from the assumptions that people would not waste biological effort for tasks that do not require it (Richter 2013).

Finally, we found support for the breadth and generality of self-focused attention. The predicted effort patterns were found for a wide range of methods, including traditional explicit manipulations of self-focus, novel implicit priming manipulations, and self-reported individual differences in trait self-focus.

The integration of these theories has clearly been fertile, and there are many problems remaining that deserve attention in future research. As one example, implicit aspects of self-regulation and effort are an intriguing point of intersection between these literatures. Theories of self-awareness have presumed that the self-evaluation follows automatically when people focus attention on the self (Duval and Silvia 2001). The present studies support this position—implicit methods of inducing self-focus worked at least as well as explicit methods—and they suggest some additional roles for self-focus, such as amplifying the effects of other implicit influences (Silvia et al. 2013). As another example, there are several interesting motivational contexts that have yet to be explored, such as cases in which people are uncertain about how hard a task will be (e.g., Richter and Gendolla 2006) and when people confront challenges that vary unpredictably in difficulty from trial to trial. Finally, the role of motivationally relevant parasympathetic changes have only recently attracted attention in motivational intensity research (e.g., Richter 2010), and it is likely that assessing both autonomic branches will provide rich insight into the control of effort (e.g., Kreibig et al. 2012). In any case, these experiments highlight the value of motivational intensity theory, which can serve as a versatile and powerful framework for a wide range of motivational problems.

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Future Thought and the Self-Regulation of Energization

21

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21.1 Future Thought and Cardiovascular Response

It is a widely held belief of the American popular culture and a credo of the self-help literature that thinking positively about attaining desired future events will help people realize those events, for example, by energizing them to invest the necessary effort to pursue the events (Ehrenreich 2009). In this chapter, we present evidence suggesting that thinking positively about realizing desired futures, if it comes in the form of positive fantasies, may actually be detrimental for effort exertion as it leads to a decreased bodily mobilization of energy. This decreased physiological energization is reflected in a dampened response of the cardiovascular system, which supplies the body with energy in form of oxygen and nutrients. According to fantasy realization theory (FRT; Oettingen 2000, 2012), however, positive future fantasies can be used to wisely self-regulate effort expenditure for pursuing desired futures if they are mental contrasted with the present reality. Indeed, we will present research suggesting that mental contrasting a desired future with present reality can be used as a self-regulation strategy leading to increased or decreased energization, depending on people‘s expectations of realizing the desired future. Such selective effort mobilization assures that people mobilize enough resources when realizing a desired future is possible and save their resources when realizing the future is impossible. Moreover, recent studies suggest that the energy mobilized by mental contrasting the desired future of solving a given task may even be used to fuel effort in a task unrelated to the desired future targeted by mental contrasting. We will discuss these findings in relation to other models of physiological self-regulation, such as motivational intensity theory (Brehm and Self 1989; Gendolla et al. 2013), the biopsychosocial model of arousal (Blascovich and Tomaka 1996), and excitation transfer theory (Zillmann 1983). Finally, we will line out implications for designing interventions geared at improving peoples' self-regulation of effort.

21.1.1 Positive Fantasies About the Future

Positive fantasies about the future are free thoughts and images about desired future events that appear in people's stream of consciousness (Oettingen and Mayer 2002). The depicted events are independent of people's experiences in their reality. A person who is very shy may, for example, envision herself giving a barnstorming speech in front of an absorbed audience or

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walking straight up to her crush to ask for a date. Positive fantasies need to be distinguished from other forms of thinking positively about the future such as beliefs or judgments about whether the desired future events will actually occur (i.e., expectations of success), or as William James noted: "Everyone knows the difference between imagining a thing and believing in its existence" (James 1890, p. 283). In contrast to positive fantasies, people's expectations (i.e., their estimated likelihood of whether the desired future events will be realized) are grounded on their past performance history. Past successes (e.g., having given an excellent presentation) strengthen people's expectations about their future performance; past failures (e.g., having flunked a test) weaken their expectations (Bandura 1997). Precisely because people estimate their expectations on the basis of their past performance, people's estimated expectations provide a valid basis for their future performance. In line with this contention, research consistently showed that positive (vs. negative) expectations predict successful performance (reviews by Bandura 1997; Heckhausen 1991; Seligman 1991).

Because positive fantasies are independent of peoples' past performance, their predictive value for future performance is less obvious. Indeed, Oettingen and Mayer (2002) hypothesized that positive fantasies may actually be detrimental for successful performance, because they may lead people to mentally enjoy the desired events in the here and now (e.g., vividly imagining oneself being awarded one's degree at the graduation ceremony). Doing so may prevent people from mobilizing the effort to actually make the events come true. To test their predictions, in one study, Oettingen and Mayer (study 1) measured fantasies about transition into work life among university graduate students: Students were asked how frequently during their everyday life they had experienced positive and negative, respectively, thoughts, images, or fantasies about graduating from university and getting a job. To obtain an estimate of the extent to which students experienced positive rather than negative fantasies, the researchers subtracted reported frequency of negative fantasies from that of positive fantasies. The researchers also measured students' expectations about transition into work life by asking them how likely they thought it was that they would find an adequate job in their field. Two years later, students were contacted again. In line with earlier findings, students with positive rather than negative expectations had received more job offers and earned higher salaries. As Oettingen and Mayer predicted however, the reverse pattern emerged with respect to positive fantasies: Students who frequently experienced positive rather than negative fantasies had received fewer job offers and earned lower salaries.

Moreover, positive fantasies about attaining the desired events also predicted lower success in starting a romantic relationship in students with a crush on a peer and lower academic success in students anticipating an exam (Oettingen and Mayer, studies 2 and 3). They also predicted slower recovery in patients who had undergone hip replacement surgery (Oettingen and Mayer, study 4), and poorer weight loss in obese patients (Oettingen and Wadden 1991). The pattern emerged for short-term and long-term pursuits, subjective and objective indicators of successful performance, different measures of fantasy (self-reported and semi-projective), and samples of different age groups and cultures (Germany and the USA). As mentioned above, Oettingen and Mayer suspected that positive fantasies are detrimental to performance because they lead people to mentally consume the desired events in their present reality and doing so should keep them from investing the necessary effort to actually pursue the events. If this assumption were true, then the impeding effect of fantasies on effort should prevent the body from mobilizing the necessary resources for effort expenditure and this process should be reflected in a physiological response.

21.1.2 Measuring Energization by Physiological Indicators

Traditionally, energization plays a key role in allowing people to pursue and realize desired events (Brehm and Self 1989; Klinger 1975).

Hull (1943) described variations in behavior as a function of two variables: direction and intensity. Direction specifies whether people approach a certain positive outcome or avoid a negative one (Atkinson 1957; Elliot 2006; McClelland 1985), and intensity refers to the force or vigor with which they do so. According to Hull's drive theory (Hull 1943), the intensity of behavior is determined by the current need state of the organism (e.g., the hours the organism is deprived of food). Unsatisfied needs activate a drive, which in turn energizes behavior. In this vein, energization has also been described as excitation, arousal, or activation (Cannon 1915; Duffy 1934). To fuel the intensity of behavior (e.g., to initiate a fight or flight response, to maintain physical exercise, or to initiate need-satisfying behavior), the organism needs to mobilize energy. In addition to bodily need states (e.g., hunger, thirst; Hull 1943), energization can be caused, for example, by drugs, threatening or novel stimuli, stimuli that prime an action mindset (words such as "action," "go"; Gendolla and Silvestrini 2010), performing difficult tasks, as well as simply thinking about upcoming challenges (e.g., when people anticipate that they will perform difficult arithmetic tasks; Contrada et al. 1984):

The mobilization of energy or bodily resources is associated with the sympathetic branch of the autonomous nervous system (ANS; Brownley et al. 2000). According to Obrist (1981), the most direct indicator of energy mobilization for effort expenditure is beta-adrenergic sympathetic discharge to the heart. Beta-adrenergic discharge directly heightens the force with which the heart contracts (i.e., myocardial contractility). A stronger myocardial contractility in turn increases the volume of blood pumped with a heartbeat (i.e., stroke volume). Stroke volume (SV) and heart rate (HR—the number of heartbeats per time unit) determine cardiac output—the total amount of blood transported through the vessels to supply the body with resources such as oxygen and nutrients per unit of time.

Because cardiac output directly potentiates systolic blood pressure (SBP—the maximum pressure exerted by the blood against the vessel walls) SBP can be used as a noninvasive proxy of energy mobilization (Wright 1996; Wright and Kirby 2001). It should be noted though that in addition to cardiac output, SBP is influenced by total peripheral resistance (TPR)—the resistance of all peripheral vasculature or diameter of the blood vessels. Peripheral resistance is unsystematically linked to sympathetic discharge, that is, sympathetic discharge may constrict some vessels and dilate others. However, even though sympathetic discharge *unsystematically* increases or decreases peripheral resistance, because it *systematically* increases cardiac output and cardiac output directly potentiates SBP, SBP is a reliable proxy for energy mobilization (Wright 1996). Indeed, a multitude of studies has successfully used SBP as an indicator of energy mobilization for effort expenditure (Wright and Kirby 2001).

Other noninvasive cardiovascular measures, such as diastolic blood pressure (DBP, the minimum pressure of the blood against the vessel walls) and HR, are less reliably linked to energization because they are also strongly influenced by other factors (e.g., DBP is, for example, mainly influenced by peripheral resistance and HR is influenced by parasympathetic activity). Therefore, to investigate whether positive fantasies lead to a decreased energy mobilization, Kappes and Oettingen (2011) experimentally induced positive fantasies and thereafter assessed participants' energization by changes in their SBP.

21.2 Positive Fantasies About the Future Dampen Energization

To test their hypothesis that positive future fantasies lead to a reduced energy mobilization that is manifested in a dampened cardiovascular response (measured by SBP), Kappes and Oettingen (2011) conducted two experiments. In two additional experiments, they assessed self-reported feelings of energization.

In the first study, female participants were led to positively fantasize about looking admirable in high-heeled shoes. High-heeled shoes are typically perceived as a fashion item that is associated with elegance and attractiveness (Kaiser 1996). Participants were either told to imagine being glamorous and admired for wearing high-heels (e.g., imagining how men would turn their heads when they would walk by; positive fantasy condition) or they were told to question whether they would actually look so glamorous and attractive in high heels (e.g., imagining how difficult it is to walk in high heels and how easily they might stumble; questioning fantasy condition). SBP was measured before and after participants fantasized about wearing high heels. As predicted, whereas participants' SBP remained stable in the questioning fantasy condition, it decreased in the positive fantasy condition.

In another study, Kappes and Oettingen (study 4) explored a context variable that may influence the link between positive fantasies and energization: whether the fantasies pertained to a currently pressing need. The researchers suspected that because satisfaction of a current need decreases energy expenditure (Atkinson and Birch 1970), fantasies that are directed at satisfying a currently pressing need would be particularly de-energizing. Participants were undergraduates at New York University. As this university is highly competitive, the researchers assumed that its students generally would have a high need for achievement. To satisfy that need for achievement, in half of the student participants a more pressing need was induced (Atkinson and Birch 1970; Blankenship 1987), the need for water. This was done by asking all participants to consume no food or liquid for at least 4 h prior to the experiment and, moreover, giving them salty crackers to eat at the start of the experiment as part of a bogus taste test. Half of the participants were then offered as much water as they wanted. For these participants the need for water was satisfied and thus the need for achievement could surface again. As predicted, for those participants, who after drinking water were again high in need for achievement, induced fantasies about an achievement-related concern (excelling in an important exam) led to lowered SBP. In contrast, in participants who were still thirsty and thus high in need for water, induced fantasies about satisfying their thirst (drinking an ice-cold glass of water) led to lowered SBP. In short, the effect of positive fantasy on de-energization depended on participants' need state. Positive fantasies decreased energy the most when they pertained to a currently pressing need.

The finding that positive fantasies lead to decreased energy mobilization was replicated in two additional studies where energization was assessed via self-reported feelings (e.g., "how active do you feel right now?"): Participants who were induced positive fantasies about winning an essay contest reported feeling less energized than those who were induced negative fantasies (study 2). In addition, participants who were asked to generate positive fantasies about successfully managing their projects and obligations in the upcoming week reported feeling less energized than those who generated neutral fantasies (study 3). Of importance, the lowered energization in participants from the positive fantasy condition actually resulted in lower success in accomplishing their projects and obligations in the upcoming week.

Across all four studies, the researchers ruled out several alternative explanations for the de-energizing effect of positive fantasies, like for example, the possibility that positive fantasies are easier to generate and/or less irritating than questioning, negative, or neutral fantasies. Including the neutral condition also allowed concluding that whereas positive fantasies decreased energization, negative fantasies increased energization. In sum, the research suggests that positive fantasies lead people to prematurely consume the desired events in their mind and thus conceal the need to mobilize resources for actually making the desired future come true. Accordingly, mentally fantasizing about having realized a desired future led to a demobilization of bodily resources that was manifested in a dampened cardiovascular response. The decreased energization led to low accomplishment and success in realizing the desired future.

21.3 Mental Contrasting Future and Reality

As outlined above, positive fantasies about the future are detrimental for energization and successful performance. However, in everyday life, people frequently fantasize and daydream about desired events (Klinger 1990; Singer and Antrobus 1972). If fantasies are ubiquitous but can hamper effort and performance, the question arises as to what can be done to make those fantasies fruitful for successfully pursuing desired futures. FRT (Oettingen 2000, 2012) explores the effect of fantasies on realizing desired futures from a self-regulatory perspective. The theory specifies that positive fantasies can be used to wisely regulate one's pursuit of desired futures if they are mental contrasted with the present reality. When people use the self-regulation strategy of mental contrasting, they first imagine having attained an important desired future (e.g., starting a romantic relationship) and immediately thereafter they imagine the present reality that stands in the way of realizing the desired future (e.g., being shy). Imagining the desired future followed by the present reality should make people recognize that they have not attained the desired future yet and need to overcome the present reality to do so. As a consequence, expectations of attaining the desired future (and overcoming the reality) become activated which then translate into performance. When expectations of successfully reaching the desired future are high, mental contrasting people engage in pursuing the desired future (i.e., they show high determination, effort, and persistence). Conversely, when expectations are low, they disengage from pursuing the desired future (i.e., they show low or no determination, effort, and persistence). Mental contrasting thus causes selective pursuit of desired futures. Selective pursuit of desired futures is adaptive because it saves resources that are inherently limited (e.g., time, energy, and attention; energy conservation principle, Brehm and Self 1989; Silvestrini and Gendolla 2013; Wright 1996): People invest their resources only for endeavors they can realize but refrain from wasting resources for endeavors they cannot realize.

FRT describes three other modes of thought that people use when thinking about desired future events (i.e., personal wishes and concerns): indulging, dwelling, and reverse contrasting. These modes of thought lead to indiscriminate pursuit of desired futures that is not based on expectations. Indulging (i.e., imagining the future only) and dwelling (i.e., imagining the reality only) fail to induce a perception of the reality as standing in the way of the desired future because people unilaterally reflect on the future or the reality. As a consequence, expectations do not become activated and do not translate into goal-directed effort and performance. Mentally elaborating reality before the future (i.e., reverse contrasting) also fails to induce a perception of reality as standing in the way of the future because the future is not a reference point for the reality, and thus the reality cannot be perceived as an obstacle (Oettingen et al. 2001). Therefore, just as after indulging and dwelling, expectations do not become activated and cannot translate into effort and performance.

A series of studies exploring mental contrasting effects on implicit cognition confirmed that mental contrasting (but not the other modes of thought) changed the meaning of participants' subjective reality: These studies suggest that when expectations were high (vs. low), mental contrasting strengthened (vs. weakened) the mental link between the desired future and the present reality as well as between the desired future and the instrumental means to overcome the reality (Kappes et al. 2012). Moreover, when expectations were high (vs. low), mental contrasting but not reverse contrasting led participants to identify idiosyncratic aspects of their reality as obstacles to reaching the desired future Kappes et al. 2013). In sum, when expectations were high, mental contrasting led people to recognize the present reality as an obstacle toward realizing their desired future, when expectations were low, mental contrasting led people to dismiss the reality as an obstacle. The other modes of thought (indulging, dwelling, and reverse contrasting) did not influence how participants understood the meaning of their reality.

The pattern that mental contrasting (vs. indulging, dwelling, and reverse contrasting) leads to selective (i.e., expectancy-based) pursuits of desired futures has been replicated in a multitude of studies. In these studies, effort and performance were assessed by cognitive (e.g., making plans), affective (e.g., anticipated disappointment in case of failure), motivational (e.g., determination), and behavioral indicators (e.g., action initiation). The pattern emerged whether these indicators were measured by self-report or observations, directly after the experiment or weeks later, whether mental contrasting was experimentally induced or unobtrusively observed, and whether expectations were measured or manipulated (Kappes et al. 2012; Johannessen et al. 2012; Oettingen 2000; Oettingen et al. 2001, 2005, 2009, 2010b, c, 2012; Sevincer and Oettingen 2013). As described above, positive fantasies about a desired future exerted their effect on poor performance through reduced energy mobilization. Accordingly, Oettingen and colleagues suspected that the effect of mental contrasting the desired future with reality on selective effort and performance would be mediated by expectancy-dependent energy mobilization, assessed by cardiovascular response (SBP).

21.3.1 Mental Contrasting Instigates Expectancy-Dependent Energization

To test the hypothesis that mental contrasting would trigger expectancy-dependent energization which would fuel subsequent effort and performance, Oettingen et al. (2009) conducted two experiments modeled after previous experimental studies that induced mental contrasting. In study 1, participants completed a computer-based questionnaire. First, they were asked to name their currently most important interpersonal wish (they named e.g., “to keep up a friendship”). The researchers then measured participants’ expectations of successfully realizing their interpersonal wish (“How likely do you think it is that the named concern will have a happy ending?”). Moreover, because people’s energization to realize a wish may also be influenced by the incentive value of the wish (Gendolla et al. 2012; Wright 1996), we assessed participants’ incentive value of realizing their wish (“How important is it to you that the named concern will have a happy ending?”). Thereafter, participants listed four aspects of the desired future of realizing their wish (e.g., “having someone to talk to”) and four aspects of the present reality that stands in the way of realizing the wish (e.g., “friend lives far away”).

Thereafter, participants were led to either mental contrast or indulge about their interpersonal wish. Participants in the mental contrasting condition mentally elaborated and wrote about two aspects of the desired future they had listed and two aspects of the present reality in alternating order beginning with a future aspect; those in the indulging condition in contrast elaborated on and wrote about each of the four listed aspects of the desired future. SBP was assessed twice while participants elaborated the aspects: The first time while participants elaborated the first aspect (T1) and the second time while they elaborated the third aspect (T2). The researchers assessed SBP at the first and third aspects because these aspects were future aspects in both conditions and therefore could be directly compared. The dependent variable was change in SBP during the mental exercise from T1 to T2. Analogous to SBP, participants’ DBP and HR were recorded. However, because DBP and HR are less consistently linked to energization than SBP, the researchers did not have as specific hypothesis for DBP and HR. Finally, participants’ commitment toward realizing the desired future was measured by self-report (e.g., “How disappointed would you feel if your concern did not come to a happy ending?”). Because strongly committed people show disappointment and frustration when failing to realize the desired events, the degree of disappointment people feel when anticipating failure in wish fulfillment is a reliable indicator for commitment (Oettingen et al. 2001; Wicklund and Gollwitzer 1982).

As predicted, in the mental contrasting condition participants showed expectancy-dependent change in SBP from T1 to T2. When expectations

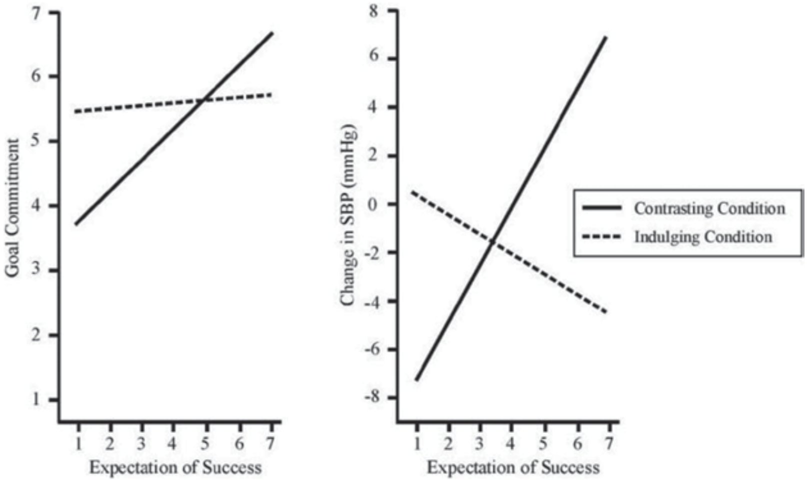

Fig. 21.1 Regression lines depict the link between expectations and goal commitment (*left*), and expectation and change in SBP in mmHG (*right*) as a function of mental contrasting and indulging. (From: "Mental contrasting and goal commitment: The mediating role of energization," by Oettingen et al. [2009], copyright © 2009 by the Society for Personality and Social Psychology. Reprinted by Permission of SAGE Publications)

were high their SBP increased, when expectations were low it decreased. This pattern indicates that participants who were induced to mental contrast *mobilized* bodily resources when they estimated that they could successfully realize their wish but *demobilized* resources when they estimated that they could not realize their wish. In contrast, indulging participants' SBP did not change (Fig. 21.1). An analogous pattern emerged for self-reported commitment: When expectations were high, mental contrasting participants reported feeling strongly committed to realizing their wish, when expectations were low, they reported feeling only weakly committed. Indulging participants reported feeling moderately committed independent of expectations. Of importance, in mental contrasting participants the effect of expectations on commitment was mediated by change in SBP (Fig. 21.2). DBP and HR were not related to participants' expectations or commitment in neither mental contrasting nor indulging participants.

Fig. 21.2 Change in SBP as a mediator for the relation between expectations and goal commitment in mental contrasting participants. [From: "Mental contrasting and goal commitment: The mediating role of energization", by Oettingen et al. 2009], copyright © 2009 by the Society for Personality and Social Psychology. Reprinted by Permission of SAGE Publications)

In study 2, the researchers conceptually replicated the above pattern. They measured energization by asking participants to self-report their feelings of energization. In addition, they observed participants' quality of performance toward realizing their wish. Specifically, they asked economics students to deliver a speech in front of a camera supposedly to help a human resource department develop a measure of professional skills. After students either mental contrasted or indulged about delivering a good speech, they were asked to indicate their subjective feelings of energization by self-report (e.g., "How full of energy do you feel with respect to the upcoming talk?"). As dependent variable, participants' quality of performance in giving the speech was assessed by their subjective self-evaluation and other-rated quality of performance. Mental contrasting participants showed expectancy-dependent energization which predicted their self-evaluated and other observed quality of performance in the talk; indulging participants showed expectancy-independent energization and quality of performance.

In sum, mental contrasting (vs. indulging) a specific wish instigated expectancy-dependent (vs. expectancy-independent) energization (assessed by change in SBP and self-report) which fuelled subsequent performance with regard to realizing that particular wish (measured by commitment and quality of performance). Because energization can be understood as a nonspecific arousal state (Duffy 1934), Oettingen and colleagues suspected that energization triggered by mental contrasting a specific desired future such as solving a given task could even be used to fuel goal-directed behavior with regard to performing a task unrelated to the primary task.

21.3.2 Energization Transfer by Mental Contrasting

As mentioned above, energization can be defined as "the extent to which the organism as a whole is activated or aroused" (Duffy 1934, p. 194). In line with this definition, Hull (1943, 1952) conceptualized energization as an unspecific activation or arousal state that indiscriminately fuels behavior: According to Hull's drive theory (Hull 1943, 1952), behavior was spurred by drive, and drive was conceptualized as an undifferentiated, universal energizer that was fuelled by the sum of all current bodily deficits/needs (hunger, thirst, pain, etc.). The nonspecific drive energized behavior, but did not determine its direction. Rather, direction was determined by habit. Habit in turn was influenced by whether the organism had learned that a particular behavior would reduce the drive in a specified situation. Thus, in Hull's conception there was no one-to-one linkage between drive and an associated behavior. The unspecific drive could energize any behavior. Hull termed this principle *irrelevant drive*. In other words, a nonspecific drive state can spur energization that facilitates behavior not primarily directed at reducing the particular bodily deficit that initially brought forth the drive. Drawing on Hull's ideas, Zillmann contented that an irrelevant drive should function analogously to physical energization in that it "indiscriminately 'energizes' and thus facilitates enacted behavior" (Zillmann 1971, p. 422).

Following up on Hull's and Zillmann's conception of energization as an unspecific motor force for behavior, Sevincer and colleagues proposed that mental contrasting a specific desired future such as solving a given task may elicit a general energization state which may then fuel effort in a task unrelated to solving the primary task. To test this proposition, the researchers conducted a series of studies: A first study (Sevincer et al. 2013) tested whether energization effects elicited by mental contrasting persist over time, because to fuel effort in an unrelated task, physiological energization effects should persist after the mental exercise. In two additional studies the researchers then tested the idea that energization (SBP) elicited by mental contrasting about successfully solving a given task (e.g., writing an outstanding essay) may fuel physical and mental effort in an unrelated task (Sevincer et al. 2014 study 1 and 2). All three studies were based on previous research that investigated the effects of mental contrasting on SBP. That is, participants first specified a wish that they would like to realize or a task they would like to solve. After indicating their expectations and the incentive value of realizing the wish, they were induced either to mental contrast or to engage in a control mental elaboration. Energization was assessed by changes in participants' SBP from baseline to after the manipulation.

The first study (Sevincer et al. 2013) investigated whether energization elicited by mental contrasting persists over time. Participants first named their currently most important interpersonal wish (they named e.g., "resolving an argument"), and indicated their expectations as well as the incentive value of realizing it. Then they either mental contrasted or they indulged about fulfilling their wish. After the mental exercise, participants engaged in two filler tasks. First, they worked on a word-search puzzle for 7 min and second, they worked on a subtask of the WILDE-Intelligence-Test (WIT-2; Kersting et al. 2008) for 13 min. The SPB measurements were taken while participants worked on each filler task. The researchers replicated the results of the previous studies (Oettingen et al. 2009); that is, mental contrasting (vs. indulging) triggered expectancy-dependent energization as assessed by changes in SBP from before to after mental contrasting versus indulging. However, going beyond the previous work, the study showed that participants maintained the expectancy-dependent energization until about 20 min after the mental exercise while they worked on the filler tasks.

Another study (Sevincer et al. 2014, study 1) tested whether energization triggered by mental contrasting one task translated into physical effort in an unrelated task. Participants were undergraduate students who wished to attend graduate school. All participants were presented with the same task: writing an excellent graduate admission essay. They indicated their expectations of writing an excellent essay and the incentive value. Thereafter, participants either mental contrasted about successfully solving their task or they engaged in control elaborations (i.e., indulging in the desired future or elaborating an irrelevant event). To assess physical effort, the researchers measured for how long participants could squeeze a handgrip (Muraven et al. 1998). Performance on this task is a measure of physical stamina, which strongly depends on the mobilization of effort and energy (Hutchinson et al. 2008; Krombholz 1985). As predicted, in the mental contrasting condition, participants' change in SBP and performance on the handgrip task depended on their expectations of writing an excellent admission essay. Mediation analysis showed that the effect of mental contrasting on handgrip performance was mediated by change in SBP from before (baseline) to after the mental exercise. Thus, mental contrasting a given task (i.e., writing an excellent essay) instigated expectancy-dependent change in SBP which translated into physical effort in a task unrelated to the primary task (i.e., squeezing a handgrip).

This pattern was successfully replicated in another study (Sevincer et al. 2014, study 2) with mental effort as the dependent variable. Participants either mental contrasted, indulged, dwelled, or reverse contrasted about excelling in an intelligence test. After the mental exercise, they were presented with an unrelated task: writing a get-well letter to a friend. Their invested effort in writing the letter was assessed by self-report. Mental contrasting but not the three other mental elaborations (indulging, dwelling, and reverse contrasting) instigated expectancy-dependent change in SBP which fuelled effort in the unrelated task: Writing the letter.

In sum, the research presented so far suggests that positive fantasies can be made fruitful for energy mobilization if they are mental contrasted with the present reality. Such mental contrasting of future with reality leads to physiological energization (assessed by SBP) that is in line with a person's expectation of realizing the desired future. The elicited energization in turn fuels subsequent behavior instrumental for wish fulfillment. Of importance, because energization can be understood as a general activation or arousal state, the elicited energization state was observed to even fuel performance in solving a subsequent task that was unrelated to the initial desired future. How these results relate to models of physiological energization will be discussed next. We will consider motivational intensity theory (Brehm and Self 1989; Wright 1996), the biopsychosocial model of arousal regulation (Blascovich and Tomaka 1996), and excitation transfer theory (Zillmann 1983).

21.4 Models of Physiological Energization

21.4.1 Motivational Intensity Theory

Motivational intensity theory (Brehm and Self 1989) specifies the variables that predict the motivational intensity (i.e., the invested effort) with which people will engage in a given task. According to the theory, the effort that people invest in a task is directly proportional to the demand of the task (or task difficulty). Thus, the more difficult the task is the more effort people will invest, as long as success is possible and justified. However, the maximum amount of effort that people exert (i.e., the potential motivation) is limited by the amount of effort that people are willing to invest with regard to the importance of success (i.e., the incentive, attractiveness or desirability of completing the task). Consequently, when the amount of effort needed to complete the task exceeds the amount of effort that people are willing to invest, people cease their effort investment. In short, people's effort investment is guided by an energy conservation principle in which the energy that people mobilize is limited by the task demand and the importance of successfully completing the task. A multitude of studies confirmed this pattern with assessing energy mobilization by cardiovascular indicators (e.g., SBP, preejection period; Richter 2013; Richter and Gendolla 2009; for summaries, see Gendolla et al. 2012; Wright 1996; Wright and Kirby 2001).

The finding that mental contrasting produces expectancy-dependent energy mobilization (assessed by SBP) is in line with motivational intensity theory by suggesting that mental contrasting elicits energization according to the energy conservation principle. That is, people mobilize energy when attaining a specific desired future (e.g., completing a certain task) is perceived as important and achievable (i.e., when incentive and expectations are high) but cease energy mobilization when attaining the desired future becomes unattractive or unachievable (i.e., when incentive value or expectations are low, Oettingen et al. 2009).

FRT and motivational intensity theory differ, however, in that whereas motivational intensity theory states that the demand of a task (or task difficulty) directly increases energy mobilization, FRT does not make predictions about how task demand affects energy mobilization. Rather, FRT specifies how people's expectations about being able to complete a task affect energy mobilization depending on people's mode of thought (mental contrasting, indulging, dwelling, reverse contrasting). Although task demand and people's expectations of completing a task are often (inversely) related—the more difficult a task the lower people's expectations of successfully completing it—the two concepts are not the same. Whereas task demand refers to the resources needed to successfully complete the task, expectations refer to people's estimated likelihood of successfully completing the task.

A number of studies on motivational intensity theory investigated the impact of outcome expectations (completing task Y will lead to outcome X) on energization. In this research, outcome expectations were operationalized as whether participants expected that successfully completing a task (an easy vs. difficult memory task) will lead to a desired outcome (participants had either a low or a high chance of winning a price if they succeed on the task; Wright and Gregorich 1989; see also Wright et al. 1992). When outcome expectations were low, participants evinced low energization, irrespective of task difficulty; when outcome expectations were high, participants' energization depended on task difficulty—the more difficult the task, the higher the participants' energization. These findings are interpreted as that people's outcome expectations determine the maximum amount of energy that people mobilize (i.e., their potential motivation, Gendolla et al. 2012).

Of importance, FRT (summary by Oettingen 2012) extends these findings in that it posits that mental processes (i.e., the four different modes of thought as specified by FRT) also need to be taken into consideration when predicting energy mobilization. Specifically, whereas mental contrasting leads to energy mobilization in accordance with the energy-conservation principle, indulging, dwelling, and reverse contrasting lead to energy mobilization that violates this principle: As people mobilize energy irrespective of their expectations of success, they fail to invest the energy that is required to successfully reach achievable desired future and to successfully let go from reaching unachievable desired futures. Consequently, they waste their energy in half-hearted pursuits of a host of desired futures.

21.4.2 Biopsychosocial Model of Arousal

The finding that mental contrasting instigates expectancy-dependent energy mobilization that is manifested in a cardiovascular response also relates to the biopsychosocial model of arousal (Blascovich and Tomaka 1996). The model posits that people's physiological reactions with regard to a stressor (an upcoming task like a mental arithmetic task) differ depending on whether people appraise the task as a challenge or as a threat. When people expect that they are able to cope with the task (i.e., they appraise their resources to exceed the task demand) they evince a challenge response. In contrast, when they expect that they are not able to cope with the task (i.e., they appraise the task demand to exceed their resources) they evince a threat response.

According to Mendes et al. (2008), the challenge response is associated with an activation state that is characterized by increased cardiac output, myocardial contractility, and HR, and decreased peripheral resistance. The threat response, in contrast, is associated with an inhibition state that is characterized by little or no increase in cardiac output, and increased myocardial contractility, HR, as well as peripheral resistance. However, our primary measure of energization, SBP, is not considered as a key concept in the model (Blascovich et al. 2003; see also Wright and Kirby 2003).

The claim that appraisal of resources exceeding task demand (challenge) leads to an activation state, while appraisal of task demand exceeding resources (threat) leads to an inhibition state is generally in line with FRT, positing that when people expect that they can (vs. cannot) successfully realize a desired future (e.g., mastering an upcoming task), mental contrasting leads to the mobilization (vs. demobilization) of energy. However, FRT goes beyond the challenge and threat model in that it specifies the mental processes (i.e., cognitive strategies or modes of thought: mental contrasting, indulging, dwelling, reverse contrasting) that influence whether people's expectations about mastering an upcoming event will translate into energy mobilization and goal-directed behavior.

21.4.3 Excitation-Transfer Theory

The finding that energization triggered by mental contrasting of solving a given task triggers energization that fuels effort in an unrelated task relates to excitation-transfer theory (Zillman 1971). Excitation-transfer theory posits that emotional activation or arousal triggered by one stimulus may enhance people's responses to another stimulus. Zillmann called this nonspecific activation or arousal state "residual excitation." To test their hypotheses, Zillmann and colleagues (summaries by Byrant and Miron 2003; Zillmann 1983) either presented participants with an arousing stimulus (e.g., engaging in physical exercise, watching an erotic movie) or with a nonarousing stimulus (e.g., engaging in an agility task, watching a neutral movie). Thereafter, the researchers assessed participants' activation state by a number of cardiovascular indicators (SBP, DBP, HR). Before the cardiovascular response, elicited by the first stimulus, decayed, participants were exposed to a second stimulus unrelated to the first stimulus (e.g., a funny cartoon, a provocation). Participants who had been exposed to an arousing first stimulus evinced a more intense response to the second stimulus (i.e., they judged the cartoons to be funnier; reacted more aggressively to the provocation) than those who had been exposed to a nonarousing stimulus, but only when they did not attribute their arousal to the first stimulus or experience. Our findings are in line with Zillmann's results by suggesting that motivational energization (or activation/arousal) triggered in one situation may transfer to a subsequent situation. They go beyond Zillmann's results in that the transferred energization may be used to fuel goal-directed behavior with regard to an unrelated task in the subsequent situation. Future research may combine the two approaches (excitation transfer theory and energization transfer by mental contrasting) by investigating whether energization triggered by mental contrasting pervades to fuel performance in an unrelated task if it is attributed to the mental contrasting procedure.

21.5 Implications for Interventions

The research presented in this chapter has implications for designing interventions using mental contrasting to regulate people's energy mobilization and in turn their everyday pursuits. A number of intervention studies already support the effectiveness of mental contrasting as a metacognitive strategy to improve people's success in fulfilling their wishes (Oettingen 2012; Oettingen et al. 2010a). Teaching mental contrasting (vs. indulging) resulted, for instance, in more effective time management and easier decision making in health-care professionals (Oettingen et al. 2010a, b, c), better academic achievement in disadvantaged school children (Gollwitzer et al. 2011), and improved health behavior in dieting students (Johannessen et al. 2012).

The finding that mental contrasting instigates expectancy-dependent mobilization of energy is directly relevant for interventions that use mental contrasting. Succesfully realizing one's desired future requires the mobilization of energy. Energy, however, is a limited resource and people are motivated to conserve their energy (energy conservation principle; Brehm and Self 1989; Richter 2013; Gendolla et al. 2012; Silvestrini and Gendolla 2013). Thus, interventions using mental contrasting may guide people to wisely spend their limited energy in their everyday life. People will conserve energy by investing it only for projects they can realize and withdraw it from projects they cannot realize.

Of particular importance for designing interventions is the observation that mental contrasting a specific desired future such as successfully solving a particular task spurs expectancy-dependent energization that fuels effort for a task unrelated to the primary task. This finding suggests that persons may be taught mental contrasting regarding a desired future for which they have high expectations that then will energize effortful performance to realize a future that was not targeted by mental contrasting. For example, a person who has high expectations of winning a sport match may mental contrast the desired future of winning the match which in turn will mobilize the energy to prepare for an upcoming exam or clean up her apartment. A person may even use mental contrasting strategically: She might mental contrast a desired future that is well in reach (e.g., solving a challenging math problem) for obtaining the energy to complete an unrelated unpleasant activity (e.g., rote learning foreign language vocabulary). In the same vein, one may develop educational interventions that strategically induce mental contrasting a desired future for which a student has high expectations to benefit performance for activities for which the student has low expectations. For example, in an academic context, a student may be induced mental contrasting about excelling in her major where she has high expectations (e.g., excelling in biology) to mobilize the effort to prepare for a test in which she has low expectations (e.g., improving in history). Finally, some contexts may call for relaxation rather than energization. For example, when a person is overexcited or is performing a progressive muscle relaxation task, mental contrasting a desired future for which the person has low rather than high expectations may help her to downregulate her energization level.

21.6 Summary

Contrary to lay belief and the credo of the self-help literature, positive thinking about the future is detrimental for realizing desired futures if it comes in the form of positive future fantasies. Indeed, positive future fantasies lead to reduced energy mobilization, assessed by cardiovascular response (SBP). Reduced energy mobilization in turn predicts low success in realizing the future fantasized about. However, positive future fantasies can be made fruitful for the self-regulation of one's everyday and long-term pursuits if they are mental contrasted with the present reality. Such mental contrasting leads to energy mobilization and subsequent pursuits that are in line with people's expectations of realizing the desired future. When expectations are high, people mobilize the necessary resources to realize the desired events; when expectations are low, they conserve their resources for more promising pursuits. Of importance, the energy mobilized by mental contrasting a desired future may even be used to modulate performance in tasks unrelated to the desired future that was elaborated in mental contrasting. These findings open the door to develop interventions directed at helping people to wisely regulate their energy mobilization for realizing important wishes and solving pressing concerns.

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Part V

Self-Regulatory Problems and Their Development

Depression and Self-Regulation: A Motivational Analysis and Insights from Effort-Related Cardiovascular Reactivity

22

Kerstin Brinkmann and Jessica Franzen

22.1 Introduction

Major depression is an affective disorder that is characterized in particular by persistent negative affect and anhedonia, i.e., a loss of interest or pleasure (Diagnostic and Statistical Manual of Mental Disorders; American Psychiatric Association 2000). It is considered one of the most burdensome mental disabilities in modern societies, with increasing prevalence rates and severe consequences not only for the individual but also for the societies' economy (e.g., Kessler and Wang 2009). Not surprisingly, a wealth of research efforts from various perspectives have been undertaken to understand the features and mechanisms of this serious disorder. Particularly well documented are cognitive impairments (e.g., reduced cognitive control) and negative cognitive biases (e.g., Gotlib and Joormann 2010). Moreover, research has been interested in depressed individuals' emotion processing and emotional reactivity (e.g., Rottenberg 2007). However, motivational deficits are also a common feature of the clinical appearance of depression. In this respect, it may be difficult to disentangle depressed individuals' other types of impairments (e.g., cognitive deficits) from underlying motivational deficits (Scheurich et al. 2008).

Given the important role of motivational deficits in depression and their potential impact on other features of depression, the aim of the present chapter is threefold: First, we present a review of the depression literature from a motivational point of view. Second, from a psychophysiological perspective, we turn to one important aspect of motivation, namely, the intensity of behavior and present hypotheses and empirical evidence for impaired adjustment of effort mobilization of subclinically depressed individuals. Finally, we outline some examples of treatment approaches that act on depressed individuals' impaired motivational functioning as presented throughout this chapter.

22.2 Self-Regulation Functioning in Depression

The literature review in the first part of this chapter is guided by the objective of taking the whole motivation process into account. Specifically, we propose an analysis of depressed individuals' self-regulation functioning starting with the setting of standards and goals, the initiation of behavior, the direction of behavior, and the related aspect of responsiveness to hedonic consequences. We then turn to the role of feedback, the persistence of behavior, and related aspects of disengagement, ruminative self-focus, and affect regulation. We aim at presenting a

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comprehensive review of the current literature of self-regulation functioning in depression by exemplarily referring to empirical evidence for each of the aspects reviewed. However, this chapter cannot claim to be exhaustive given space concerns and the selective focus on several important aspects of motivation. The choice of these aspects is based on the four dimensions of motivated behavior (i.e., the initiation, direction, intensity, and persistence of behavior; see Geen 1995) and on a self-regulation perspective. A self-regulation perspective is particularly useful because it comprises the whole process of goal-directed behavior, including goal setting, action initiation and maintenance, attention control, and affect regulation (see Carver and Scheier 1998; Klenk et al. 2011).

We are limiting our motivational analysis to theory and research on major depressive disorder and subclinical depression. In brief, major depression is a recurrent disorder characterized by a depressed mood or a loss of interest or pleasure for at least 2 weeks. Moreover, at least four of the following symptoms must be present in a depressive episode: weight change, insomnia or hypersomnia, psychomotor agitation or retardation, loss of energy, feelings of worthlessness, difficulties concentrating or indecisiveness, and suicidal ideation (American Psychiatric Association 2000). Subclinical depression—which is also referred to as dysphoria—is characterized by symptoms that do not meet the threshold for a diagnosis of a depressive episode. However, dysphoric individuals often present similar, albeit minor, impairments and are at an elevated risk for developing major depression (Fergusson et al. 2005; Judd et al. 2002). Theories of depression mainly refer to major depression. However, empirical evidence often comes from both clinical and subclinical samples. Throughout this chapter, we consider studies from both kinds of samples.

22.2.1 Standards and Goal Setting

The self-regulation process typically starts with goal setting. Prominent theories of depression argue that depressed individuals tend to set goals or standards that exceed the expected or obtained outcomes (see Ahrens 1987, for a review). However, in the past decades, no clear empirical consensus has been reached concerning this assumption. On the one hand, it is well established that clinical and subclinical depression is related to maladaptive forms of perfectionism (e.g., Wheeler et al. 2011). On the other hand, only some goal-setting studies have confirmed that dysphoric individuals set higher standards but found no differences in the expectancy to reach their goals (e.g., Golin and Terrell 1977). Other studies have revealed lower self-efficacy expectancies in subclinical depression but found no differences in goal setting (e.g., Qian et al. 2002). However, when simultaneously considering standard-setting and self-efficacy expectancies, results converge on the fact that clinically and subclinically depressed individuals show a negative discrepancy between standards and expectancies, i.e., they set higher minimal standards for themselves than they reach or expect to reach (e.g., Ahrens 1987; Tillema et al. 2001).

Related to lower outcome expectancies are findings indicating that depressed individuals report approach goals as less likely to happen and avoidance goals as more likely to happen and that they perceive less control over goal outcomes (e.g., Dickson et al. 2011). However, depressed individuals do not consistently report a higher number of avoidance goals (e.g., Dickson et al. 2011). Taken together, theories of depression and empirical research suggest that the self-regulation process of clinically and subclinically depressed individuals might be impaired by maladaptive goal- and standard-setting and by lower expectancies of (positive) outcomes.

22.2.2 Initiation of Behavior

Following goal setting, one of the critical moments in the self-regulation process is the initiation of actions. The failure to act on one's intentions has been identified as a common problem (see Gollwitzer and Sheeran 2006). In the particular case of depression, the cognitive-initiative account by Hertel and colleagues (e.g., Hertel 2000) suggests that memory impairments of depressed individuals are due to a lack of spontaneously developed initiative and to difficulties in the initiation of strategies. This assumption converges with the view of initiation as being an approach-related action associated with left frontal activity, both of which have been found to be reduced in depression (Nitschke et al. 2004). Moreover, it also converges with the view that the initiation of strategies (e.g., in a task that requires switching) is related to impaired frontal lobe executive functioning in depression (Lafont et al. 1998). According to the cognitive–initiative account, attention-focusing instructions and highly structured tasks might help overcoming these cognitive impairments (Austin et al. 2001; Hertel 2000). In sum, theory and empirical findings suggest that action initiation and strategy initiation are impaired in clinical and subclinical depression and a crucial aspect to act on.

22.2.3 Direction of Behavior

As foreshadowed above, the direction of behavior in terms of approach or avoidance is an important aspect of self-regulation. Several theories postulate that depressed and dysphoric individuals are characterized by deficits in approach-related positive affect. Specifically, behavioral theories suggest that depressed individuals learn from their experiences that their actions are not followed by positive reinforcement. As a consequence, the behavior leading to positive consequences is given up in favor of avoidance, withdrawal, and passivity. Such avoidance tendencies in turn produce, sustain, or worsen depressive symptoms (Beck et al. 1979; Jacobson et al. 2001).

Depue and Iacono (1989) argue that depression is characterized by a deficient activity of the behavioral facilitation system—a basic system that mobilizes behavior and that provides a motivational contribution to the process of active engagement in the environment. In a similar vein, a number of studies based on reinforcement sensitivity theory (Gray 1982) demonstrate that depressed and dysphoric individuals report lower levels of the behavioral activation system (BAS) and higher levels of the behavioral inhibition system (BIS; see Bijttebier et al. 2009, for a review). Finally, it is well documented that clinically and subclinically depressed individuals show reduced electrocortical activity in left prefrontal regions that are associated with approach behavior (see Thibodeau et al. 2006, for a review).

Related to the direction of behavior is an intriguing analysis of empirical evidence for low serotonergic function in depression by Carver et al. (2008, 2009). Based on two-mode models of self-regulation, the authors conclude that depressive inaction is characterized by the interaction of low serotonergic function—which is linked to deficient effortful control—and reduced incentive sensitivity. According to this perspective, reduced approach tendencies in depression cannot be overcome because of deficits in a higher-order reflective control system (see also Chap. 2 in this volume).

Taken together, several important theories as well as empirical evidence suggest that clinical and subclinical depression is characterized in particular by reduced approach behavior and deficits to overcome this tendency. What is more, a hypoactive BAS, resting electrocortical frontal asymmetry, and low serotonergic function can be considered as trait-like vulnerability markers of depression.

22.2.4 Responsiveness to Reward and Punishment

A related aspect of behavioral approach and avoidance tendencies is the responsiveness to hedonic consequences like reward or punishment. In the past two decades, a number of behavioral and neuroscientific studies have been conducted on clinical and subclinical depression. Several behavioral studies demonstrated that dysphoric and depressed individuals are less sensitive to monetary rewards in terms of a less liberal response bias compared to nondepressed individuals (e.g., Henriques and Davidson 2000). However, they did not consistently find this effect in a monetary punishment condition. More recently, some studies revealed that compared to nondepressed individuals, clinically and subclinically depressed participants show a lower response bias toward the more frequently reinforced stimulus (e.g., Liu et al. 2011; Pizzagalli et al. 2009). Moreover, several behavioral studies showed a reward-based decision making deficit in depressed individuals (e.g., Kunisato et al. 2012).

Numerous studies using brain-imaging techniques have investigated depressed individuals' sensitivity to reward and some of them also to punishment. These studies generally revealed dysfunctions of cortical and subcortical components involved in the neural reward circuit not only in depressed individuals (see Eshel and Roiser 2010; Nestler and Carlezon 2006, for reviews) but also in recovered patients (McCabe et al. 2009) and in daughters of depressed mothers (Gotlib et al. 2010). Furthermore, depression has been linked to a reduced frontal electroencephalogram asymmetry during anticipation of reward (Shankman et al. 2007) and to a blunted feedback-related negativity to monetary gains and losses (e.g., Foti et al. 2011).

Recently, several authors (e.g., Berridge 2003) suggested to divide reward processing into different components: wanting or the anticipatory phase, which is defined as the motivation to obtain rewards, and liking or the consummatory phase, which is defined as the hedonic response to rewards. During anticipation, most of the behavioral and neuroscientific studies revealed that depressed and dysphoric individuals show reduced motivation to obtain rewards (e.g., Chentsova-Dutton and Hanley 2010; Treadway et al. 2012; but see also Dichter et al. 2012). The consummatory phase has been studied less. Most of these studies showed decreased responsiveness to rewards in depression (e.g., Forbes et al. 2009; but see also Smoski et al. 2011).

In sum, numerous studies have investigated reward processing using behavioral and neuroscientific measures. They consistently show a hyposensitivity to rewards in clinical and subclinical depression. In contrast, fewer studies have investigated punishment sensitivity, and the results are less consistent, showing sometimes hypo- and sometimes hypersensitivity in depression.

22.2.5 Feedback Reactivity

As a particular case of reward and punishment sensitivity and an important aspect of self-regulation, reactivity to positive and negative feedback has also been subject of numerous studies. Concerning negative feedback in particular, several studies have shown that once depressed individuals have made a mistake, they commit more subsequent mistakes (e.g., Elliott et al. 1997; Steffens et al. 2001). This abnormal effect of negative feedback on subsequent performance in depression has also been demonstrated using brain-imaging techniques (e.g., Elliott et al. 1998). In their review, Eshel and Roiser (2010) suggest two alternative interpretations for this well-documented effect, which receive both some empirical support from research with event-related potentials:

Using the error- or feedback-related negativities as measures of the electrophysiological reactivity to errors or negative feedback, some studies demonstrated larger feedback-related negativities in depressed and remitted depressed individuals (e.g., Santesso et al. 2008). These results suggest that depressed individuals are hypersensitive to negative feedback, in the sense that negative feedback leads to failure-related thoughts that, in turn, interfere with subsequent performance. On the other hand, there is also evidence for depressed individuals' reduced feedback-related negativity in error trials following error trials (e.g., Ruchsow et al. 2004). These findings point to difficulties evaluating negative feedback and using it to improve future performance and suggest thus a hyposensitivity to negative feedback in depression.

Similarly, studies comparing reactivity to both negative and positive feedback diverge on the question whether depression is characterized by increased sensitivity to negative compared to positive feedback or whether depression is characterized by a global reduction in sensitivity to reinforcement (see Chase et al. 2010). Evidence for a negative bias comes, for instance, from a study showing that elderly depressed individuals make worse mistakes after negative but not positive feedback (von Gunten et al. 2011; but see also

Chase et al. 2010). However, other studies have demonstrated a blunted behavioral and neural response to both negative and positive feedback in depressed individuals (e.g., Steele et al. 2007).

In sum, the literature converges on the conclusion that self-regulation in clinical and subclinical depression might be impaired by an altered response to negative feedback. However, it is still unclear if this impairment should be interpreted as a hypo- or a hypersensitivity to punishment, and if negative feedback has a more important impact on depressed individuals than positive feedback.

22.2.6 Persistence and Disengagement

In order to effectively regulate one's behavior, it is sometimes important to persist, even in the face of obstacles, whereas in other circumstances disengagement from an unattainable goal is warranted. In the case of depression, both facilitated and impaired disengagement have been postulated and observed. On the one hand, classic theories of depression posit that depressive symptoms are associated with facilitated disengagement from unattainable goals and thus with the conservation of resources (see Wrosch and Miller 2009). Similarly, evolutionary psychologists have postulated that facilitated goal disengagement in a depressed mood serves an adaptive function to preserve resources and to avoid danger or loss (e.g., Nesse 2000). On the other hand, depression has been associated with the inability or unwillingness to abandon unattainable goals or values (e.g., Carver and Scheier 1998; Pyszczynski and Greenberg 1987).

Concerning the persistence on a specific ongoing task, there is evidence that dysphoric participants persist less long on frustrating or insoluble laboratory tasks than nondysphoric participants (Ellis et al. 2010). This earlier task disengagement—and related poorer performance outcomes—of dysphoric individuals has been shown to be independent of the kind of stop rule provided: In a study by Brinkmann and Gendolla (2014), dysphoric participants persisted less long on an item generation task, independent of whether they were instructed to stop when they "felt it was a good time to stop" or whether they were instructed to stop when they "no longer enjoyed the task"—a finding that diverges from induced negative mood (see Martin et al. 1993). With respect to the consequences of task persistence, it has been shown that dysphoric individuals' facilitated disengagement from obsolete plans can have positive consequences, for instance, when relearning new rules (Van den Elzen and MacLeod 2006). Similarly, research by Wrosch and colleagues has demonstrated that the capacity to disengage from unattainable goals is related to subsequent decreases in depressive symptoms and increases in well-being (e.g., Dunne et al. 2011; Wrosch and Miller 2009).

The empirical evidence discussed thus far suggests that clinical and subclinical depression is associated with decreased task persistence and facilitated goal disengagement, at least with respect to concrete actions. Even though this comes with undesirable decreases in task performance, these results accord with the assumption that depression might sometimes serve an adaptive function.

22.2.7 Rumination and Self-Focus

In the preceding section, we have discussed evidence suggesting lower task persistence and facilitated behavioral disengagement in depression. However, from a cognitive point of view, it is well established that depression is related to impaired attentional disengagement and rumination. In this section, this maladaptive case of disengagement is discussed.

Ruminative responses have been defined as "behaviors and thoughts that focus one's attention on one's depressive symptoms and on the implications of these symptoms" (Nolen-Hoeksema 1991, p. 569). Such recurrent negative thoughts play an important role in the onset and maintenance of depression. Studies conducted in the framework of response style theory (Nolen-Hoeksema 1991) consistently demonstrate that the experimental induction of rumination increases negative mood in dysphoric individuals, whereas a distraction induction reduces negative mood in dysphoric individuals (see Nolen-Hoeksema et al. 2008, for a review).

From a self-regulation perspective, Pyszczynski and Greenberg (1987) have postulated that following a negative life event or failure, depressed individuals are unable to disengage from an unattainable goal but instead engage in a depressive self-focusing cycle, which intensifies their negative affect. Similar to the work by Nolen-Hoeksema and colleagues, their studies show that distraction from perseverating on negative self-content and self-discrepancies may deactivate negative self-schemas and alleviate negative biases (Pyszczynski et al. 1989).

Rumination has also been linked to deficient cognitive control and to attentional disengagement. The impaired disengagement hypothesis by Koster et al. (2011) states that depressed individuals have difficulties switching their attention away from negative self-referent material and show prolonged processing of negative stimuli (e.g., Sanchez et al. 2013). Even though empirical evidence is not unequivocal (van Deurzen et al. 2011), depressed individuals' impaired disengagement from the elaborative processing of negative material is thought to play an important role in the perseverance of negative mood states (Joormann and Siemer 2011). In sum, theory and research presented in this section point to the fact that subclinically and clinically depressed individuals are inclined to rumination and show impaired attentional disengagement from negative material.

22.2.8 Affect Regulation

Sustained negative affect is the core feature of depression. Moreover, the inability to effectively regulate one's negative affect is a well-established problem of depressed individuals. Joormann and colleagues (e.g., Joormann and Siemer 2011) suggest that cognitive biases in attention, interpretation, and memory and deficits in cognitive control (i.e., difficulties in inhibiting the elaborative processing of negative material) may be responsible for depressed individuals' difficulties in effectively using emotion regulation strategies. A number of recent studies document that clinically, subclinically, and remitted depressed individuals indeed report using more frequently maladaptive emotion regulation strategies like rumination and using less frequently adaptive strategies like reappraisal (see Aldao et al. 2010, for a review).

Another common strategy for regulating one's negative affect is the recall of positive memories. Several studies suggest that clinically, subclinically, and remitted depressed individuals have difficulties using such mood-incongruent recall of positive memories to effectively regulate their negative affect (e.g., Joormann et al. 2007; Josephson et al. 1996). Finally, there is evidence that not only the regulation of negative affect but also the upregulation or amplification of positive affect is impaired in clinical and subclinical depression (Werner-Seidler et al. 2013). Taken together, individuals experiencing clinical or subclinical symptoms of depression have difficulties with respect to the effective self-regulation of their affect. Moreover, maladaptive affect regulation seems to be a trait-like vulnerability that persists after remission and that predicts the future course.

22.2.9 Summary

In this first part of the chapter, we have outlined self-regulation functioning in clinical and subclinical depression, passing the steps of goal-directed behavior from the setting of a goal or standard, the initiation, the direction, and the persistence of an action to goal disengagement and related aspects of rumination and affect regulation. Throughout the sections, we have pointed out in which ways depressed individuals' functioning differs from normal functioning. To start with, depressed individuals set higher standards for themselves than they expect to reach and they have difficulties in the spontaneous initiation of actions and task strategies. Moreover, depression is characterized by reduced approach behavior, by reduced responsiveness to an action's hedonic consequences, and by a maladaptive responsiveness to negative feedback. Finally, depressed individuals show facilitated goal or task disengagement but impaired attentional disengagement from negative material. This latter case is related to depressed individuals' propensity to ruminative self-focus and difficulties in effective affect regulation.

In the second part of this chapter, we have a closer look at one aspect of the self-regulation of behavior that has not been discussed thus far, namely, the intensity of behavior. The intensity of behavior, i.e., the vigor and engagement with which individuals pursue their goals is an important aspect of self-regulation that has largely been neglected in the depression literature thus far. From a psychophysiological point of view, we present hypotheses and evidence for the impaired adjustment of effort mobilization in subclinically depressed individuals. Finally, we exemplarily propose some treatment approaches that act on some of the aspects of impaired self-regulation functioning presented throughout this chapter.

22.3 Intensity of Behavior and Effort Mobilization in Dysphoria

As foreshadowed above, the intensity aspect of behavior refers to the vigor and engagement with which individuals pursue their goals. Conceptualizing the intensity of behavior as the momentary mobilization of effort at a point in time in the process of goal pursuit (see also Gendolla and Wright 2009), we have conducted a series of studies and tested several factors that are expected to moderate the effort mobilization of dysphoric individuals. In the following sections, we briefly present the theoretical background of these studies and the operationalization of effort mobilization by individuals' cardiovascular response. Then, we describe evidence for the moderating impact of task difficulty and task context on effort mobilization. Finally, we report evidence for dysphoric individuals' reduced effort mobilization for rewarding and punishing consequences.

22.3.1 Intensity of Motivation and Cardiovascular Response

Based on a resource conservation principle, the motivational intensity theory (Brehm and Self 1989) states that individuals mobilize effort proportionally to task difficulty as long as success is possible and justified: The more difficult a task is, the more effort people invest. When the task is perceived as impossible or when the perceived task difficulty exceeds the importance of success, people should withhold effort. This relationship holds for the case that task difficulty is clear and fixed. In contrast, when task difficulty is fixed but unknown (i.e., unclear task difficulty) or when the task has no fixed difficulty standard (i.e., unfixed task difficulty), effort mobilization should proportionally rise with success importance: The more important a task and its outcomes are, the more effort people invest.

In his integrative model, Wright (1996) proposed that effort mobilization can be operationalized by assessing individuals' cardiovascular response during goal pursuit. According to this analysis, two noninvasive cardiovascular parameters should be particularly well suited for operationalizing effort mobilization because these parameters are influenced by the contractility of the heart muscle and thus by the impact of the sympathetic nervous system on the heart: pre-ejection period (PEP; in milliseconds) and systolic blood pressure (SBP; in millimeter mercury). The PEP is the time interval from the onset of left ventricular excitation until the opening of the aortic valve. It is considered as a direct measure of the force of myocardial contraction and thus as a reliable index of sympathetic activation. SBP is the maximum pressure against the blood vessels following the ejection of the blood. It is mainly influenced by the force of myocardial contraction and may thus be an indicator of sympathetic activation. Diastolic blood pressure (DBP; in millimeter mercury) is the minimum blood pressure between two heartbeats. It is less influenced by myocardial contractility and thus not considered as a reliable indicator of effort mobilization. Finally, heart rate (HR; in beats per minute) is jointly determined by the sympathetic and parasympathetic nervous systems and may under some circumstances reflect sympathetic activation (see Brownley et al. 2000). Over two decades of research within Wright's integrative model has corroborated that cardiovascular reactivity follows the predictions of motivational intensity theory as described above (e.g., Gendolla et al. 2012a, b; Wright and Kirby 2001; Wright and Stewart 2012).

22.3.2 Impact of Task Difficulty and Task Context

Considering that clinical and subclinical depression is characterized by persistent negative affect, we have applied the principles of motivational intensity theory (Brehm and Self 1989) and the reasoning of the mood–behavior model (Gendolla 2000) to systematically investigate depressed individuals' effort mobilization. According to the mood–behavior model, moods can have an informational impact on evaluations that, in turn, determine behavior. In the context of goal pursuit, we hypothesized that depressed mood should lead to a mood-congruent appraisal of task demand, i.e., to higher perceived task difficulty. For the five quasi-experimental studies reported below, we recruited extreme groups of undergraduate students with low scores ("nondysphoric") versus high scores ("dysphoric") on self-report depression scales. According to the dimensional perspective of psychopathology, we considered dysphoric participants to have subclinical symptoms of depression that differ quantitatively but not qualitatively from clinical depression. The dependent variable of the studies reported in the remainder of this chapter was participants' cardiovascular reactivity, i.e., the change in cardiovascular activity from a rest to a task period. As outlined above, we focused on PEP reactivity and—whenever this parameter was unavailable—on SBP reactivity.

The first two studies (Brinkmann and Gendolla 2007) tested the predictions for tasks with unfixed difficulty, i.e., without fixed performance standard. In the first study, participants were presented with a list of letter series and were asked to correctly memorize within 5 min as many series as possible. Results corroborated that dysphoric participants showed higher SBP reactivity at the beginning of the performance period than nondysphoric participants. This finding was replicated in a second study using a concentration task. During the whole performance period, dysphoric participants showed stronger SBP reactivity than nondysphoric participants. These results suggest that tasks that ask to "do one's best" can elicit high effort mobilization in dysphoric individuals.

Then, we investigated the joint impact of dysphoria and a clear difficulty standard on participants' cardiovascular reactivity (Brinkmann and Gendolla 2008). Participants performed either an easy or a difficult version of a concentration task (Study 1) or a memory task (Study 2). In both studies, results revealed the expected crossover interaction pattern: In the easy condition, dysphoric participants showed stronger SBP reactivity than nondysphoric participants. In the difficult condition, however, nondysphoric participants showed stronger SBP reactivity (see Fig. 22.1). Moreover, task demand appraisals assessed before task performance indicated that dysphoric participants perceived the memory task in Study 2 as more difficult than did nondysphoric participants. Together, these findings corroborate the hypothesis that depressed mood leads to higher perceived task difficulty, which, in turn, leads to higher effort mobilization for easy tasks but to disengagement for difficult but still possible tasks because of too high subjective demand.

In order to experimentally show the hypothesized role of an informational mood impact on task demand appraisals, we conducted another study that made use of a discounting manipulation, which aimed at drawing people's attention to possible mood influences (Brinkmann et al. 2012). We presented dysphoric and nondysphoric participants with a memory task without fixed performance standard. Half of the participants received an additional cue suggesting that their current mood might have an impact while they were working on the task. Results corroborated earlier findings when no cue was provided: Dysphoric individuals had higher SBP reactivity

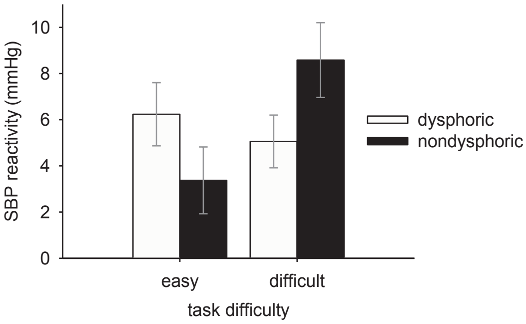

Fig. 22.1 Cell means and standard errors of systolic blood pressure reactivity during performance of an easy versus difficult memory task in Study 2 by Brinkmann and Gendolla (2008). Does depression interfere with effort mobilization? Effects of dysphoria and task difficulty on cardiovascular response. (Copyright: American Psychological Association. Reprinted with permission)

than nondysphoric individuals. In contrast, when participants received the cue about possible mood influences, the SBP reactivity pattern was reversed. This means that mood had lost its informational value for task demand appraisals, which resulted in lower perceived task demand and thus lower SBP reactivity in dysphoric participants. These findings suggest that, when a cue was provided, dysphoric participants managed to reduce the impact of depressed mood on their task demand appraisals and on subsequent effort mobilization.

In summary, the findings of these five studies show that depression is not necessarily characterized by a general motivational deficit and disengagement of effort mobilization. Rather, when task difficulty is unfixed or easy, dysphoric individuals mobilize even more effort than nondysphorics. The results of these studies also qualify previous research that does not unequivocally find either enhanced or attenuated cardiovascular reactivity in depression and dysphoria (e.g., Carroll et al. 2007) and underline the importance of considering task difficulty and task context.

22.3.3 Impact of Success Importance

Success importance is another important concept of motivational intensity theory (Brehm and Self 1989). Among other variables, success importance is determined by rewards and punishments. It follows that such hedonic consequences have a direct impact on effort mobilization when task difficulty is unclear or unfixed: The more positive or negative the consequences are, the more effort mobilization is expected (see also Wright 1996). As outlined above, behavioral and neuroscientific studies have demonstrated depressed and dysphoric individuals' reduced responsiveness to reward and, less consistently, to punishment. In the following, we report five quasi-experimental studies that investigated dysphoric individuals' effort mobilization for obtaining rewards or avoiding punishments during tasks with either unclear or unfixed task difficulty.

In the first two studies, dysphoric and nondysphoric participants worked on mental tasks and could earn a monetary reward or avoid a monetary loss depending on their performance outcome (Brinkmann et al. 2009). Study 1 demonstrated that nondysphoric individuals showed high SBP reactivity when expecting to lose money, whereas dysphoric participants showed low SBP reactivity. Study 2 revealed that nondysphoric individuals showed higher SBP and PEP reactivity in the reward condition than in the neutral condition. In contrast, dysphoric participants showed a blunted cardiovascular response across all conditions. These findings thus suggest a general insensitivity to both monetary reward and punishment in dysphoria.

A following study by Franzen and Brinkmann (2014) aimed at investigating reward and punishment responsiveness in dysphoria on both cardiovascular and behavioral levels. Working on a recognition memory task, one third of the participants earned small amounts of money for correct responses, one third lost small amounts of money for incorrect responses, and one third neither earned nor lost money. As expected, reactivity of PEP was higher in both incentive conditions compared to the neutral condition for nondysphoric participants, while it was blunted across all three conditions for dysphoric participants (see Fig. 22.2). On the behavioral level, results revealed that nondysphorics performed better following a monetary loss than did dysphorics. This study thus confirms that dysphorics have

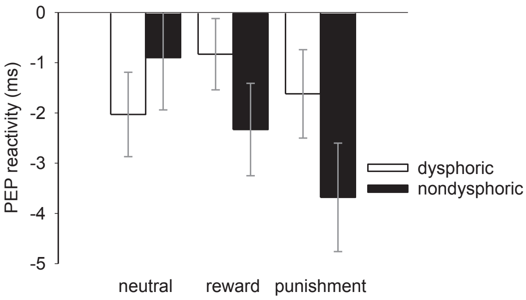

Fig. 22.2 Cell means and standard errors of pre-ejection period reactivity during performance of a recognition memory task in anticipation of monetary rewards or punishments in the study by Franzen and Brinkmann (2014)

a motivational deficit during both reward and punishment anticipation and that they show an altered behavioral response to punishment.

In order to investigate the linear increase of effort mobilization with increasing reward value as suggested by motivational intensity theory (Brehm and Self 1989), another study by Brinkmann and Franzen (2013) manipulated monetary reward at three levels. Participants worked on a memory task with unclear performance standard, expecting no reward, a small monetary reward, or a high monetary reward for successful overall task performance. As expected, nondysphorics gradually mobilized more effort in terms of PEP reactivity dependent on reward value, whereas dysphorics did not mobilize more effort during reward anticipation compared to the condition without reward. This study suggests that dysphoric individuals' insensitivity to monetary reward generalizes across varying reward levels.

Finally, a study by Brinkmann et al. (in press) took into account the fact that not only monetary gains or losses determine the importance of success: Social consequences are also important motivators and at the same time susceptible to impaired effectiveness in depression (Forbes and Dahl 2012). Dysphoric and nondysphoric participants worked on a 5-min memory task. Half of them received the vague instruction that "in case they performed well," they would have the possibility to enter their name in the study's public "best list." As expected, nondysphoric participants' SBP reactivity was higher when they anticipated getting this kind of social approval for good performance. In contrast, dysphoric individuals had low SBP reactivity regardless of the presence or absence of the social reward. These findings expand prior evidence for reward insensitivity in depression to social rewards.

Our studies on reward and punishment responsiveness in subclinical depression confirm that dysphoric individuals' effort mobilization is blunted regardless of the kind or amount of incentives at stake. Our motivational analysis thus suggests that the self-regulation of effort mobilization is indeed impaired in subclinical depression and converges with the findings of impaired self-reported, behavioral, and neural reward responsiveness in depression reported above.

22.3.4 Summary

Taken together, our program of research leads us to conclude that there is no general motivational deficit in subclinical—and presumably also clinical—depression. Rather, one can observe a maladaptive adjustment of effort mobilization: Dysphoric individuals do not seem to take into account information about task difficulty and success importance in an adaptive way. It is of note that recent cardiovascular findings suggest that the effects reported above might be mood-state dependent and thus reflect motivational deficits rather than stable biomarkers of depression (Salomon et al. 2013). Our findings have important implications for the treatment of depression. First, being aware of the impact of negative affect on task demand appraisals, it is important to avoid the impression of tasks being too difficult but rather start with easy or "do your best" tasks (see below). Second, in order to raise the level of maximum effort that a person is willing to invest (see Brehm and Self 1989), treatments have to act on alleviating anhedonic symptoms (see below).

22.4 Conclusions and Implications

Throughout this chapter, we have reviewed evidence for impaired self-regulation functioning in clinical and subclinical depression. Understanding impaired self-regulation is important as this knowledge is the basis for proposing specific treatments that allow depressed individuals to develop a more adaptive self-regulation of their behavior. Fortunately, there exist a number of treatment approaches that are targeted on specific aspects of depression. To conclude this chapter, we exemplarily focus on reward sensitivity and goal setting and present three specific therapies that are suited for alleviating these impairments in depression.

First, behavioral activation is an appropriate treatment to cope with insensitivity to reward or with depressed individuals' tendency to set too high goals. This structured approach has emerged in the 1950s (Bennett-Levy et al. 2004) and has been proven effective for clinical depression (e.g., Cuijpers et al. 2007; Hopko et al. 2003). Behavioral activation aims at helping depressed individuals to reengage in pleasant activities, which will increase reinforcement from the environment, and in turn elicit the experience of pleasure. What is more, behavioral activation proposes to start with the identification of small and doable goals. Then, depressed individuals ought to gradually identify and achieve higher goals. In sum, behavioral activation techniques should increase reward sensitivity, avoid the setting of unachievable goals, and counteract the vicious cycle of ruminative self-focus (Dimidjian et al. 2008).

Second, mindfulness-based cognitive therapy (MBCT; Segal et al. 2013) could also be proposed to remitted depressed patients to increase reward sensitivity. This program is specifically designed to prevent depressive relapse. During each session, formal (e.g., sitting meditation, body scan) and informal (e.g., walking, yoga, cultivating mindfulness in daily life) meditation practices are suggested in combination with features of cognitive therapy for depression (e.g., identify the warning signs of depression). Concerning positive affect in particular, one exercise invites participants to think about a recently experienced pleasant event and to analyze it while being aware of related thoughts, feelings, and bodily sensations. Another exercise focuses on identifying nourishing activities during a typical day and on making a list of pleasurable activities that can be programmed when one feels bad. A number of studies have demonstrated the efficacy of MBCT not only for the reduction of depressive symptoms (e.g., Ma and Teasdale 2004) but also for increasing positive emotions and reward experience (Geschwind et al. 2011).

Finally, positive psychotherapy aims at increasing positive emotions, engagement, and meaning and should allow depressed individuals to rediscover pleasure (Seligman et al. 2006). Specifically, the module "savoring" invites participants to take the time to consciously enjoy something that one usually hurries through in daily life (e.g., eating a meal, taking a shower). Then, participants describe what they did, how they did it in a different way than usually, and how they felt compared to how they usually feel. Another module invites participants each evening to write down three good things that happened during the day and to explain why they think these events happened.

To conclude, clinical and subclinical depression is characterized by dysfunctional self-regulation of behavior. Fortunately, a number of specific treatments exist, among which we have exemplarily outlined three. A detailed knowledge of dysfunctional self-regulation in depression is crucial for the development of further treatment approaches and for individually tailoring them to the specific symptoms of the individual patient.

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Perinatal Developmental Origins of Self-Regulation

23

Jens Henrichs and Bea R. H. Van den Bergh

23.1 Introduction

The “developmental origins of health and disease” (DOHAD) hypothesis emphasizes the importance of perinatal experiences in influencing developmental patterns and phenotypic variations in mental and physical health and disease (Barker et al. 1989; Gluckman and Hanson 2004). According to this hypothesis, developmental programming is a process by which a perinatal environmental condition during a sensitive developmental period has a long-lasting and/or permanent impact on the development of cells, tissues, organs, including the brain, and associated physiological and metabolic systems (Barker et al. 1989; Gluckman and Hanson 2004). Exposure to adverse environmental factors early in life can modulate developmental programming resulting in a higher vulnerability for poor somatic and mental health outcomes across the life span and a large body of evidence illustrates this link (Barker et al. 1989; Gluckman and Hanson 2004; Monk et al. 2013; Raikkonen et al. 2011). Recently, an extended concept of the DOHAD hypothesis has been introduced by proposing the DOBHAD hypothesis which emphasizes programming effects on early brain development and subsequent behavioral development (Van den Bergh 2011). As neurodevelopment is a continuing and remarkably rapid process during the perinatal period and infancy (Gale et al. 2006; Gazzaniga et al. 1998; Kolb et al. 2012), the developing brain is particularly sensitive to adverse environmental conditions early in life. Exposure to adverse environmental conditions may modulate programming of early neural development predisposing the individual to later neurodevelopmental problems (Monk et al. 2013; Van den Bergh 2011). High levels of maternal anxiety, depression, or stress during pregnancy represent adverse environmental conditions that have frequently been shown to be associated with altered offspring neurodevelopmental outcomes, such as self-regulation at the emotional, cognitive, and behavioral level later in life (Huizink et al. 2004; Monk et al. 2013; Raikkonen et al. 2011; Seckl and Holmes 2007; Van den Bergh 2011; Van den Bergh et al. 2005b). Although one cannot rule out that shared genetic factors and postnatal differentiation effects also partly explain this link (Lupien et al. 2009), animal models and natural experiments in humans showed that prenatal exposure to stress can induce developmental programming of offspring self-regulatory outcomes (e.g., Huizink et al. 2004; Laplante et al. 2008).

This chapter focuses on the effect of maternal anxiety, depression, and stress during pregnancy on offspring self-regulation. The development of

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self-regulation is crucial for successful adjustment throughout life. Whereas in infancy, regulation is mainly provided by caregivers, self-regulation already starts to develop at birth (or even before; e.g., sleep states) and gradually develops further (McCartney and Phillips 2006; Rothbart et al. 2004; Rothbart et al. 2011). Adequate caregivers' support of initial self-regulatory tendencies is vital from birth onwards (Fox and Calkins 2003).

Self-regulation has been defined as the processes and abilities that make it possible to modulate (i.e., facilitate or inhibit) reactivity, which refers to motor, physiological, attentional, and emotional responses to internal and external stimuli (Rothbart and Derryberry 1981; Rothbart et al. 2011). Self-regulation allows the individual to display adequate behavior and to appropriately respond to situational demands in accordance with his or her age and reactivity pattern: for example, inhibiting reactive fearfulness that is too strong or engage it when it is appropriate and, likewise, facilitate or inhibit reactive approaching tendencies (Rothbart et al. 2004; Van den Bergh and Mennes 2006). Self-regulation may include (1) emotional control, (2) attention, planning, and other cognitive strategies, as well as (3) behavioral strategies (McCartney and Phillips 2006). Appropriate/adequate self-regulation exerts positive effects on somatic and mental health (Kubzansky et al. 2011) or one may even state that somatic and mental health imply appropriate self-regulation. Psychological problems are often characterized by an imbalance of any kind between reactivity and self-regulation (i.e., one of the two or both aspects have abnormal levels; Fox and Calkins 2003; Van den Bergh and Mennes 2006). Due to such an imbalance, individuals may be unable to meet situational demands and to display age-appropriate levels of adaptation (Van den Bergh and Mennes 2006). Increased irritability, fuzziness, and sleeping and feeding problems may reflect strong reactivity to endo- or exogenous stimuli or, in other words, high levels of reactivity or failed (self)-regulation (Van den Bergh and Mennes 2006). Attention problems, problems in inhibitory control, and externalizing and internalizing problems across the life span also indicate an imbalance between reactivity and self-regulation (Van den Bergh and Mennes 2006). This chapter addresses self-regulatory processes and abilities at the behavioral, emotional, and cognitive level from birth onwards.

The developmental programming effects of prenatal exposure to maternal anxiety, depression, and stress on offspring self-regulation may partly be explained by an increased activity of the maternal hypothalamic–pituitary–adrenal (HPA) axis and its hormonal end products (i.e., two glucocorticoids, cortisol, and cortisone; Huizink et al. 2004; Raikkonen et al. 2011; Van den Bergh 2011; Van den Bergh et al. 2005b). Glucocorticoid hormones organize and synchronize events related to day and night activity, regulate the stress response, and facilitate adaptive processes (de Kloet et al. 2005b). When maternal glucocorticoids are not biologically inactivated by the placental enzyme 11B-hydrosteroid dehydrogenase type 2 (11-BHSD2) and pass the placental barrier, they might alter fetal development, the regulation and development of the fetal neuroendocrine stress system, and (subsequent) neurodevelopmental patterns (Huizink et al. 2004; Raikkonen et al. 2011; Van den Bergh 2011). Maternal and fetal cortisol levels are correlated (Gitau et al. 1998). Previous research showed that maternal prenatal stress (in animals) and maternal anxiety and depression (in humans) during pregnancy downregulate placental 11-BHSD2 (Mairesse et al. 2007; O'Donnell et al. 2012; Raikkonen et al. 2011), possibly restricted by genotype (Lucassen et al. 2009). Moreover, while glucocorticoids are crucial for fetal tissue proliferation and differentiation, exposure to excessive levels of glucocorticoid hormones can reduce fetal growth (Fowden and Forhead 2004) and also impair neurodevelopment (Antonow-Schlorke et al. 2003) as cortisol is able to cross the blood–brain barrier (Zarrow et al. 1970). Prenatal stress and associated gene–environment interactions influencing the HPA axis may also alter early neurodevelopment (Raikkonen et al. 2011). Anxiety, depression, and stress experienced by the mother during pregnancy may also affect the development of the fetus and its brain via other possible pathways, such as maternal lifestyle (e.g., continued smoking and malnutrition during pregnancy), au-

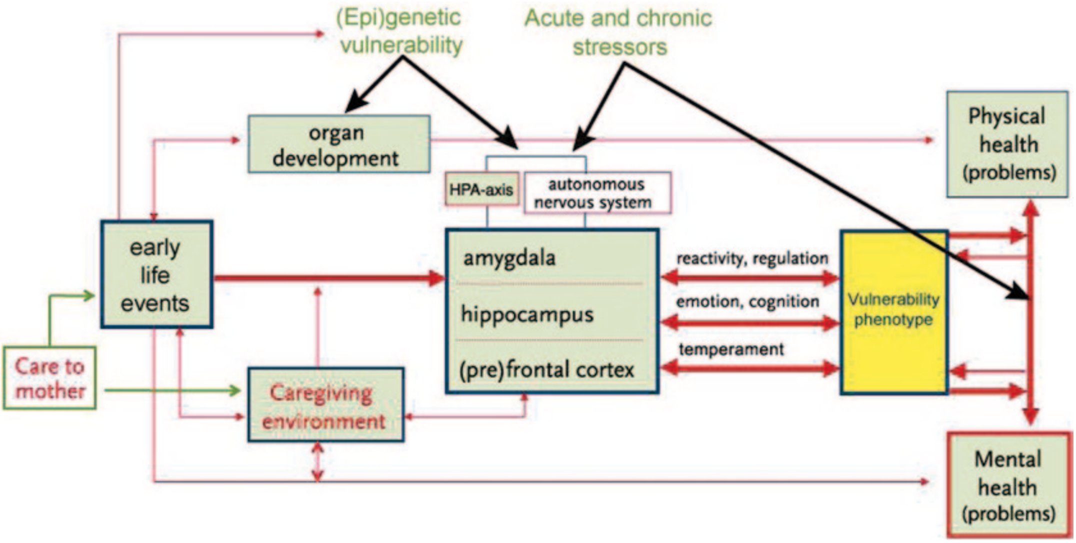

Fig. 23.1 Mechanisms of perinatal origins of self-regulation. (Based on Van den Bergh 2011)

tonomous nervous system physiological stress-regulatory mechanisms, and placental functioning (e.g., blood supply, nutrient transport, and 11-BHSD2), as presented in Fig. 23.1 and/or depicted in more detail in earlier reviews (Huizink et al. 2004; Kajantie and Raikkonen 2010; Monk et al. 2013; O'Donnell et al. 2009; Raikkonen et al. 2011; Seckl and Holmes 2007; Van den Bergh et al. 2005b).

Alterations of epigenetic mechanisms due to the prenatal exposure to maternal stress hormones may also play a role in developmental programming of neurodevelopmental outcomes, such as self-regulation (Van den Bergh 2011). Epigenetic modifications represent altered gene functions which cannot be accounted for by alterations in nucleotide sequence (Graff and Mansuy 2008). Epigenetic mechanisms comprise DNA methylation, histone modifications, chromatin remodeling, and others (Graff and Mansuy 2008; Meaney 2010). These mechanisms are important for many vital functions, including brain functions, synaptic plasticity, and memory formation, and their alteration is implicated in the etiology of cognitive and psychiatric disorders (Graff and Mansuy 2008; Szyf 2013; Van den Bergh 2011). Biological attributes of prenatal exposure to maternal stress, anxiety, or depression may thus alter gene expression via epigenetic modifications leading to modulation of the programming of brain development (Ben-Ari 2008; Szyf 2013; Van den Bergh 2011). Interestingly, evidence of two recent studies in humans indeed demonstrates that maternal mood during pregnancy and pregnancy-related anxiety can influence the methylation status of the glucocorticoid receptor (GR) gene (NR3C1) as analyzed based on cord blood samples taken from babies at birth (Hompes et al. 2013; Oberlander et al. 2008). Moreover, experiences of intimate partner violence by the mother during pregnancy were linked to the methylation status of the GR gene in the offspring at age 10–19 years (Radke et al. 2011). This gene and its expression is important for the level of activity of the HPA axis and the related stress response (de Kloet et al. 2005a; McGowan et al. 2009), as the GR plays a crucial role in the regulation of the negative feedback inhibition of the endocrine response to a stressor (McGowan 2012). In rats, experimentally induced prenatal stress alters 11-BHSD2 gene expression via changes in DNA methylation in both the placenta and the fetal brain (Pena et al. 2012).

Via the co-occurring and partly interdependent mechanisms described above, prenatal exposure to maternal anxiety, depression, or stress may alter the development of various brain structures and diverse brain developmental processes throughout pregnancy. In the first two pregnancy trimesters, neuron proliferation, migration, and differentiation take place and the fetal brain architecture is formed (Rakic 2006). In the third pregnancy trimester (ca. 26–40 weeks of gestation), axon and dendritic growth, synaptogenesis, and the formation of adult-like neural networks occur (Ben-Ari 2008; Fox et al. 2010), which enables the development of areas important for, e.g., receptive language and other higher neuropsychological abilities (Tau and Peterson 2010). From the 29th week of gestation, increased connectivity develops in motor, (somato)sensory, and executive control networks (Ben-Ari 2008; Fox et al. 2010). A vast amount of animal models has demonstrated that exposure to prenatal stress may have impacts on various brain structures, at both the microscopic and macroscopic level, including the hippocampus, amygdala, corpus callosum, anterior commissure, cerebral cortex, cerebellum, and hypothalamus, that are involved in self-regulatory functioning later in life (Charil et al. 2010). Prenatal stress-induced changes in these brain regions included alterations in proliferation, migration, and differentiation of brain cells, synaptic and dendritic density, and in GR density. Prenatal stress also reduced tissue volume in these different brain regions. Moreover, animal research suggests that the association between exposure to prenatal stress and altered self-regulatory functioning in adult offspring, such as higher levels of anxiety and changes in circadian rhythm, locomotor activity, and paradoxical sleep, is mediated by prenatal stress-induced alterations in offspring brain functions regulating HPA axis feedback mechanisms, as indicated by a prolonged stress hormone secretion and a reduced number of central GR (Maccari et al. 2003). Thus, in line with the DOBHAD perspective, this suggests that alterations in developing brain structures and developmental brain processes may mediate the association of prenatal exposure to maternal anxiety, depression, or stress with various offspring self-regulatory problems across the life span (Van den Bergh 2011).

This chapter summarizes prospective observational studies in humans investigating the association of prenatal exposure to maternal anxiety, depression, and stress with different types of offspring self-regulation from infancy to adulthood. We present findings based on different types of assessment techniques (i.e., questionnaires, observation scales, neuropsychological tasks, endocrine and physiological measures, and brain imaging techniques). As brain development is most rapid during pregnancy, infancy, and early childhood and the DOBHAD perspective suggests that programming effects are not restricted to the prenatal period but also occur postnatally (Kolb et al. 2012; Van den Bergh 2011), we also address the influence of postnatal environmental factors on this association. The results of three human studies on the moderating effect of genetic factors on the association of maternal anxiety, depression, or stress during pregnancy with offspring self-regulation are also described. Finally, future directions for epidemiological and clinical research and public health implications are discussed.

23.2 Consequences of Maternal Anxiety, Depression, and Stress During Pregnancy for Offspring Self-Regulation from Birth Onwards: Evidence from Human Studies

Table 23.1 summarizes prospective observational studies examining the association of maternal anxiety, depression, and stress during pregnancy with offspring self-regulation in infancy, childhood, adolescence, and early adulthood measured with questionnaires, standardized observations, neuropsychological tasks, endocrine and physiological measures, and neuroanatomical/physiological brain (electrical) imaging techniques. The large majority of these studies revealed significant associations of maternal anxiety, depression, or stress during pregnancy with offspring self-regulation even after adjustment for maternal anxiety/depression/stress experienced post partum and/or other potential pre- and postnatal confounders, including maternal smoking and/or alcohol use during pregnancy, educational level, ethnicity, family income, gestational age, birth weight, and child gender. In several studies, these associations were also controlled for the intake of medications during pregnancy (e.g., antidepressants) or paternal pre- and/or postnatal psychological symptoms. Studies investigating

Table 23.1 Maternal anxiety, depression, or stress during pregnancy and offspring self-regulatory outcome from infancy onwards

Author(s) and year of publication	Child age	Prenatal exposure or measure of maternal prenatal anxiety, depression, or stress	Pregnancy trimester or weeks of gestation	Offspring outcome(s)
Field et al. (2010)	2 days	Anxiety or depression or comorbid depression and anxiety	20 (mean)	Cortisol levels, norepinephrine, dopamine, serotonin, frontal EEG
Rieger et al. (2004)	3–5 days	Total distress	30–34	Neonatal regulation problems (NBAS)
Diego et al. (2004)	1 week	Depression	26	Cortisol, norepinephrine, and dopamine level, frontal EEG asymmetry
Hernández-Reif et al. (2006a)	12 days	Depression	–	Attentiveness and arousal (NBAS)
Lou et al. (1994)	4–14 days	Life events stress	–	Prechtl's neurological examination
Hernández-Reif et al. (2006b)	16 days	Depression	–	Frontal EEG asymmetry, heart rate accelerations/decelerations (EKG)
Ponirakis et al. (1998)	Birth, 1 day, 3–4 weeks	Anxiety (state and trait), maternal cortisol	≤6, 32–34	Medical records (e.g., Apgar scale), cardiac vagal tone (EKG Porges' method)
DiPietro et al. (2008)	6 weeks	Fetal reactivity to maternal stimulation (viewing of video)	32	Infant negative reactivity observed during standard infant development assessment procedure
Stapleton et al. (2012)	6–8 weeks	Perceived partner support and relationship quality	–	Infant temperament
Hunter et al. (2012)	76 days	Current maternal anxiety disorder	–	Auditory sensory gating
Van den Berg et al. (2009)	2 months	Elevated depressive symptoms	20	Excessive infant crying
Van Batenburg-Eddes et al. (2009)	3 months	General anxiety	20	Observations of infant neuromotor development (Prechtl)
Baibazarova et al. (2012)	3 months	Maternal and fetal cortisol, perceived stress (PSS), state anxiety	Second trimester	Infant temperament (mixed results)
Davis et al. (2004)	4 months	Anxiety (state) and depression	32	Infant behavioral reactivity (HIBRP)
McGrath et al. (2008)	2, 6 months	Depression	Third trimester	Ratings of infant temperament
Field et al. (1985)	3–5 months	Psychosocial pregnancy problems	Third trimester	Mother–infant interactions (CCTI)
Rothenberger et al. (2011)	5 months	Perceived stress, depression, negative life events	Each pregnancy trimester	Infant affective reactivity to novel stimuli (observations)
Wurmser et al. (2006)	3 and 6 months	Negative life events	6 weeks	Infant crying (5-day 24 h behavior diary)
Van der Wal et al. (2007)	3–6 months	Depressive symptoms, anxiety (pregnancy-specific), parenting stress; job strain	7–40	Excessive infant crying
Austin et al. (2005)	4–6 months	Anxiety (trait); depression, life events stress	Third trimester (32)	Difficult infant temperament (SITQ)
Brennan et al. (2008)	6 months	Depression and anxiety (DSM-IV)	26	Infant cortisol level before and after an infant stress test
Henrichs et al. (2009)	6 months	Anxiety (pregnancy-specific; general)	12, 20	Temperament (IBQ-R); infant difficulties

Table 23.1 (continued)

Author(s) and year of publication	Child age	Prenatal exposure or measure of maternal prenatal anxiety, depression, or stress	Pregnancy trimester or weeks of gestation	Offspring outcome(s)
Pluess et al. (2011)	6 months	Anxiety (general) and serotonin transporter polymorphism as moderator	20, cord blood	Infant negative emotionality (IBQ-R)
Van den Bergh (1990, 1992)	1 week, 12 weeks, 7 months	Anxiety (state and trait)	12–22, 23–31, 32–40	Prechtl's neurological examination, behavioral state observation, feeding score, mother–infant interaction (ITQ, ICQ, BSID)
Grant et al. (2009)	7 months	Anxiety	35–39	Cortisol level of the child, pre and post still face procedure
Vaughn et al. (1987)	4–8 months	Anxiety (trait)	21, 26–34, 35	Infant temperament (ITQ-revised)
Huizink et al. (2002, 2003)	8 months	Pregnancy-specific anxiety, perceived stress, maternal cortisol	15–17, 27–28, or 37–38	Infant mental development (BSID-MDI); observations and parent report of infant temperament (attention regulation and difficult behavior)
Brand et al. (2006)	9 months	9/11	–	Infant temperament (IBQ)
Yehuda et al. (2005)	9 months	9/11	28–40	Cortisol level of the child
Otte (2013); Otte et al. (2011), van den Bergh et al. (2012, 2013)	2 and 9 months	Anxiety (state)	9–15	Infant auditory processing (ERP oddball paradigm)
Weikum et al. (2012)	36 weeks of gestation (in utero), 6 and 10 months	Depression (HAM-D)	Second and third trimester	Speech perception tasks
Gerardin et al. (2011)	3 days, 12 months	Depression	Third trimester	Neonatal motor skills and regulation states (NBAS); infant anxiety, activity/impulsivity, and sleep problems (ITSEA)
Davis and Sandman (2010)	3, 6, 12 months	Maternal cortisol, pregnancy-specific and state anxiety, perceived stress, and depression	15, 19, 25, 31, 37	Mental and psychomotor development (BSID-MDI and BSID-PDI)
Tollenaar et al. (2011)	5, 8 weeks, 5, 12 months	Maternal circadian cortisol levels, general and pregnancy-specific anxiety and stress	Last trimester	Infant cortisol reactivity to stressors
Keim et al. (2011)	12 months	Trait anxiety and depressive symptoms	20	Infant cognitive development (MSEL), nonlinear associations
Dierckx et al. (2009)	14 months	Maternal psychiatric symptoms (BSI)	20	Cardiac vagal modulation assessed with heart rate variability (nonsignificant)
Bergman et al. (2010a)	17 months	In utero (fetal) cortisol	17	Infant fear reactivity (Lab-TAB; nonsignificant)
Bergman et al. (2010b)	14–17 months	Maternal prenatal cortisol (and infant–mother attachment as moderator)	17	Infant cognitive development (BSID-MDI)
Blair et al. (2011)	2 years	State and pregnancy-specific anxiety	15, 19, 25, 31, 37	Temperament (ECBQ)

Table 23.1 (continued)

Author(s) and year of publication	Child age	Prenatal exposure or measure of maternal prenatal anxiety, depression, or stress	Pregnancy trimester or weeks of gestation	Offspring outcome(s)
DiPietro et al. (2006)	2 years	Anxiety (general: POMS and STAI), stress (DSI, PSS); depression (POMS, CES-D); pregnancy-specific stress (PES)	24, 28, 32	Motor and mental development (BSID-MDI/-PDI; IBR)
Brouwers et al. (2001)	3 weeks; 1 year; 2 years	Anxiety (state and trait)	32	Orientation (NBAS), cognitive development (BSID-MDI), task orientation and motor coordination (IBR)
Gutteling et al. (2005b)	27 months	Perceived stress Pregnancy-related anxiety	15–38	Behavioral problems (CBCL), temperament (ICQ), attention regulation (BSID)
Velders et al. (2011)	3 years	Maternal and paternal depressive symptoms and hostility, perceived family functioning	20	Internalizing (including anxious/depressed and emotional reactive behavior) and externalizing problems (maternal and paternal report using CBCL)
Velders et al. (2012)	14 months and 3 years	Maternal psychological symptoms and moderating effects of variation in the glucocorticoid receptor gene at rs41423247	20	Infant cortisol reactivity, childhood internalizing and externalizing problems (maternal and paternal report using CBCL)
Kok et al. (2013)	3 years	Perceived prenatal family and general stress and mediating/moderating effects of COMT Val158Met genotype and maternal discipline	20	Child compliance (coded observations during mother–child disciplinary tasks)
Henrichs et al. (2011)	18, 24, 37 months	Perceived prenatal family stress reported by both parents	20	Word comprehension (MCDI), nonverbal cognitive development (PARCA), effortful control (observational assessments)
Van Batenburg-Eddes et al. (2013)	3 and 4 years	Anxious and depressive symptoms reported by both parents (cross-cohort consistency study)	20	Attention problems and emotional problems (CBCL or SDQ; little evidence found)
de Bruijn et al. (2009)	14–54 months	Anxiety, depression	Each trimester	Behavioral and emotional problems (CBCL); saliva cortisol after stressors
Martin et al. (1999)	6 months, 5 years	Psychological distress	1–16, 17–28, 29–40	Temperament (ITQ, PTQ)
Laplante et al. (2004)	2 years	Ice storm	4–24	Cognitive development (BSID-MDI), language production (MCDI)
Laplante et al. (2008)	5.5 years		–	IQ (WISC)
Niederhofer and Reiter (2004)	6 months, 6 years	Pregnancy risks	16–20	Temperament (ITQ), school grades and marks
Martini et al. (2010)	Birth, 4–5 years or older	Anxiety disorder before birth (DSM-IV), prenatal self-perceived stress	–	Apgar score (nonsignificant), ADHD, separation anxiety disorder, conduct disorder
Loomans et al. (2011, 2012)	5 years	State anxiety (STAI)	16	Neurocognitive functioning assessed with a computerized reaction time task and a reaction time choice task; mother- and teacher-reported behavioral and emotional problems (SDQ)

Table 23.1 (continued)

Author(s) and year of publication	Child age	Prenatal exposure or measure of maternal prenatal anxiety, depression, or stress	Pregnancy trimester or weeks of gestation	Offspring outcome(s)
Gutteling et al. (2004, 2005a, 2006)	4–6 years	Daily hassles, anxiety, perceived stress, life events, maternal cortisol	16	Cortisol level of the child at first school day; after inoculation memory (TOMAL)
O'Connor et al. (2002, 2003)	4 and 7 years	Anxiety (CCI)	18, 32	Emotional and behavioral problems (SDQ)
Rodriguez and Bohlin (2005)	7–8 years	Perceived stress	10, 12, 20, 28, 32, 36	ADHD (DSM-IV)
Beversdorf et al. (2005)	8 years	Life events (SSRS)	21–32	Autism (DSM-IV)
Buss et al. (2010)	6–9 years	Pregnancy-specific anxiety	19, 25, 31	Gray matter density in various (MRI study)
Davis and Sandman (2012)	6–9 years	Maternal cortisol and pregnancy-specific anxiety	19, 25, 31	Anxiety symptoms (CBCL)
Buss et al. (2011)	6–9 years	Pregnancy-specific anxiety	15, 19, 25, 31, 37	Executive functioning (inhibitory control (Flanker task) and visuospatial working memory (sequential memory test)
Buss et al. (2012)	6–9 years	Maternal cortisol	15, 19, 25, 31, 37	Affective problems and larger amygdale volume in girls
O'Connor et al. (2005)	10 years	Self-rated anxiety	18, 32	Cortisol level of the child
Khashan et al. (2008)	10 years	Death of a close relative	0–12	Schizophrenia (ICD8/ICD10)
Braithwaite et al. (2013)	6 months, 4–13 years	Anxiety (CCI) and serotonin transporter 5-HTTLPR as moderator	18, 32	Infant temperament (ITQ), behavioral/emotional problems (no moderation effects)
Huizink et al. (2008)	14 years	Chernobyl	First, second, and third trimester	Saliva cortisol and testosterone levels
O'Donnell et al. (2013)	15 years	Anxiety (CCI) and depression (EPDS)	18, 32	Saliva cortisol (diurnal pattern and awakening response based on 4 occasions during one day)
Van den Bergh and Marcoen (2004); Van den Bergh et al. (2005a, 2006, 2008); Mennes et al. (2006, 2009)	8–9 years, 14–15,17 years	Anxiety (state and trait)	12–22	ADHD symptoms (CBCL, TRF), computerized encoding task and stop task, vocabulary and block design (WISC-R), sustained attention (CPT), depression (CDI), cued attention, N-back, Go/NoGo, dual task (ERP), response-shifting
Kinney et al. (2008)	–	Hurricane	24–40	Autism (DSM-III-R/DSM-IV)
Li et al. (2009)	–	Bereavement due to loss of significant other	During pregnancy or up to 1 year before pregnancy	Autism (ICD-8/-10; nonsignificant)

ADHD attention-deficit hyperactivity disorder, *AER* auditory evoked responses, *BSI* brief symptom inventory, *BSID* Bayley scales of infant development, *BSID-MDI* Bayley scales of infant development–mental development index, *BSID-PDI* Bayley scales of infant development–psychomotor development index, *CCI* crown crisp index, *CBCL* child behavior checklist, *CCTI* Colorado child temperament inventory, *CDI* child depression inventory, *CPT* continuous performance task, *C-SSAGA-A* child semi-structured assessment of genetics and alcoholism, *DSI* daily stress inventory, *DSM(-R) diagnostic and statistical manual* (-revised), *ECBQ* early childhood behavior questionnaire, *ECG* electrocardiogram, *EPDS* Edinburgh postnatal depression scale, *ERP* event-related potential, *HAM-D* Hamilton depression scale, *HIBRP* Harvard infant behavioral reactivity protocol, *IBQ* infant behavior questionnaire, *IBR* infant behavior the moderating or mediating influence of genetic and/or postnatal environmental factors on the association of maternal anxiety, depression, or stress during pregnancy with offspring self-regulation are also presented in Table 23.1. The results of the different studies shown in Table 23.1 are arranged by offspring age at the last follow-up measurement.

23.2.1 Neonatal Period

In neonates, maternal anxiety, depression, or stress during pregnancy were related to poorer neurodevelopmental functioning as assessed with the Brazelton Neonatal Assessment Scale or Prechtl's neurological assessment (Brouwers et al. 2001; Gerardin et al. 2011; Hernandez-Reif et al. 2006b; Lou et al. 1994; Rieger et al. 2004) and to neuroendocrine alterations (i.e., changes in cortisol, norepinephrine, dopamine, and serotonin levels; Diego et al. 2004; Field et al. 2010). Inconsistent findings were reported with regard to neonatal Apgar scores, which indicate general health status after birth (Martini et al. 2010; Ponirakis et al. 1998). Yet, neonates prenatally exposed to maternal anxiety, depression, or stress also had altered behavioral states and displayed alterations in (neuro)physiological functioning as indicated by, for example, altered heart rate variability and vagal tone and greater relative right frontal EEG asymmetry (Diego et al. 2004; Field et al. 2010; Hernandez-Reif et al. 2006a; Ponirakis et al. 1998; Van den Bergh 1990, 1992).

23.2.2 Infancy

Studies using parent-report measures to assess self-regulatory outcomes of infants of mothers with anxiety, depression, or stress during pregnancy showed that these infants were perceived as having more sleeping and feeding problems and temperamental difficulties, such as negative emotionality, irritability, and activity problems (Austin et al. 2005; Baibazarova et al. 2013; Blair et al. 2011; Brand et al. 2006; Gerardin et al. 2011; Henrichs et al. 2009; Huizink et al. 2002; McGrath et al. 2008; Van den Bergh 1990, 1992; Vaughn et al. 1987), and as displaying more excessive crying (van den Berg et al. 2009; van der Wal et al. 2007), and poorer verbal and nonverbal cognitive skills (Henrichs et al. 2011; Laplante et al. 2004). Studies using standardized observational measures of infant development revealed that infants of mothers with (increased levels of) anxiety, depression, or stress during pregnancy displayed poorer interactions with their mother (Field et al. 1985), were more irritable (DiPietro et al. 2008) and more reactive (Davis et al. 2004, 2007; Rothenberger et al. 2011), cried more (Wurmser et al. 2006), and had more attention regulation difficulties (Huizink et al. 2002) and more neuromotor development problems (van Batenburg-Eddes et al. 2009). In comparison to controls, infants of depressed mothers treated with selective serotonin reuptake inhibitors (SSRIs) during pregnancy displayed accelerated development of speech perception at age 6 and 10 months, whereas infants of mothers with depressed mood but not SSRI-treated during pregnancy showed poorer perceptual speech development at age 6 months only (Weikum et al. 2012).

Research using the Bayley Scales of Infant Development as measure of infant cognitive and psychomotor development reported inconsistent results. In several studies, infants of prenatally highly anxious, depressed, or stressed mothers displayed lower scores on the Bayley Scales of Infant Development at 8, 12, and 24 months (Brouwers et al. 2001; Huizink et al. 2003; Laplante et al. 2004). Yet, interestingly, two other

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record, *ICD international classification of diseases, ICQ infant characteristics questionnaire, IQ* intelligence quotient, *ITQ* infant temperament questionnaire, *ITSEA* infant-toddler social emotional assessment, *MCDI* MacArthur communicative development inventory, *MDD* major depressive disorder, *MSEL* mullen scales of early learning, *Lab-TAB* laboratory temperament assessment battery, *NBAS* Brazelton neonatal behavioral assessment scale; *PARCA* parent report of children's abilities, *PES* pregnancy experience scale, *POMS* profile of moods scale, *PSS* perceived stress scale, *PDI* psychomotor development index, *PTQ* preschool temperament questionnaire, *SDQ* strengths and difficulties questionnaire, *SITQ* short infant temperament questionnaire, *SRRS* social readjustment rating scale, *STAI* state-trait anxiety inventory, *TOMAL* test of memory and learning, *TRF* teacher's report form, *WISC* Wechsler intelligence scale for children, *WPPSI* Wechsler preschool and primary scale of intelligence studies (DiPietro et al. 2006; Keim et al. 2011) addressing the effects of maternal anxiety, depressive symptoms, or stress during pregnancy on infant cognitive development as measured during a test administered at 12 or 24 months, respectively, observed curvilinear associations. These findings suggest that mild to moderate levels of maternal psychosocial distress during pregnancy may accelerate infant developmental outcome. Similarly, a recent study showed that maternal perceptions of a high-quality, supportive partner relationship during pregnancy had beneficial effects on infant mental health at age 6–8 weeks (Stapleton et al. 2012).

Conflicting results were also observed regarding the association of physiological measures of stress during pregnancy (i.e., maternal saliva/plasma cortisol or amniotic cortisol) with infant cognitive and behavioral outcome. For example, findings by Davis and Sandman (2010) suggest that maternal cortisol during pregnancy can exert opposite effects on infant cognitive development depending on the timing of exposure. Yet, early morning maternal cortisol levels in late pregnancy (Huizink et al. 2003) or cortisol levels taken from amniotic fluid at 17 weeks of gestation (Bergman et al. 2010b) were negatively related to infant cognitive development at age 8 months or 17 months, respectively. In contrast, Baibazarova et al. (2013) found no significant associations of maternal cortisol during pregnancy and amniotic cortisol with infant fearfulness and distress to limitations at age 3 months. Similarly, Bergman et al. (2010a) observed no association between amniotic cortisol levels at age 17 weeks of gestation and infant fear reactivity at age 17 months. Remarkably, the few studies assessing both maternal psychosocial stress during pregnancy (i.e., anxiety, depression, or perceived stress) and physiological measures of stress during pregnancy (i.e., maternal or amniotic cortisol) failed to find evidence that any of these physiological stress indices mediate the association of maternal psychosocial stress during pregnancy with offspring self-regulatory outcome (Baibazarova et al. 2013; Bergman et al. 2010a; Davis et al. 2007; Gutteling et al. 2006). The absence of detecting such mediating effects may be explained by: (a) the possibility that in most observational prospective human cohort studies, the number of mothers experiencing high/extreme levels of stress during pregnancy is relatively low; (b) the fact that the used physiological measures only concern crude proxy measures of the maternal biological stress system or placental function; and/or (c) the lack of measurement precision regarding the cortisol measures used in previous research. Therefore, future studies should, for example, use more refined and repeated measures of maternal diurnal cortisol patterns during pregnancy that accurately assess the time point of collected saliva samples during a day and are based on more frequent assessments of the diurnal cortisol pattern (e.g., instead of four times a day, eight times a day). Future research should also address the mediating effects of other indicators of physiological/endocrine stress during pregnancy (e.g., maternal heart rate variability) or placental function (e.g., 11-BHSD2 gene expression or uterine blood supply) on the association of maternal psychosocial stress during pregnancy with child outcome.

Nevertheless, most studies addressing the effects of maternal anxiety depression, or stress during pregnancy, on infant (neuro)physiological outcomes found significant associations. Whereas, maternal anxiety, depression, or stress during pregnancy were related to altered infant cortisol reactivity at age 5 weeks, and 2, 3, 5, 6, 7, 9, 12, and 14 months (Brennan et al. 2008; Grant et al. 2009; Tollenaar et al. 2011; Velders et al. 2012; Yehuda et al. 2005), one study by Dierckx et al. (2009; *n* = 528) did not observe an association between maternal psychological symptoms during pregnancy and infant heart rate variability at age 14 months. A study by Hunter et al. (2012) observed an association of maternal anxiety disorders during pregnancy with less inhibition of P50 auditory sensory gating in infants aged 76 days. This performance deficit was mitigated by exposure to antidepressants during pregnancy (Hunter et al. 2012). The first results of an ongoing prospective cohort study in Tilburg, the Netherlands, suggest that maternal anxiety during pregnancy is related to altered auditory sensory processing in early infancy as assessed with an auditory oddball event-related paradigm (ERP; Otte 2013; Otte et al. 2011; Van den Bergh et al. 2012, 2013).

Remarkably, some recent studies suggest that both genetic factors as well as postnatal environmental factors moderate the association of maternal anxiety, depression, or stress during pregnancy with infant self-regulation. Variation in the GR gene at rs41423247 moderated the association of maternal psychological symptoms during pregnancy with infant cortisol reactivity (Velders et al. 2012). Based on a study sample ($n = 1513$) derived from the Generation R study, a population-based prospective cohort study in Rotterdam, the Netherlands, it was shown that infants carrying the short allele of the serotonin transporter gene (5-HTTLPR) were more negatively emotional when mothers reported high anxiety during pregnancy (Pluess et al. 2011). However, data from the Avon Longitudinal Study of Children and Parents (ALSPAC) cohort ($n = 3946$) in the UK did not replicate the moderating effect of 5-HTTLPR on associations between maternal anxiety during pregnancy and infant temperament (Braithwaite et al. 2013). Regarding postnatal factors, one study showed that secure infant–parent attachment ameliorated the negative effects of prenatal exposure to maternal cortisol on infant cognitive development (Bergman et al. 2010b).

23.2.3 (Early) Childhood

Preschoolers and children of mothers with anxiety or depressive symptoms or (di)stress during pregnancy were rated by their mothers, fathers, teachers, an external observer or tester, or themselves as displaying poorer attention, cognitive functioning, and effortful control and as having more attention/hyperactivity problems, behavioral and emotional problems, and academic problems (Davis and Sandman 2012; de Bruijn et al. 2009; Gutteling et al. 2005b, 2006; Henrichs et al. 2011; Laplante et al. 2008; Loomans et al. 2011; Martin et al. 1999; Niederhofer and Reiter 2004; O'Connor et al. 2002, 2003; Rodriguez and Bohlin 2005; Van den Bergh and Marcoen 2004; Velders et al. 2011, 2012). A population-based prospective cohort study in Amsterdam, the Netherlands, revealed that maternal anxiety during pregnancy was related to altered cognitive control as measured with a computerized neuropsychological assessment program in 922 5-year-olds (Loomans et al. 2012). Buss et al. (2011) also observed an association of maternal pregnancy-specific anxiety with computerized assessments of poorer executive functioning in 6–9-year-old children. Self-perceived stress or stressful life events experienced by the mother during pregnancy were related to a higher risk of psychopathological disorders in childhood, including separation anxiety disorder, ADHD, conduct disorder, or schizophrenia (Khashan et al. 2008; Martini et al. 2010; Rodriguez and Bohlin 2005). Studies investigating the association of the experience of major life events (e.g., bereavement) or major stressors (e.g., a hurricane) by the mother during pregnancy with the risk of offspring autism, however, reported inconsistent results (Beversdorf et al. 2005; Kinney et al. 2008; Li et al. 2009). Similarly, a recent cross-cohort consistency study based on two large-scale prospective cohort studies in the Netherlands and the UK only observed little evidence for intrauterine effects of maternal anxious and depressive symptoms during pregnancy on offspring behavioral and emotional problems after statistically controlling for demographic and obstetric confounders, paternal prenatal anxiety and depression, and maternal postnatal psychological symptoms (van Batenburg-Eddes et al. 2013).

Several studies indicated that maternal anxiety, depression, or stress during pregnancy were also related to altered childhood physiological functioning, such as alterations in cortisol levels or reactivity (Gutteling et al. 2004, 2005a) and to changes in neuroanatomical structures in childhood (Buss et al. 2010; Buss et al. 2012). Maternal pregnancy-specific anxiety in midpregnancy was related to reduced gray matter volumes in several brain regions, including the prefrontal cortex, the premotor cortex, the medial temporal lobe, the lateral temporal cortex, the postcentral gyrus, as well as the cerebellum extending to the middle occipital gyrus and the fusiform gyrus (Buss et al. 2010). Higher maternal cortisol levels in early pregnancy were related to a larger right amygdala volume in girls aged 7 years but not in boys (Buss et al. 2012). In the same study, higher maternal cortisol levels in early pregnancy were linked to more affective problems in girls and this relation was mediated by amygdala volume (Buss et al. 2012).

Also in children, some evidence has been found that genetic and postnatal environmental factors influence the association between maternal anxiety, depression, or stress during pregnancy and offspring self-regulatory functioning. Based on the earlier described Generation R study, Velders et al. (2012) observed that variation in the GR gene at rs41423247 moderated the effect of maternal psychological symptoms during pregnancy on behavioral and emotional problems in 1727 children aged 3 years. However, Braithwaite et al. (2013) did not observe moderating effects of 5-HTTLPR on associations between maternal prenatal anxiety and childhood behavioral problems from age 4 to 13 years. With regard to postnatal environmental factors, Kok et al. (2013) showed that the link between prenatal family stress as reported by the mother and child committed compliance at age 3 years was mediated by maternal positive discipline.

23.2.4 Adolescence and Adulthood

A pioneering small-scale prospective cohort study in Belgium ($n = 86$ at enrollment) revealed associations of maternal anxiety during pregnancy with several aspects of self-regulation in adolescence and early adulthood. Maternal anxiety during pregnancy was associated with difficulties of adolescents in cognitive control when performing computerized cognitive tasks assessing prefrontal cortex functioning and with lower intelligence subtests scores of adolescents at the age of 14–15 and 17 years (Mennes et al. 2006; Van den Bergh et al. 2005a, 2006). Adolescent girls of mothers with increased anxiety during pregnancy had higher levels of depressive symptoms (Van den Bergh et al. 2008). At age 17 years, adolescents of mothers with higher levels of anxiety between 12 and 22 weeks of gestation had altered event-related brain potentials assessed with EEG during a gambling task, requiring endogenous control (Mennes et al. 2009). Finally, measures of functional magnetic resonance imaging in young adults indicated that differences associated with the level of maternal anxiety during pregnancy were observed in the activation patterns of a number of crucial prefrontal brain areas (Mennes 2008).

Previous research also suggests that maternal mood and stress during pregnancy are related to alterations in physiological systems and HPA axis functioning in (pre-)adolescence (Huizink et al. 2008; O’Connor et al. 2005). Maternal mood during pregnancy was related to individual differences in awakening cortisol at age 10 and 15 years (O’Connor et al. 2005; O’Donnell et al. 2013) and prenatal exposure to a stressor (i.e., Chernobyl) was related to elevated cortisol and testosterone levels at age 14 years (Huizink et al. 2008). Finally, in girls aged 14–15 years, changes in the cortisol diurnal profile were an intermediate in the relation between maternal anxiety during pregnancy and depressive symptoms in adolescence (Van den Bergh et al. 2008). This suggests that altered offspring HPA axis functioning may mediate the association of maternal anxiety during pregnancy with offspring self-regulation.

23.2.5 Discussion and Conclusions

A large body of human evidence presented in this chapter suggests that alterations in offspring self-regulation from infancy until young adulthood can originate in utero due to the prenatal exposure to maternal anxiety, depression, and stress. In the following discussion, several theoretical conceptualizations of the effects of early experience on self-regulatory skills later in life stemming from work in the fields of developmental neuroscience, stress research, epigenetics, and the developmental origins hypothesis of behavior, health, and disease are addressed in an integrative manner. Importantly, all these conceptualizations share the idea that individuals differ in their susceptibility to environmental factors early in life. Finally, we discuss future directions for the study of perinatal origins of self-regulation and public health implications of the findings are summarized in our chapter.

Environmental conditions play a crucial role in the ontogenesis of the brain influencing both gene expression and continuing neural specialization (Karmiloff-Smith et al. 2012; Meaney and Szyf 2005). The acquisition of self-regulatory abilities is closely related to the development of the prefrontal cortex which starts early in life and continues into early adulthood (Kolb et al. 2012; Shonkoff 2012). As early in life the basic circuitry of the prefrontal cortex underlying self-regulatory abilities later in life, such as higher cognitive functions, is formed (Tsujimoto 2008), early experience can set up developmental trajectories of the prefrontal cortex and, thus, exert lifelong effects on developmental patterns of self-regulation (Kolb et al. 2012). Alterations in self-regulation due to early experience are possibly mediated by synaptic changes or reorganizations in neural circuits of the prefrontal cortex (Kolb et al. 2012). Experience may alter synaptic connections in certain neural networks, a phenomenon that has been termed as neural plasticity (Kolb et al. 2012). When confronted with adverse environmental conditions early in life (e.g., prenatal stress), neural plasticity may concern an evolutionary-based adaptation mechanism (Lee and Goto 2013). Changes in fetal neurodevelopment, in particular alterations of synaptic networks in the prefrontal cortex, due to adverse prenatal environmental influences may represent adaptations to cope with expected adversity later in life (Lee and Goto 2013). Thus, self-regulatory problems, such as neuropsychiatric disorders, can be seen as evolutionary-based adaptation strategies against environmental adversity (Lee and Goto 2013).

Yet, the degree of (neural) plasticity early in life or, in other words, the degree to which developing (neural) structures of a certain fetus are susceptible to environmental adversity in utero may differ per developing organism. This implies that not all individuals prenatally exposed to adverse environmental conditions may develop self-regulatory problems later in life. These individual differences in outcome patterns may be caused by individual variations in the genetic blueprint and/or by the unique interaction patterns between genes and the environment that characterize the ontogenesis of each individual (Belsky and Pluess 2009). According to Belsky's *differential susceptibility* hypothesis, some individuals carrying, for example, certain "plasticity genes" are "more malleable or susceptible than others to both negative and positive environmental influences" (Belsky et al. 2009; Belsky and Pluess 2009). The earlier described study by Pluess et al. (2011) tested this hypothesis with regard to the moderating effects of a polymorphism in the serotonin transporter gene (5-HTTLPR) on the association of maternal anxiety during pregnancy with infant negative emotionality at age 6 months. Yet, the results of this study were supportive of the classic stress–diathesis or vulnerability model viewing certain individuals as particularly vulnerable to environmental adversity (Burmeister et al. 2008). Pluess et al. (2011) namely found that infants carrying the 5-HTTLPR short allele displayed more negative emotionality when mothers reported increased levels of anxiety during pregnancy, while there was no difference between genotypes on infant negative emotionality when maternal anxiety during pregnancy was low. Moreover, in a later study by Braithwaite et al. (2013), the moderating effect of 5-HTTLPR was not replicated. Nevertheless, more research is needed to determine whether *plasticity genes* or *vulnerability genes* (Belsky et al. 2009) are involved in the association between prenatal experience and self-regulation later in life. Furthermore, to elucidate individual differences in programming sensitivity (Nederhof and Schmidt 2012) and (dis-)continuity of effects, longitudinal studies following-up the developmental trajectories of children prenatally exposed to both high and low levels of maternal anxiety, depression, and stress are needed. Such research should take the interaction of genetic predisposition, (the timing of) early-life environmental conditions, and environmental contexts later in life into account (Daskalakis et al. 2013).

Notably, animal research has convincingly shown that prenatal stress-induced alterations of brain and HPA axis functioning in the offspring mediates the association between exposure to prenatal maternal stress and self-regulatory functioning later in life (Lupien et al. 2009; Maccari et al. 2003). However, so far, only two human prospective studies have provided evidence suggesting that alterations in a brain structure (i.e., the amygdala) of the offspring (Buss et al. 2012) or changes in offspring HPA axis functioning (Van den Bergh et al. 2008), as indicated by alterations in cortisol diurnal profile, are intermediates in this association. Therefore, more human research is needed identifying neuroanatomical and (neuro)physiological/endocrine markers in the child mediating the association between maternal anxiety, depression, or stress during pregnancy and offspring self-regulation.

Interestingly, animal models (e.g., Maccari et al. 1995) and one human study (Bergman et al. 2010b) suggest that early adequate maternal care may ameliorate or even reverse the negative long-term effects of prenatal exposure to maternal stress. Reversibility of epigenetic modifications may explain these observations (Szyf et al. 2007). In rats, exposure to environmental agents later in life can reverse epigenetic marks, induced by modulation of developmental programming early in life, in, for example, the GR exon 1_7 promoter region, which is involved in the neuroendocrine stress response (Szyf et al. 2007; Weaver et al. 2004). These epigenetic marks were elicited by exposure to altered maternal care (i.e., low maternal levels of pup licking and grooming and of engagement in arched-backed nursing, LG-ABN) early in life (Szyf et al. 2007; Weaver et al. 2004). Adult offspring of rat dams displaying high levels of pup licking and grooming in the first week of life demonstrated elevated GR expression in the hippocampus, increased sensitivity to negative feedback sensitivity to glucocorticoids, and more modest HPA axis stress responses than adult offspring of mothers that engaged in low levels of pup licking and grooming (Liu et al. 1997; Szyf et al. 2007). Treating adult offspring of low-LG-ABN mothers with the histone deacetylase inhibitor trichostatin A caused demethylation of the GR gene via histone acetylation (Szyf et al. 2007; Weaver et al. 2005). This treatment also resulted in increases in occupancy of the promoter with the transcription factor nerve growth factor-inducible protein A, which, finally, led to elevated expression of the GR exon 1_7 promoter (Szyf et al. 2007; Weaver et al. 2005). This epigenetic reversal was related to behavioral alterations so that the stress response in histone deacetylase inhibitor-treated adult offspring of low-LG-ABN mothers no longer differed from the stress response of offspring of high-LG-ABN mothers (Szyf et al. 2007; Weaver et al. 2005). Thus, reversing epigenetic programming may modulate gene expression and, in turn, also alter endocrine stress responses and associated behavioral patterns via changes in gene expression in the brain (Szyf et al. 2007).

Reversibility of the effects of early experiences on the brain (e.g., prenatal exposure to maternal anxiety, depression, or stress) may also be explained by metaplasticity (i.e., the concept that plastic alterations in the brain due to early experience may be moderated, that is exacerbated or ameliorated, by later plasticity; Abraham and Bear 1996; Kolb et al. 2012).

However, so far, only one human study suggests moderating influences of the child–parent relationship on the association between maternal stress during pregnancy and infant self-regulatory outcomes (Bergman et al. 2010b). Therefore, replication of this work is warranted. Moreover, although some evidence exists suggesting epigenetic changes in the human GR gene (NR3C1) due to prenatal exposure to maternal anxiety or mood (Hompes et al. 2013; Oberlander et al. 2008), the mediating or moderating effects of epigenetic changes on the association of maternal anxiety, depression, and stress with offspring self-regulation have not been studied. Nevertheless, the work by Bergman et al. (2010b), research in epigenetics, and the concept of metaplasticity suggest that behavioral interventions in early postnatal life may reduce or even reverse the adverse effects of prenatal exposure to early-life stress on self-regulatory outcome later in life. To increase their effectivity, such interventions should not only address the improvement of cognitive, emotional, and behavioral aspects of self-regulation in the offspring via psychoeducation and coaching caregivers in adequate parenting skills but also strengthen the caregiving environment via training parents themselves in these aspects of self-regulation (Shonkoff 2012). This latter training may, in particular in vulnerable parents, increase their employability and the emotional, social, and economic stability of the whole family (Shonkoff 2012). Testing the effectivity of such interventions via randomized controlled trials may also allow examining reversibility effects among offspring displaying self-regulatory problems due to prenatal exposure to maternal anxiety, depression, or stress.

Using prospective follow-up studies, new measures identifying infants at risk of developing poor self-regulation later in life should be developed, as most traditional parent-report and standardized tests of aspects of self-regulation in infancy (e.g., early verbal and nonverbal cognitive development) only show low predictive validity regarding subsequent self-regulatory functioning (e.g., Honzik 1983; Rice et al. 2008). Neurophysiological measures of infant self-regulation (e.g., ERP paradigms) offer promise as they have been shown to be strong predictors of developmental outcome later in childhood (e.g., Molfese 2000). Long-term prospective studies should examine whether such measures may concern a promising tool to identify early neural markers of self-regulatory problems later in life, such as behavioral problems, learning difficulties, and neuropsychiatric disorders in childhood, adolescence, and adulthood, that may originate in utero due to prenatal exposure to maternal anxiety, depression, or stress (Kushnerenko et al. 2013).

This chapter demonstrated that prenatal exposure to high levels of maternal anxiety, depression, or stress is a risk factor of poor self-regulation later in life. More interventional research is needed testing whether stress reduction programs for anxious/depressed/stressed pregnant women (e.g., mindfulness interventions) exert beneficial effects on offspring development and self-regulation. Finally, to develop and improve intervention programs to prevent or reduce the effects of developmental programming due to maternal anxiety, depression, or stress during pregnancy, more observational longitudinal research is needed identifying molecular, neuroanatomical, and (neuro-)physiological mechanisms and postnatal environmental factors involved in these effects.

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Self-Regulation Through Rumination: Consequences and Mechanisms

24

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24.1 Introduction

When confronted with negative events, such as an argument with our spouse or criticism by the boss, oftentimes we engage in mental activity reflecting on these events. Typically, we aim to understand why these events occurred, how we contributed to such events, and how to avoid them in the future. Despite the adaptive consequences of reflecting on one's feelings, research indicates that persistent thinking about negative feelings may have negative consequences. In the context of depression, for instance, such persistent negative thinking, termed "rumination," has been found to be one of the most important risk factors for the development of depressive symptoms (Nolen-Hoeksema et al. 2008). Moreover, even in nondepressed, healthy individuals, rumination can be observed and also leads to negative cognitive as well as affective consequences (Watkins 2008).

In this chapter, we discuss rumination as an important self-regulatory strategy. We begin by introducing some of the basic conceptualizations of rumination where different theories have highlighted stable as well as momentary aspects of rumination. Then, we discuss the research on the cognitive and biobehavioral consequences of rumination in more detail. In order to understand the persistent nature of rumination, we will then turn to the psychological mechanisms underlying rumination. Finally, we discuss some of the future directions in experimental research on rumination including recent innovative approaches to reduce excessive rumination.

24.2 Definition of Rumination

There are many different conceptualizations of rumination (for a review, see Smith and Alloy 2009). Here we will discuss the main approaches to this concept. One of the most dominant theories of rumination is the response styles theory (RST), where rumination is conceived as "behaviors and thoughts that focus one's attention on one's depressive symptoms and on the implications of these symptoms" (Nolen-Hoeksema 1991, p. 569). Within this definition, several features are important. First, it states that rumination is focused on (depressed) *mood state* instead of certain *cognitive themes* (Joormann and Gotlib 2010; Nolen-Hoeksema et al. 2008). Then it mentions the content of rumination to indicate that people try to use it purposefully to understand and control their negative affect (Nolen-Hoeksema 2000). Finally, this conceptualization proposes a very close link between rumination

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and depressive symptoms (Nolen-Hoeksema et al. 2008). It is noteworthy that, despite some supportive evidence for each of these features, there is still extensive discussion about these features.

In the RST, rumination can be not only an intrapersonal process but also a social process where individuals engage in ruminative processing together co-rumination (Nolen-Hoeksema 1991). Unlike the RST, in which communicating feelings to others can be considered a component of rumination, other researchers contend that the basic component of rumination is cognitive ideation, because it is usually thought that rumination has negative consequences (Giorglo et al. 2010) while repetitive emotional expressions can sometimes be useful (Derlega et al. 1993). Additionally, several models have defined rumination as being part of a pattern of "persistent negative thought" where these negative thoughts do not necessarily merely involve thinking about negative affect but also include other types of thinking such as anxious anticipation (Brosschot 2010).

According to RST (Nolen-Hoeksema 1991), rumination is considered a trait-like response style to distress as research observed stable tendencies in responding with rumination to distress. This conceptualization led to the development of measures of trait rumination. The most commonly used measure is the ruminative response scale (RRS; Nolen-Hoeksema and Morrow 1991), a 22-item scale that assesses ruminative responding to sad mood. The RRS has high internal consistency and acceptable concurrent validity (Nolen-Hoeksema and Morrow 1991). Factor analysis of this questionnaire revealed two subtypes of rumination: reflective pondering and brooding (Treynor et al. 2003). Reflective pondering is a more adaptive form of rumination that indicates the amount of thinking about potential solutions to reduce negative affect, whereas brooding is maladaptive and indicates passively focusing on symptoms of distress and on the meaning of those symptoms. This distinction is nowadays frequently applied in the literature although in clinically depressed individuals the distinction between these two factors is blurred (Whitmer and Gotlib 2011).

In contrast to theories that consider rumination as a stable trait, some views proposed that rumination is stress-reactive and variable across time (for reviews, see Martin and Tesser 2006; Smith and Alloy 2009). Indeed, research indicates that meaningful differences can be found between trait and state rumination using measures that allow measuring fluctuations in rumination. For example, Moberly and Watkins (2008) found that momentary rumination (assessed via two items that inquire about the extent to which participants are currently focused on their feelings and problems) predicted subsequent negative affect independently from the prediction by trait rumination. Other studies found interactive effects of state and trait rumination. For instance, state rumination was related to impaired cardiovascular recovery from emotional stress, but only among those who are low in trait rumination (e.g., Key et al. 2008). Moreover, some studies have demonstrated poor stability across time of trait rumination (e.g., Kasch et al. 2001), and recent diary studies have shown significant variation in rumination across days and even hours of the day (e.g., Genet and Siemer 2012; Takano and Tanno 2011). Taken together, these findings support the notion of rumination as a variable process where there are separate influences of trait versus state rumination.

Other contemporary models emphasize the notion that rumination is a transdiagnostic risk factor for a variety of disorders, instead of being depression specific (e.g., Watkins 2008). This has led to the development of several measures, such as the repetitive thinking questionnaire (RTQ; Mahoney et al. 2012) and the perseverative thinking questionnaire (PTQ; Ehring et al. 2011), that examine repetitive thinking in a wide range of situations instead of focusing specifically on negative affect. In different disorders, rumination may take a somewhat different form. For instance, in the cognitive model of social phobia, Clark and Wells (1995) suggest that the content of rumination is concentrated on social interaction, instead of negative affect (Kashdan and Roberts 2007). In such theories, the notion of rumination is generally used interchangeably with that of post-event processing, where socially anxious individuals dwell on previous social encounters and failures (Mellings and Alden 2000). Research has implicated repetitive negative thinking not merely in affective disorders but has also indicated that rumination plays an important role in health and somatic problems such as hypertension (e.g., Brosschot et al. 2010; Gerin et al. 2012).

24.3 Physiological Aspects of Rumination

In recent years, there has been marked progress in understanding the underlying neurobiological and physiological mechanisms associated with rumination.

24.3.1 Neural Mechanisms of Rumination

Most research on the neural mechanisms of rumination has been performed on both healthy and depressed individuals by having them undergo experimental tasks with emotional or self-relevant stimuli. It has been observed that depressed persons show enhanced amygdala activity in response to negative stimuli and this is correlated with self-reported measures of rumination (Siegle et al. 2006, 2002). This finding has been confirmed and refined by another functional magnetic resonance imaging (fMRI) study showing that the amygdala response while upregulating negative mood was correlated with trait rumination also in healthy controls, thus suggesting that in depressed as well as in nondepressed individuals similar neural mechanism are involved in repetitive thinking (Ray et al. 2005).

However, hyperactive amygdala reactivity is by no means the only brain response involved in rumination. Cooney et al. (2010) have demonstrated that a much more complex network (perhaps multiple networks) is associated with the tendency to ruminate. In that study, depressed individuals who were engaged in rumination showed increased activation in important areas, such as the amygdala, the subgenual cortex, the rostral anterior cingulate/medioprefrontal cortex, the dorsolateral prefrontal cortex, the posterior cingulate cortex, and the parahippocampus. This result confirms that rumination recruits a wide range of brain areas that are typically involved in emotional processing, self-focus, self-referential thinking, attentional control, and autobiographical memory.

More recently, depressive brooding has become the focus of increasing research. This maladaptive form of rumination has been associated with a variety of negative consequences, such as both concurrent and future depressive symptoms over 1 year (Treynor et al. 2003; Siegle et al. 2004); therefore, the understanding of its specific neural substrate is an important area of research. For instance, Berman et al. (2011a) reported that depressed individuals with higher brooding scores are characterized by increased spatial variability in the activation of the left inferior frontal gyrus. Despite this intriguing finding, such research on brooding (and rumination) has been carried out in mixed samples consisting of both depressed and nondepressed individuals, so that the related findings could have been confounded by features specific for clinical depression such as impaired attentional control. Consequently, Vanderhasselt et al. (2011) tried to bridge this gap by selecting healthy brooders with no history of previous depressive episodes. This study demonstrated that those with higher levels of depressive brooding reported also increased activity in the right dorsolateral prefrontal cortex when successfully disengaging from negative information. In sum, this study shows that depressive rumination impacts specifically on emotional task performance and is associated with neural substrates that can be distinguished from depression.

Parallel to investing the neural basis of rumination during task, researchers have increasingly focused their attention on the activity of the brain when not in a task context (i.e., resting state) and an associated neural network that has raised much interest (Broyd et al. 2009). This neural network, termed default mode network (DMN), has been documented to be highly active during rest (Raichle et al. 2001) as well as to be associated with many higher order functions, such as self-referential thinking (Northoff et al. 2006). Because of this, it has been proposed that the DMN could shed new light on depression and rumination (Marchetti et al. 2012). Indeed, specific DMN brain areas have consistently been associated with rumination. Berman et al. (2011b), for instance, reported that during rest, temporal synchronization (i.e., functional connectivity) between the subgenual cortex and the posterior cingulate correlated with higher levels of trait rumination. Interestingly, this correlation was driven only by brooding scores, but not by reflective pondering.

24.3.2 Cortisol Levels and Rumination

Stress is a psychobiological reaction demanding cognitive, emotional, and physiological adjustments to threats or challenges to one's well-being. When an individual faces a stressor, such as receiving harsh critic from the boss, a complex sequence of adjustments takes place to prepare the body for responding. Once the stressor has disappeared, it is important that the body returns to baseline (homeostasis). In fact, physiological activation and subsequent return to homeostasis is regulated by the hypothalamic–pituitary–adrenal axis (HPA) by releasing cortisol, a stress-related steroid hormone.

As rumination is continuously reactivating mental representations related to negative affect and stress, rumination could elicit and maintain inappropriately high levels of cortisol. Despite this straightforward hypothesis, the extant literature on the relationship between rumination and cortisol proves to be more complicated, and we will discuss some of the key findings here (Zoccola and Dickerson 2012). State rumination after stress manipulation in the laboratory has been consistently associated with increased levels of cortisol (Byrd-Craven et al. 2008; Zoccola et al. 2008), whereas the link between trait rumination and stress-related hormone reaction is unclear. In fact, it has been reported that the association between trait rumination and cortisol can be positive (Roger and Najarian 1998), negative (Zoccola et al. 2008), or absent (van Santen et al. 2011). It is also noteworthy that studies examining rumination in the context of depression oftentimes failed to find a positive relation between depression-related rumination and cortisol response. Instead, they showed no or a negative association (Kuehner et al. 2007; Young and Nolen-Hoeksema 2001). On the contrary, a robust positive relationship has been documented between cortisol levels and stress-related (state) rumination (Byrd-Craven et al. 2008; Roger and Najarian 1998; Zoccola et al. 2008).

Taken together, these findings show that differential effects of rumination on cortisol levels can be detected, if the state versus trait specificity or the topic of the repetitive thinking is taken into account. In studies showing evidence for a positive relation, rumination mainly has an effect on the duration of the stress response rather than elevating initial reactivity (Byrd-Craven et al. 2008). Although it is tempting to claim a causal influence of perseverative thinking on the HPA axis, alternative models that entail mutual influences have been proposed as well (Zoccola and Dickerson 2012) and empirical data for strong conclusions is lacking.

24.4 Affective and Cognitive Consequences of Rumination

There is an extensive literature on the consequences of rumination. Where one could be inclined to think that negative affect elicits a reflective response that could enhance insight into the nature of one's negative feelings and problems, most research indicates that rumination is mainly associated with negative consequences. Here, especially depressive brooding—the evaluative and passive style of focusing on negative feelings and problems—has been associated with negative consequences. We will briefly describe these consequences below.

A major negative consequence of rumination is enhanced negative affect. Studies where rumination is induced in participants show this as an important short-term consequence (Lyubomirsky and Nolen-Hoeksema 1995). Experimental studies testing the short-term effects of rumination have typically used the rumination induction procedure developed by Nolen-Hoeksema and Morrow (1993). This procedure increases ruminative thinking and has been shown to heighten negative affect and prolong negative mood in individuals with heightened depression risk (Morrow and Nolen-Hoeksema 1990; Nolen-Hoeksema and Morrow 1993) and in clinically depressed participants (Donaldson and Lam 2004; Lavender and Watkins 2004; Watkins and Moulds 2005; Watkins and Teasdale 2001). It is specifically the negative, evaluative, and judgmental type of self-focused attention that is considered maladaptive (Rude et al. 2007). Importantly, negative affect is also considered an important trigger of rumination (see Smith and Alloy 2009 for a review). Hence, there seems to be a mutually reinforcing link between rumination and negative affect.

At the long term, affective consequences of rumination are depressive symptoms such as sustained negative affect. Numerous studies have demonstrated that rumination is associated concurrently with depressive symptoms (Treynor et al. 2003) and, more importantly, prospectively with the onset (Nolen-Hoeksema 2000), severity (Just and Alloy 1997; Nolen-Hoeksema and Morrow 1991), and duration (Nolen-Hoeksema 2000) of depression. Furthermore, recovery from depression has been linked to rumination where higher levels of rumination predict slower and incomplete recovery (Kuehner and Weber 1999; Schmaling et al. 2002). Thus, rumination is considered one of the key cognitive risk factors for depression.

In addition to the affective consequences, rumination also has several unwanted cognitive consequences. There are a number of studies showing that inducing rumination hampers problem solving and task performance (Watkins and Brown 2002). This led Watkins and Brown (2002) to propose that state rumination leads to cognitive impairment by overloading limited executive resources. This effect seems especially pronounced in individuals with elevated depression scores, since Philippot and Brutoux (2008) found that a rumination induction made it more difficult for dysphoric (but not for nondysphoric) participants to ignore distracting words in a Stroop task. In this context, it is also interesting that individuals high in trait rumination perform less well on the Wisconsin Card Sorting Task (WCST), which suggests lower levels of cognitive flexibility (Davis and Nolen-Hoeksema 2000).

This brief overview of the consequences of rumination indicates that rumination is a problematic self-regulatory strategy. This begs the question which processes contribute to excessive rumination.

24.5 Why Ruminate?

In addressing the question of factors contributing to rumination, it is useful to distinguish between voluntary rumination and involuntary rumination. That is, within and across individuals, parts of rumination are clearly linked to intentionally trying to understand negative affect and events occurring, whereas at other moments rumination occurs unintentionally (according to some even unconsciously; Brosschot 2010). Different theories of rumination have been proposed to account for these different aspects of rumination.

In the broad context of self-regulation, the goal progress theory (Martin et al. 1993) proposes that it is the failure to progress towards higher order goals that initiates rumination. From this perspective, rumination is strictly linked to both motivation and the self. In fact, an assumption of the theory is that the more central to one's self-concept the unattained goal is (for instance, finding a romantic partner), the greater and more pressing the ruminative response is in turn. In line with this, relief from rumination is possible only when one attains the goal, gets clear feedback about sufficient progress to it, or disengages from it (Martin and Tesser 2006).

Alternatively, in the self-regulatory executive function (S-REF) theory, rumination is generated when people find that their present state is different from their intended one (Wells and Mathews 1996). The maintenance of rumination is explained by overly positive metacognitive beliefs about rumination being a helpful strategy to understand and reduce negative affect (Papageorgiou and Wells 2001).

Both theories described above consider rumination as an intentional and voluntary process. Yet, individuals characterized by high levels of rumination find it extremely difficult to stop when rumination is interfering with their functioning. Several information-processing theories have been put forward to explain this observation.

A key proposal in information-processing theories is that individuals with high levels of rumination have difficulties disengaging attention from negative information or expelling negative information from working memory (Gotlib and Joormann 2010; Koster et al. 2011). These models propose that information processing is biased to favor negative material in high ruminators at the expense of other information, which hinders more adaptive emotion regulation strategies such as cognitive reappraisal. There is substantial support for these models, where several studies found attentional bias as well as biases in the updating of working memory in high ruminators (Bernblum and Mor 2010; Joormann and Gotlib 2008; Koster et al. 2013). However, there have been a substantial number of studies where cognitive impairments were observed in high ruminators in the absence of emotional material (e.g., De Lissnyder et al. 2011). The latter finding suggests that cognitive impairments are more broad and not necessarily emotion specific which demands a theoretical explanation.

Recently, Whitmer and Gotlib (2012) proposed a new model called the attentional scope model of rumination, which provides an integrated way to explain the consequences of rumination. The basic assumption is that trait ruminators have a narrower attentional scope than nonruminators. More specifically, they postulate that individuals who have a narrow attentional scope when not in a negative mood will show a high tendency to ruminate, because their attentional resources will be constrained to a limited set of focal thoughts. In some circumstances, such a constrained attentional focus is adaptive when for instance concentrating on homework. However, in conditions of distress, negative mood will narrow attentional scope and, as a result, magnify focusing on a single feeling or problem, while ignoring much external information. In contrast, individuals who have a broad attentional scope tend to ruminate less even when they are in a depressed mood, because their attentional scope will be broad enough to protect them from becoming absorbed by a focal feeling or problem.

It is noteworthy that, different from other models, this model posits that trait ruminators should exhibit a narrower attentional scope independent of mood. Besides, other than biasing by negative information (Joormann 2010; Koster et al. 2011), individuals could focus their attention on all kinds of information when it is relevant to the task (Friedman and Förster 2010). So, instead of inhibiting the negative information, this model posits that trait ruminators could maintain the relevant information but will have difficulties inhibiting this information when the situation changes and the information is not relevant any more. Despite the absence of direct tests of this hypothesis, many of the findings at the level of working memory and perception can also be explained by the attentional scope model of rumination.

The information-processing explanations of depressive rumination are also supported by some of the neurobiological findings. In a recent fMRI study (Foland-Ross et al. 2013), an emotional working memory task was administered in a sample with major depression to elucidate neural correlates of difficulties in cognitive control. In the depressed individuals, the dorsal anterior cingulate and parietal and bilateral insular cortices were activated significantly more when negative words had to be removed from working memory. In contrast, nondepressed participants exhibited stronger neural activations in these regions for positive than for negative material. Surprisingly, no unique correlations were observed with rumination but this may have been due to high levels of depression which are strongly confounded with rumination. These findings suggest that different neural mechanisms are involved in expelling negative material in depression where future studies should further investigate whether and how this contributes to rumination.

24.6 Future Directions in the Study of Rumination

There are a number of research lines that appear particularly promising to enhance understanding and modification of rumination. Here, a major challenge is how to clarify and understand biobehavioral cascades in relation to rumination. There is some research examining the psychophysiological consequences of rumination, which shows that rumination and sustained processing of emotional information causes decreased ability to recover from emotional stimuli. Such effects have been supported by studies measuring vagal tone, heart rate variability, and the cortisol response (see Siegle and Thayer 2004). Provided that rumination is associated with prolonged stress, it is interesting that recent research also suggests an important role of rumination in influencing physical illness where, for instance, rumination plays an important role in recovery from chemotherapy (Berman et al. 2013). More broadly, provided that depression is associated with inflammation (Berk et al. 2013), it would be highly interesting to better understand the long-term biological consequences of rumination as prolonged stress associated with rumination could contribute to inflammation.

Moreover, it is likely that there are dynamic cascades between the cognitive and biobehavioral consequences of rumination that deserve more fine-grained investigation. Such cascades could occur in several ways. It is possible that when individuals ruminate and experience increased levels of stress, that experiencing stress can give rise to more ruminative thought ("why am I feeling this way?"). In addition, rumination is also associated with reduced levels of activity (several items of the RRS for instance refer to withdrawal from social contact to analyze feelings). By social withdrawal, rumination could both lower activity levels where isolation may magnify the focus on problems and their emotional impact.

Below, we describe several approaches that could shed more light on such cascading and dynamic effects associated with rumination.

24.6.1 Dynamic Systems Approach

Despite that most of the theories center around explaining the initiation and persistence of rumination, a clear and empirical way to test temporary fluctuations in rumination is to a large extent absent. What is lacking is indeed a conceptual frame that may efficaciously account for fluctuations of ruminative thinking and its co-occurrence with negative mood, self-focus, and motivational states (Smith and Alloy 2009).

In that regard, a powerful tool is offered by dynamic systems theory (DST), which explicitly aims at capturing individual and group-level trajectories (Kelso 1995). DST is a metatheoretical framework that, originally derived from mathematics and physics, has successfully been applied in many domains where time is an importance variable, such as developmental and clinical psychology (Carver and Scheier 1998; Granic and Hollentesin 2003). Within the DST framework, it is possible to represent a certain phenomenon as a set of elements co-varying over time (i.e., system) and, in turn, capitalize on the enormous amount of information that dynamics provide. Concepts, like "state space," "attractor," and "repellor" are usually adopted to analyze temporal dynamics.

A *state space* is a schematic map where all the possible states of a system are included. For instance, by representing simultaneously both state mood (i.e., positive, neutral, or negative) on the x-axis and attention (i.e., internally oriented vs. externally oriented) on the y-axis, the two-dimension system would consist of six possible states (e.g., positive-internal, neutral-internal, etc.). Hence, a single subject (or group) trajectory could be shown transiting from one state to another across time and, by doing so, provide valuable information not only in terms of general intensity (i.e., mean) but also of temporal dynamics (i.e., variability and flexibility). For instance, two trajectories could show the same mean with regard to both mood and attention, but show very different temporal patterns when time is taken into account.

Furthermore, although it is theoretically possible that all the states of the state space are visited with the same frequency (i.e., equiprobability), it is much more likely that one state (or a subset of states) is visited more often than others. In other words, it is more probable for a trajectory to enter a specific state than to exit (Heylighen 1992). Such a state is defined as *attractor*. On the other hand, by applying the same logic, it is also possible that some states are constantly avoided, as their probability to be visited is null or close to zero. Consequently, they are considered as *repellors*.

Research on rumination could clearly take great advantage from applying DST. Given a certain state space,[1] it would be interesting to investigate whether high ruminators compared to low ruminators tend to preferentially select a specific state over time (i.e., *attractor*), such as being internally focused and experiencing negative mood at the same time. Adopting this perspective would provide many benefits. For instance, not only would it be possible to ascertain what state absorbs ruminators most but also what state high ruminators stay far away from.

Despite these promising perspectives, no novelty is without costs. In fact, DST demands repeated measures and the availability of short but psychometrically sound measures of state rumination is pivotal. Unfortunately, so far most of the experience sampling studies, that potentially meet the DST requirements, have made use of a single item or very few items with unknown psychometric properties to measure rumination (e.g., Genet and Siemer 2012). We here stress the necessity to adopt valid questionnaires that could be viable for repeated and reliable assessment of state rumination, such as the recently developed momentary ruminative self-focus inventory (MRSI; Mor et al. 2013).

In sum, DST seems to be a very promising perspective both to propose new hypotheses and to reinterpret our current findings about rumination.

24.6.2 Resting State Studies

Moments where individuals are not actively engaged in a task are contexts that may give rise to enhanced levels of ruminative thought. At the neural level, there is increasing research examining the relation between rumination and the DMN using resting state paradigms. However, given the very specific context and the loud background noise, at present it is unclear to what extent the fMRI research is representative of normal resting state (Gaab et al. 2008). Therefore, behavioral studies examining rumination during resting state are particularly promising.

A recent behavioral study investigated whether resting state indeed provides an important context for ruminative self-focus and negative affect. In this study, individuals were at rest, while being randomly probed about their attentional focus. This focus could either be internally or externally oriented (Marchetti et al. 2013a). Being internally focused predicted increased levels of state rumination and, in turn, a worsening in mood. This rest-related toxic effect held only in people at high risk of depression. Moreover, a questionnaire study recently showed that the trait tendency to engage in daydreaming (as a proxy of resting state) specifically predicted individual levels of depression, but only to the extent to which both trait self-focus and brooding were involved too (Marchetti et al. 2013b).

In sum, given the absence of external stimulation and the proneness to become self-focused, resting state seems to be a promising field of inquiry for rumination. Nevertheless, new theoretical and empirical efforts are needed in order to account for and reconcile both neuropsychological and cognitive data.

24.6.3 Examining Causal Mechanisms of Rumination

The current chapter underscores that there are many different possible factors contributing to rumination. In order to stringently test the causal involvement of certain mechanisms of rumination, an increasing number of studies are using

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[1] This construct can be operationalized in different ways, such as by means of the state space grids (Hollenstein 2007).

experimental manipulations. Especially in the domain of information processing, novel methodologies have been developed to manipulate basic cognitive processes (e.g., working memory) or cognitive biases (e.g., attentional bias for negative material). Such training procedures can be used either to induce certain processing styles in healthy samples or to reduce certain impairments in high ruminators or depressed individuals (see Koster et al. 2009).

For instance, as discussed earlier, the link between cognitive impairments and rumination has been demonstrated in several correlational and prospective studies, but no clear inferences about the nature of this association can be made. It is possible that rumination depletes working memory resources (e.g. Philippot and Brutoux 2008) or, alternatively, working memory impairments may lead to rumination (e.g., Gotlib and Joormann 2010). To examine the functional role of cognitive impairments, the expected causal factor, being working memory functioning, has to be manipulated to subsequently monitor the effects on ruminations.

Currently, there is an extensive debate about the efficacy of working memory training and the transferability of training effects (Shipstead et al. 2012). A major challenge of working memory training procedures is to obtain transfer of training to new tasks and contexts. In recent years, several studies have shown promising results using a working memory training paradigm. For instance, Jaeggi et al. (2008) used a dual n-back task to train working memory. This training involves monitoring and updating two streams of information, which becomes gradually more difficult. They found, next to improvements on the training task, considerable gains in fluid intelligence scores compared to a control group. However, these results have been challenged based on inappropriate designs (absence of an active control condition) and inappropriate transfer tasks that do not tap aspects of working memory (Shipstead et al. 2012).

Although the efficacy of working memory training in improving working memory performance in healthy individuals is still under debate, working memory training did show interesting effects in the context of psychopathology or traits that are characterized by reduced working memory performance (Owens et al. 2013; Siegle et al. 2007). The results of these studies suggest that the dual n-back training might be a valid tool to manipulate working memory within an experimental design when individuals have impaired cognitive control. Such training has interesting potential to examine the influence of cognitive processing on rumination. Moreover, if working memory training proves to cause sustainable beneficial effects, it could complement existing treatments or (relapse) prevention programs.

Conclusion

Rumination is a problematic self-regulation strategy that is associated with negative consequences on mood and cognition. We have discussed some of the key mechanisms explaining why individuals are susceptible to rumination. Major new developments in the study of rumination have been introduced which are likely to deepen our understanding of the dynamics of rumination and might also indicate new ways to reduce rumination.

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Biological Aspects of Self-Esteem and Stress

25

Jens C. Pruessner and Mark Baldwin

25.1 The Role of Personality in Coping with Stress

Psychological stress begins with the perception of a threat, such that situational demands are experienced as exceeding the individual's available resources for coping. This sets in motion a cascade of psychological and neuroendocrinological responses, including the activation of the hypothalamic–pituitary–adrenal (HPA) axis with the subsequent release of cortisol, an endocrine marker of the stress response. The activation of the HPA axis under acute threat can be considered a basic adaptive mechanism in response to alterations in demand, as one of its functions is to increase the availability of energy substrates in different parts of the body, and allow optimal adaptation to changing demands from the environment. However, psychological stress—and the emotions that tend to accompany threat perception such as anxiety and fear—can interfere with performance and the effective self-regulation of behavior. Moreover, prolonged (chronic) activation of the HPA axis can lead to negative outcomes including suppression of the immune system and subsequent illness, increased blood pressure, and heightened risk of infections and other serious conditions such as diabetes and hypertension (e.g., McEwen 1998, 2002).

Thanks to Lazarus (1966), who has devoted much of his work to the study of stress, behavioral scientists now know much about the interindividual variability in the stress response. Lazarus noted early on that stressful conditions per se fail to produce reliable effects on task performance (Lazarus et al. 1952). Keeping all situational variables constant, the same stressor can have a minimal effect, lead to performance improvements, or result in significant performance impairments across different people. This led Lazarus and others to suggest that individual differences in motivational and cognitive variables are likely to interact with situational components. What is considered threatening for some, and thus stressful and performance impairing, might be considered as stimulating by others, and thus produce beneficial effects on performance.

Subsequent research identified the appraisal process as crucial in explaining the impact of psychological variables on the stress response. Any internal or external stimulus is perceived as stressful only if it is appraised as harmful or threatening. According to Lazarus, this is a two-stage process, where the primary appraisal of a stimulus as benign/irrelevant versus threatening/challenging is followed by a secondary appraisal that compares the demand of the situation with the available resources, and in the case where the demands exceed the resources the individual is

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becoming stressed. The importance of appraisals (Lazarus 1966) has received recent validation with the identification of “social evaluative threat” as the single most important factor in determining the stressfulness in laboratory studies (Dickerson and Kemeny 2004). The social appraisal could thus be considered a special form of the secondary appraisal process proposed by Lazarus, where the social demands of the situation are compared to the (perceived) social resources. Obviously, a number of personality factors could play a significant role here as well.

25.2 The Importance of Self-Esteem and Locus of Control in the Perception of Stress

Over the years, we have conducted a series of studies to test the notion that the personality variables self-esteem and locus of control play a central role in the appraisal of many situations as threatening, and thus contribute to the experience of stress. Self-esteem is broadly defined as the value people place on themselves. Locus of control refers to the belief that the outcome of events is either more dependent on one’s own actions (internal) or others (external; DeLongis et al. 1988; Lo 2002; Petrie and Rotheram 1982; Whisman and Kwon 1993). Epidemiological studies have shown that low self-esteem is associated with negative life outcomes, including substance abuse, delinquency, unhappiness, depression, and worsened recovery after illnesses (e.g., Hoyle et al. 1999; Leary and McDonald 2003). On the other hand, high self-esteem has been linked to happiness and longevity (Baumeister et al. 2003). In studies of aging, a positive self-concept and internal locus of control predict successful aging, predicting independence, cognitive stability, and general health (Baltes and Baltes 1990; Markus and Herzog 1991).

Not surprisingly, internal locus of control and self-esteem are usually highly correlated. The key link of these variables to the experience of stress lies in their impact on the appraisal of a given situation. We postulate that in the appraisal of whether a given situation might be threatening and harmful, or benign, self-esteem and internal locus of control systematically interact with situational factors. If a person attributes little importance to him or herself, and thinks that he or she has little impact on the outcome of his or her own actions, this person will more quickly appraise situations as uncontrollable and unpredictable, and consequently will be more likely to experience situations as threatening, and harmful.

25.3 Endocrinological Evidence for the Role of Self-Esteem and Locus of Control in the Perception of Stress

The first evidence for the impact of self-esteem and locus of control on stress perception emerged when we exposed participants to repeated psychological stress, using the Trier Social Stress Test (TSST; Kirschbaum et al. 1993). In this standardized laboratory stress paradigm, participants have to give an impromptu speech and perform serial subtraction tasks in front of an audience, usually for about 10 min. The audience consists of two to three persons who are instructed to maintain a neutral expression, being neither explicitly rejecting nor confirmative in their facial expression or gestures. In addition, the task is audio- and video-recorded and participants are instructed that the recording will later be analyzed by trained psychologists for verbal and nonverbal contents. During the speech, the audience interacts with the participant only to indicate the amount of time that is left to talk, or to ask specific questions. In the case that a participant has nothing more to say, they remind the participant that there is time left to continue the speech. During the serial subtraction task, the participant is interrupted only when making a mistake. The participant is then corrected and instructed to start the task over.

The TSST is specifically designed to induce a significant amount of social-evaluative threat, combined with uncontrollability, and indeed has been shown to be a powerful stressor, stimulating the HPA axis and leading to significant increases of free cortisol within 15–30 min following the

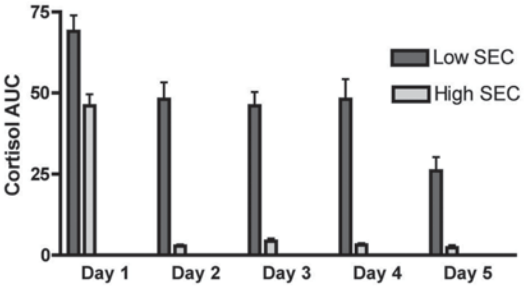

Fig. 25.1 Cortisol responses (area under the curve) on repeated exposure to the Trier Social Stress Test (TSST) on 5 subsequent days in participants with high self-esteem and high locus of control (High SEC; $n=13$) and low self-esteem and low locus of control (Low SEC; $n=7$)

onset of the task (e.g., Kirschbaum et al. 1992). In this first study, we aimed to validate the hypothesis that in humans, repeated exposure to the same stressor would lead to quick habituation of the stress response (Ursin et al. 1978). To test the habituation of the stress response, a total of 20 young healthy male college students were exposed to the TSST on 5 subsequent days. For this purpose, the TSST was modified using different speech topics and serial subtraction tasks on each day.

Notably, we found that only 13 of the 20 participants showed the typical habituation pattern, with a normal stress response on day 1 being significantly reduced on day 2, and no longer present on the subsequent days. In the seven remaining participants, however, the cortisol stress response continued to be present on all days, and only showed a tendency to decline toward the end of the testing period (Fig. 25.1). When analyzing the psychological variables, it became apparent that low internal locus of control and low self-esteem were the best predictors of failing habituation of the cortisol stress response to repeated stress exposure (Kirschbaum et al. 1995). This can be interpreted as a sign that these personality variables at least interact with, if not determine, people's appraisal of a situation during repeated exposure to a stressor.

We attributed the absence of differences in the stress response between the two groups of participants on day 1 to the effect of novelty. The novelty of the situation might have made it unpredictable and uncontrollable for everybody on the first exposure, and might thus have "masked" the impact of personality variables on stress perception and response. Thus, one conclusion at the time was that, to reveal the effect of personality variables on the stress appraisal and response, one will likely require at least two exposures to the same stressor.

At the same time, additional benefits can be gained from exposing participants to more than two repetitions of the same stressor. When looking at the strength of the correlations between the magnitude of the endocrine stress response and the personality variables, we noticed that the correlations grew stronger with repeated exposure. That is, the magnitude of the correlation between the combined stress response of the first 2 days was stronger than the first day alone, the magnitude of the correlation of the first 3 days was stronger than the first 2 days, and so on. In fact, the strongest correlations were found between the aggregated stress responses of all 5 days combined and the personality variables (Pruessner et al. 1997). Because the effects of novelty were likely an influence only on day 1, it can be speculated that other factors must have been at play.

One such factor could have been statistical in nature: Any error associated with the endocrine measures would be presumably random, and by aggregating across several endocrine measures the errors would have cancelled each other out, thus increasing the strength of the association. At the same time, there is likely also an influence of the change of the endocrine response dynamic over time at play here, because the group with low self-esteem and low internal locus of control continued to respond strongly to the psychosocial stressor, while the group with normal to high levels of self-esteem showed completely absent stress responses starting at day 3. Thus, the participants with greatly varying personality profiles moved further away from each other endocrinologically, over time. Because the correlational strength of the endocrine/personality relationship was not as strong when looking at the endocrine profile of later days alone, there is likely a combination of factors at play here, with the above two contributing significantly, and other factors also likely playing a role.

It can be argued that personality variables tend to have relatively weaker effects when situational factors are very strong. In a second study, we thus reduced the threatening aspects of the situation and found that self-esteem and locus of control could then have an impact on the perception of stress already on the first exposure to a stimulus. In this study, we combined computerized mental arithmetic with induced failure to invoke stress. In the experimental design used in this task, 52 students performed the task on computer terminals in front of them. Half of the students were exposed to a difficult version leading to low performance compared to an easy version of the task with high performance for the other half. The students played the task in three 3-min segments, and had to announce their performance score after each segment to the investigator, who wrote the scores down on a board for everyone to see. Saliva sampling before, during, and after the task allowed us to assess the cortisol dynamics in relation to this paradigm (Pruessner et al. 1999).

Notably, this task only triggered a significant cortisol release among participants who were in the low-performance group *and* had low self-esteem combined with low internal locus of control. Neither low performance alone nor low self-esteem and internal locus of control alone were significant predictors of cortisol release, supporting the notion that these personality variables produce effects only in interaction with a potentially stressful situation (Fig. 25.2). In line with the appraisal perspective we outlined at the beginning of the chapter, we suggest that people's appraisal of the situation is at the core of this interaction. In addition, we conclude from this study that the milder form of stress enabled us to see personality effects despite the fact that we used a single exposure paradigm. If a potential stressor is mild enough so that it will lead to a perception as threatening only in those participants that experience low self-esteem and low internal locus of control, then the association with the endocrine stress response is likely to emerge at the initial exposure. Subsequent research from other laboratories has confirmed the link we observed between low self-esteem and the stress response (e.g., Ford and Collins 2010; see also Martens et al. 2008).

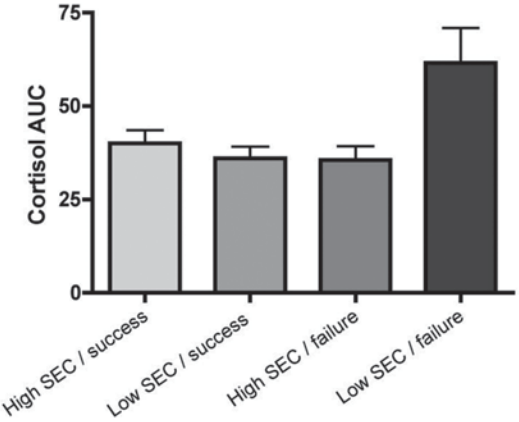

Fig. 25.2 Cortisol stress responses to the Trier Mental Challenge Task (TMCT) in four groups of participants, separated for high and low self-esteem and locus of control, and high and low performance in the mental arithmetic. The performance was manipulated by the investigator

25.4 The Hippocampus as a Possible Mediator of the Relationship between Self-Esteem, Locus of Control, and Stress

Studies on brain correlates of personality variables and endocrine function in humans have only recently started to appear. Nevertheless, initial evidence points to a critical role of the hippocampus at the interface of personality and stress responses. The hippocampus is one of the major limbic system structures involved in the regulation of the stress response (Fuchs and Flugge 2003), and variations in hippocampal volume have shown to be systematically linked to excessive HPA axis activity (Sapolsky 1999; Sapolsky et al. 1986). Early models postulated that associations between hippocampal volume and HPA axis activity might represent the consequence of excessive exposure of the hippocampus to glucocorticoids, due to their powerful neurotoxic properties (Sapolsky et al. 1986).

More recently however, evidence has surfaced that questions the role of glucocorticoid neurotoxicity in affecting hippocampal volume (Swaab et al. 2005). Instead, neurodevelopmental factors might have a more dominant effect in determining hippocampal volume, and in turn HPA function (Engert et al. 2010; see also below). Functionally, the hippocampus is the primary structure for memory contextualization, and it is here that a link to self-esteem and locus of control could occur. When faced with a potentially threatening and harmful situation, people may activate memories of past events to inform their appraisal of the current event. However, if specific situational and environmental characteristics associated with negative past events cannot be recalled, this lack of awareness of situational circumstance can lead to an overgeneralization of negative past events, and thus an increased likelihood to consider the current situations as stressful as well. Thus, poor contextualization due to impaired hippocampus function could be linked to higher stress responses on the one hand, and lower self-esteem on the other (for related arguments, see Goosens 2011; Pham et al. 2005). Another question that is linked to this argument is whether smaller is always worse, and bigger is always better, when referring to variations in brain volume and functional consequences. It is probably oversimplifying to think of this relationship in a strictly linear fashion, but it can be assumed that there is at least a certain range of normality where this association is linear.

We thus tested the hypothesis of a link between hippocampal volume, personality variables, and stress responses in 20 healthy young male college students. All participants underwent an extensive psychological procedure for the assessment of personality variables, including self-esteem and locus of control (Krampen 1991; Rosenberg 1979). In addition, participants underwent structural magnetic resonance imaging (MRI) employing a structural T1-weighted acquisition protocol, which produces high-resolution (isotropic 1 mm) images of the cerebrum (Mazziotta et al. 1995). Our in-house manual segmentation protocol was then applied to all images after nonuniformity correction, signal-intensity normalization, and Tailarach-like transformation for standardization of brain size. The manual segmentation then allows for volumetric assessment of the hippocampus (Pruessner et al. 2000). Finally, all participants were exposed to a computerized stress task, similar to the mental arithmetic task described earlier. Saliva samples before, during, and after the task accompanied the testing to assess the cortisol stress response.

Results first replicated earlier findings of mental arithmetic stress: Only the participants with low self-esteem and low internal locus of control showed a significant release of cortisol. Extending earlier findings however, a correlation emerged between the cortisol stress response and self-esteem ($r=-0.45$, $p<0.05$). Furthermore, a strong correlation emerged between the cortisol stress response and the total hippocampal volume ($r=-0.53$, $p=0.03$), supporting the idea that the size of the hippocampus is related to the regulation of the HPA (Fig. 25.3a). Finally, supporting our initial hypothesis, we also observed a link between internal locus of control and hippocampal volume ($r=0.66$, $p=0.006$; Fig. 25.3b), and self-esteem and hippocampal volume ($r=0.58$, $p=0.02$; Fig. 25.3c).

Testing for the specificity of the effect with regard to the hippocampus, total brain gray matter was employed as control structure in correlations with both personality variables and cortisol response. None of the correlations with total brain gray matter were significant, suggesting that the observed relationships were indeed specific to the medial temporal lobe area and the hippocampus. This was the first research we are aware of linking self-esteem to hippocampal volume, although the finding has been independently replicated since (Kubarych et al. 2012).

25.5 Personality Variables, Brain Structures, and Stress Responses in a Developmental Context

An obvious follow-up research theme that arises from these results is to better understand the observed relationships among personality variables,

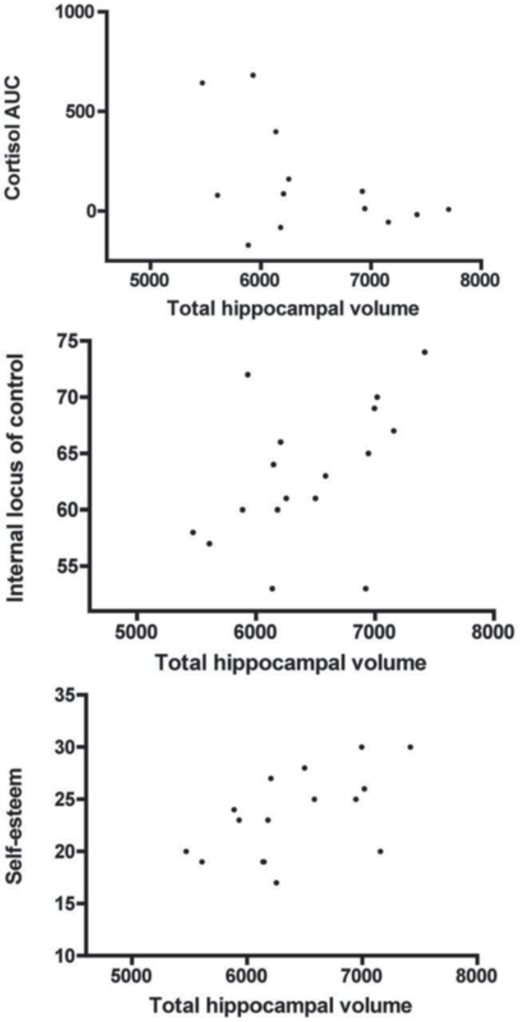

Fig. 25.3 Correlation between hippocampal volume and cortisol stress responses to a mental arithmetic task (**a**), hippocampal volume and locus of control (**b**), and hippocampal volume and self-esteem (**c**) in a group of 16 healthy young male college students

hippocampal volumes, and stress responses. Future research will have to address the direction of the observed relationship between personality, neural structures, and endocrine responses, as well as the origin of these relationships. While we are not at a point where we can present conclusive answers, a number of observations allow us to carefully formulate some hypotheses backed up by recent findings.

According to the "glucocorticoid cascade hypothesis" (Sapolsky et al. 1986), periods of excessive and chronic stress could lead to damage in those areas of the brain that are rich in receptors for glucocorticoids—prominently among them, the hippocampus. Because the hippocampus is further involved in the inhibition of subsequent activity of the HPA axis (through glucocorticoid receptors on its surface it becomes aware that cortisol has been released and signals to the hypothalamus to shut down further HPA axis activity—a process called negative feedback), a damaged hippocampus would be impaired in its ability to relay the negative feedback signal, and thus an excessive or prolonged activation of the axis after stress would occur. This model would explain why lower hippocampal volume is associated with higher cortisol stress responses (the hippocampus is less capable of shutting down HPA axis activity), and it could further explain why those with higher stress responses could have lower self-esteem (the smaller hippocampus would be not as good as a bigger hippocampus in memory contextualization). What it would not explain necessarily is how the hippocampus would become damaged in the first place: Is a onetime traumatic stressor sufficient, or is a period of chronic stress required? There is further a potential developmental process in which reduced hippocampal volumes with stress and aging become associated with changing levels of cortisol and self-esteem. While the early studies by Sapolsky et al. (1986) in rodents could produce some evidence for such a scenario, studies in humans that have been performed since have produced rather inconsistent results.

The question of glucocorticoid toxicity in the human brain is a very rich field of studies, and it would be beyond the scope of the current chapter to try and list all of the evidence. However, there is one piece of evidence that is particular compelling in suggesting that a strict model of toxicity might not work as suggested, at least in humans. This evidence comes from patients diagnosed with Cushing's syndrome, a condition with excessive glucocorticoid production often caused by a tumor in the pituitary, who display cognitive disturbances. Moreover, upon assessment of their brain function and integrity, these patients present with reduced hippocampal volumes. However, once the underlying reason for their excessive glucocorticoid production is found and they are successfully treated (e.g., by surgery to remove the tumor from their brain), Cushing patients' cognitive function and their hippocampal volume return to normal. Furthermore, the incidence of neurodegeneration and dementia in old age among Cushing's patients is not higher than in the general population, suggesting that no permanent damage has been done. This despite the fact that the disease has led to excessive glucocorticoid production sometimes for years, with the highest possible glucocorticoid exposure for a significant portion of their life. If anyone should suffer from glucocorticoid neurotoxicity, this population should certainly be affected! In the light of these findings, some authors have suggested that glucocorticoid exposure represents an insult from which people can recover (Müller et al. 2001). The observed lower hippocampal volumes during the presence of high cortisol levels could be discussed as a consequence of transient intracellular changes in water and electrolyte content (Swaab et al. 2005).

So if it not glucocorticoid toxicity, what else could cause the association between hippocampal volumes and cortisol regulation? An alternative to this model brings neurodevelopmental factors into the focus, and here the picture is perhaps a bit more consistent. There are by now a substantial number of studies which support the idea that distinct events during critical development periods can shape the developing brain, which might in turn influence the personality, and the stress response. Studies looking at pre- and postnatal adversity like malnutrition, toxic exposure, physical or sexual abuse, parental neglect, etc. have shown that these factors can be additive in affecting the volume of key structures in the brain, including the hippocampus, the anterior cingulate, and the precuneus, all structures involved in personality, emotion, and stress regulation (e.g., Engert et al. 2010; Heim et al. 2013). Thus, specific events during critical development periods might determine the development of the brain, which in turn might influence the functioning of key systems, including the stress system.

We could demonstrate partial support for the neurodevelopmental model in a recent study where we first established a link between early-life adversity (in the form of self-reported early-life maternal care), and then showed how the correlation was mediated by the hippocampal volume of the participants. If the size of the hippocampus determines memory contextualization capabilities, this variation could then have personality- and stress-related consequences. The impaired source monitoring would lead to an overgeneralization of the experience of failure and rejection, and consequently to a self-perception of being a failure or being socially rejected in general, which might produce low self-esteem and low locus of control during childhood and adolescence (Davidson et al. 2002; Kernis et al. 1989; Showers 1992). The observed higher cortisol responses would then not be a direct consequence of smaller hippocampal volume, but of the increased stress perception due to consistent unfavorable appraisals of ambiguous situations. Thus, the effect of early-life adversity on the hippocampus would in turn have an effect on the developing personality, which again in turn could then shape the endocrine stress response.

Of course, the question arises why overgeneralization should then not also be an issue for positive life events, in other words, a general lack of source monitoring for both positive and negative life events with no consequences on self-perception. One possible explanation here could be seen in the stress-specific function of the hippocampus within the limbic system. There is evidence that it is specifically the hippocampus together with the anterior cingulate that is involved in the stress response (Sinha et al. 2004). It is also known that the anterior cingulate is particularly involved in error monitoring, which means its involvement is restricted to situations where a mismatch between expectations and reality occurs (Wang et al. 2005). These circumstances would make a specific role of the hippocampus in reaction to negative life events more probable.

The neurodevelopmental model changes the direction of the overall association—both hippocampal volume and personality traits are seen as a consequence of early-life adversity factors, which then in turn determine the cortisol stress response. It would also create a more static association, because variations in current or chronic stress would not result in enduring changes in the brain structure or function. At the same time, the neurodevelopmental model puts a much greater emphasis on the importance of factors in early life, reminiscent of psychoanalytical theories and models. This possibility currently receives increased attention in the literature (Del Giudice et al. 2011). The variations in hippocampal volume as a consequence of critical development periods early in life could then be speculated to have other consequences as well (memory, cognition, executive function), creating a model of developmental trajectory based on critical development periods. Evidence to support the neurodevelopmental model comes from smaller retrospective studies (Engert et al. 2010; Pruessner et al. 2004), but systematic studies on this topic will have to follow to provide broader support such a view.

Taken together, based on our findings to date, we suggest that reduced hippocampal volume might play a role in the development of low self-esteem. This may in turn produce a higher susceptibility to perceive ambiguous situations as threatening, and thus stressful. The idea that hippocampal volume variation might be the cause for adverse functional and behavioral consequences, rather than their consequence has found further support in conjunction with risk factors for developing post-traumatic stress disorder (PTSD), in a study investigating hippocampal volume in twin brothers. Here, in participants who developed PTSD as a consequence of participating in the Vietnam War, the researchers observed lower hippocampal volume compared to participants who went to war, but did not develop PTSD. Intriguingly, however, lower hippocampal volume could also be observed in the PTSD participants' twin brothers—who never went to war—suggesting that the hippocampal volume might be a risk factor for, rather than a consequence of, developing PTSD (Gilbertson et al. 2002).

As mentioned, the possibility that hippocampal volume might play a causal role in the personality/coping interface is supported by the fact that we found consistent results even among relatively young adults. Recently, we have reported on variations in hippocampal volume in young populations (Lupien et al. 2007; Pruessner et al. 2001), suggesting that there is a considerable range of hippocampal volumes present in participants of all ages. At the same time, self-esteem is known to be a stable trait with considerable intraindividual stability throughout life (Markus and Herzog 1991). This supports a model in which variations in brain morphology could become a pathway to certain personality characteristics early in life, but further longitudinal studies are needed to examine these changes over time, and provide validation for these assumed associations.

25.6 Toward Improving Stress Regulation by Modifying Self-Esteem

Notwithstanding the existence of a general tendency toward stability in self-esteem, a strong experimental test of the causal role of self-esteem in the stress response would involve temporarily manipulating levels of self-esteem to examine any impact on the stress response. Parenthetically, this research question touches on a broader issue in the self-esteem literature regarding whether self-esteem can offer any benefits beyond heightened subjective well-being (see, e.g., Baumeister et al. 2003). Our view is that it most certainly can, and we have conducted several studies to test this notion.

Dandeneau and Baldwin (2004) developed an attentional training manipulation in which a participant is shown a grid of 16 people's faces, with 15 of them scowling and only one smiling warmly. The participant's task is to identify as quickly as possible the location of the sole smiling face. The hypothesis was that performing this task over approximately 100 trials would train and facilitate a response of disengaging from the distracting frowning faces, rather than dwelling on them as had been shown to be the normal response of individuals with low self-esteem (Dandeneau and Baldwin 2004). Indeed, this task successfully modified attentional responses, and also boosted participants' scores on standard measures of self-esteem (Baldwin and Dandeneau 2009; Dandeneau and Baldwin 2004; Dandeneau et al. 2007).

In one study that combined this manipulation with a stressful situation, Dandeneau et al. (2007, Study 3a) asked a sample of students to use the attentional training manipulation (or a control task) each day across the week before the final exam in their social psychology course. By the morning of the exam, the group using the find-the-smile task reported lower levels of perceived stress about the exam, less anxiety during the exam, and marginally higher academic self-esteem after the exam compared to controls.

A second study was conducted in a workplace, which can also be a stressful context particularly when—as for telemarketing operators—it is saturated with social evaluation and repeated experiences of rejection and outright hostility. A sample of telemarketers performed the attentional training task (or control) each day before their shift for 1 week. Those undergoing the attentional training showed improved emotional regulation, reporting lower stress levels, and higher self-esteem on daily measures. Cortisol release was assessed five times across the final day of the week, and participants undergoing attentional training had 16.8 % lower cortisol than controls. Moreover, on a measure of cortisol reactivity that examined peak levels of cortisol release, the attentional training group was 35.5 % lower than controls. Finally, the self-esteem boosting training also influenced behavioral self-regulation: By the end of the week, those in the training condition were scoring higher on quality control ratings and also performing significantly better (i.e., making more sales) on the job.

In sum, the Dandeneau et al. (2007) research has confirmed the causal role of self-esteem in the stress response. More specifically, an attentional training task that increased people's self-esteem also led to improved regulation of the physiological aspects of the stress response (including cortisol release, which can have adverse physiological effects). In addition, the attentional training led to improved regulation of behavioral outcomes due to reduced subjective stress and anxiety that might otherwise interfere with performance.

Conclusions

A person's response to stress is known to be linked to a number of psychological variables. A case can be made that specific personality variables, especially self-esteem and locus of control, play a central role in the appraisal of many situations, and thus contribute to the experience of stress. The studies described here provide evidence that participants with low self-esteem and low locus of control tend to show increased and more consistent release of cortisol in response to standardized laboratory stress tests. This effect is observable during stressful experiences, as well as in the failure of the cortisol response to habituate to repeated stress exposure.

We have further shown how this endocrinology/personality link is systematically associated with hippocampal volumes. The hippocampus is an important structure in the formation of memory, emotional regulation, and the regulation of the stress response. Variations in hippocampal volume have been postulated and shown to be systematically linked to HPA axis dysregulation, but intriguingly, the direction of this dysregulation is inconsistent across studies. We conclude that the dysregulation at the psychological level is due, at least in part, to impairments in memory associated with reduced hippocampal function: If specific situational and environmental characteristics associated with negative past events cannot be recalled, this lack of awareness of situational circumstance can lead to an overgeneralization of negative past events, and therefore an increased likelihood to consider the current situations as stressful as well. Thus, poor contextualization mediated by the hippocampus could be linked to abnormal stress responses on the one hand, and lower self-esteem on the other.

Taken together, the research that we have reviewed in this chapter highlights the importance of considering individual differences in self-esteem and locus of control in understanding people's behavioral and endocrinological responses to stress. In this way, our research contributes to a deeper understanding of the biobehavioral foundations of self-regulation.

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A Basic and Applied Model of the Body–Mind System

26

W.M. Bernstein

26.1 Introduction

Two hundred years of scientific research have produced a large set of varied, valid psychological concepts to explain the person. Important ideas have come from many different fields and schools of thought. Dialogue between schools has often been limited or contentious. But the *dogmas* of behaviorism and psychoanalysis, for example, promoted the development of the fields at first. Laws of classical and instrumental conditioning, habit hierarchies and drive are valid. And, Freud's ideas have gained renewed respect from scientific psychology (e.g., Westen 1999; Solms and Turnbull 2002; Northoff 2011).

While behaviorism excluded study of mental experience, the earliest experimental psychologists made it their focus. The Weber–Fechner law, developed by psychophysicists in the nineteenth century, describes how the *sensed intensity* of an external stimulus varies in a nonlinear fashion with changes in stimulus energy. The neurological basis for the effect has been identified in the brain's "number neurons," which apparently run on an algorithmic and not a liner basis (e.g., Dehaene 2003). In any case, Weber–Fechner may have been the first scientific clue that raw sensation does not reflect external reality exactly. The normal person becomes aware that "there is more to reality than meets the eye" at about 3 years of age (cf. Brenner 2006).

We are prepared as never before to integrate valid axioms of behaviorism, psychophysics, psychoanalysis, neurobiology, and social cognition. It may seem a wretchedly complex task to understand the person as an entity functioning simultaneously at biological, psychological, and social levels. But the subject matter is already organized very exquisitely. The mind sits in the brain, the brain sits in the body, and, the body is often in real or imagined social situations. Knowing something of each of the adjacent fields promotes understanding of how a body and a mind might add up to a whole, more or less functional human being.

Because standards for scientific methods are common to all subfields, we have a chance to integrate adjacent biological and psychological areas after the manner of genetics and molecular biology, neurology and neuropsychology, psychoanalysis and neuropsychoanalysis, and so on. The map representing the boundaries of the various fields and schools of thought is changing rapidly. This creates some urgency to articulate integrative concepts that workers from all the relevant neuroscience fields can understand, if not agree with entirely.

I started a project to link related neuroscience fields by using noncontroversial, axiomatic assumptions from each one (Bernstein 2011, 2014). The ideas come from biology and evolution, psychoanalysis, behaviorism, psychophysics,

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ethology, neurophysiology, neuropharmacology, developmental psychology, cognitive psychology, social psychology, organization psychology, clinical psychology, clinical neurology, and clinical psychopharmacology. The most general, organizing concepts are platonic philosophy and cybernetics.

The first part of this chapter describes my basic concepts. The second part illustrates how some of the thinking can be applied in diagnosing and treating mental illnesses. For the sake of clarity, I should first indicate my most foundational assumption: The most potent *reinforcers* and *incentives* of human behavior derive from a motive to learn valid concepts about reality; and, to use such knowledge to describe, predict, and control the self and, at least, some part of the external world. In short, learning is the greatest pleasure and desire.

This is consistent with Fritz Heider's (Heider 1958) characterization of the person as *a naïve scientist* who is motivated to understand the causes of his own and other people's behaviors. Heider's idea overlaps, in part, with *Freud's* concept of the *reality principle* (e.g., Freud, 1920). The essential feature of both ideas is that thinking might enhance control of the person's behavior beyond that achievable by hardwired responses to sensation (i.e., instincts). In ethology, instincts are termed *fixed action patterns;* and, *unconditioned stimuli* are called *releasers*. For example, sensory data indicating the shadow of a predator release *fixed actions* in potential prey such as crouching (e.g., Tinbergen 1951). Any early varieties of mice that evolved an instinct to approach objects that resembled carnivorous snakes have become extinct. That is, instinctive responses that have been *conserved* over evolution are, at least, based on some *face-valid* interpretations of the meaning of sense data from the exteroceptors that is generated somewhere in the nervous system.

If instinctive responding was effective 100 % of the time, one would not need to think too much. The problem for the individual is that instincts do not work all the time. Evolution has not anticipated every last idiosyncratic aspect of everyone's current situation. Rather, instincts are effective "most of the time" in the environments in which they developed. Accordingly, one may need to postpone enactment of instinctive urges, and decide "in the moment" how to best respond to a situation that presents a nonzero probability of resulting in pain or injury; pleasure; or, as happens usually, some degree of both. This sort of containing, explaining, predicting, and deciding involves use *of semantic concepts* in the brain's neocortex.

26.2 Sensations, Concepts, and Feelings

Formal and *naïve* scientific theories are made of *semantic concepts.* To my way of thinking, *semantic concepts* include words, arithmetic, and mathematics. They function to group or organize the sensory attributes of objects. For example, the word "lion" contains visual, auditory, and social attributes such as "yellow," "roars," and "predator." Words can also encode inferences about causal connections between *sensations* and other *concepts*. These are "the verbs" of concept usage such as x causes y, x and y are in bidirectional causal relations, x and y each partially cause z, and so on. *Attribution theory* considers cognitive and motivational variables that affect implicit and explicit rules for explaining reality.

Conscious deliberative, and unconscious automatic activation of *semantic concepts* in the neocortex can function to contain and explain *sense data* from exteroceptors (eyes, ears, etc.); and, information arising from inside the body and the brain (interoception). I define *feelings* as the subjective experience caused when *semantic concepts* contain and explain *sensations* and *other concepts*. Schachter and Singer (1962) used the term "emotion" for what I call *feeling*.

Conceptual, inferential processes give rise to *expectations* of the likelihood of experiencing pleasure and/or pain as a result of approaching or avoiding objects in the external world and in the mind. Pleasure *expectations* promote decisions to move the body's muscles to grasp something with the hand, for example; and, decisions to move focal attention in order to apprehend something with the mind. *Expectations* that exteroceptively or interoceptively sensed objects are likely to cause pain or injuries promote decisions to avoid such things. *Expectations* of pain and pleasure based on highly valid concepts of nature tend to generate more accurate predictions of events than *expectations* based on less valid ideas; and, hence, improve the durability and success of individuals and social organizations.

By the time raw data from the external world or the interior of the body reach the neocortex, it has been processed subcortically to varying degrees by different methods (e.g., Kalivas et al. 1993). It is likely the sense data have been *equipartitioned* into packets of equal numbers of sensory details (e.g., Snyder and Mitchell 1999; Snyder et al. 2006). For example, an entire prime number cannot be completely contained by any set of equipartitioned structures. So, registration of a prime number would result in some number of equal numbered packets and some *remainder*. Snyder believes that the abilities of *autistic savants* to do various arithmetic skills, such as recognizing prime numbers faster than any computer, are due to their having some "privileged access" to equipartitioned sense data that all normal individuals once had as infants. With development of semantic concepts, most adults have difficulty turning concepts off, that is, they have trouble intentionally accessing in focal attention raw sensation.

I call equipartitioned packets of sensory data *protoconcepts.* If sense data are adequately contained in *protoconcepts,* and responded to competently by subcortical brain areas using congenital standards to make decisions, there is no reason to think conceptually. So, perhaps it is *the remainders,* the data that cannot be contained in neat packets, which stimulate thinking and the activation or creation of semantic concepts proper (cf. Bion 1962).

Freud (e.g., 1895) used the term "primary process thinking" to describe what occurs in dreaming sleep and in regressive forms of mental illness such as psychosis. Today, Panksepp and Wright (2012) use the term "primary processing" to describe something that occurs in the brain stem. A term that might cause less confusion is *initial processing*. That is, Freud and Panksepp are trying to describe the first phases of information processing of raw sense data. Regression of normal mental processes is related to sleep and to psychotic processes.

There is no reason to think conceptually of such data if it can be contained and, thereby, explained, by equipartitioning or *protoconcepts*. *Protoconcepts* are used to assess the face-valid meaning of sense data. For example, "To what degree do the sense data match representations of wanted or feared things stored in the nervous system by way of 'species learning' coded genetically, and/or things learned in the life of the individual?" Good enough matches stimulate tendencies to perform *fixed actions* involving *approach, avoidance, or immobilization* that are sometimes enacted by muscles.

But instinctive urges can be *suppressed, refined, denied,* or somehow transformed in countless ways. These transformations come from the *secondary processing* of information that occurs in the *neocortex* lying above the brain stem and limbic system. Usually, individuals who have learned to use valid concepts to generate accurate predictions of the likely results of enacting instinctive or more sophisticated responses to stressors will be successful at work and love.

In contrast, those with *post-traumatic stress syndromes* face an uphill struggle to use inferential thinking to regulate their sensations of fear. This is, in large part, because the subcortical *amygdala* has already made a decision, about 2 ms before sense data can reach the neocortex, to activate fear and avoidance behaviors (e.g., LeDoux 1996). In other words, the regulating effect of conceptual thinking on sensation is activated only after instinctive, fear avoidance tendencies have gained momentum. Most people do not suffer from disabling anxiety disorders. But in all people, initial information processing precedes secondary processing. It is the way the brain is wired. Hence, we react to the world initially as did phylogenetically earlier animals.

The motive to understand objects at levels deeper than *instinctive face validity* are in constant, dynamic relations with reflexive, instinctive tendencies (cf., Lieberman and Eisenberger 2004). Individuals living in complex social environments are consistently being exposed to *releasers of fixed actions* such as the secondary sexual characteristics of potential mates (e.g., Bernstein 1984; Bernstein et al. 1983).

Miller (e.g., 1944) depicted classically the underlying asymmetries in approach pleasure and avoid pain motives. Avoidance motives are activated close to presumably dangerous objects and increase quickly in strength with decreasing distance. Compared to avoidance tendencies, drives to approach objects to learn about them are stimulated at relatively far distances; and, have a less steep increase in strength as the distance from objects of curiosity decreases. This universally observed asymmetric pattern puts safety first, thus increasing the odds the individual will be alive in order to enjoy the pleasures of food, sex, science, art, and everything else.

Heider placed the motive to approach knowledge in the capital position in the hierarchy of forces controlling the individual (cf. E.O. Wilson 1984, 1999). Freud's *pleasure principle* described the tendency of immature individuals to act in order to gain immediate gratification of desires. He described the control of urges, in part, as "the vicissitudes of the instincts" (e.g., Freud 1915). Behaviorists or learning theorists would say behavior becomes *shaped* by learning. Control may involve *suppression, expression, displacement, denial,* and innumerable other methods. The centrally important variables controlling the person are the *concepts* and *expectations* held by them, proximal social agents, and overarching culture forces such as corporations, nations, and economies (e.g., Katz and Kahn 1973; Bernstein and Burke 1989).

26.3 Focal Attention

Following Allan Snyder at the University of Sydney, Australia (e.g., Snyder and Mitchell 1999; Snyder et al. 2004, 2006), I assume that either *sense data or concepts* can be in focal attention at any one moment. Intentional and automatic switching between activation in awareness of concepts or sensations can be considered the "skill of skills" in cognitive control. I think mental habits that regulate attention are determined largely by the same sorts of variables identified by the behaviorists. And, activating concepts is neurologically not too different from stimulating a muscle.

All people develop habits to focus on pleasurable sensations, thoughts, or feelings; and to avoid painful subjective experiences. In effect, the *naïve scientist* is able to switch more or less competently between collecting raw data and applying theories to explain it because he has learned, and uses effectively "sensory interpreting concepts" that are valid enough, or in the words of the British psychoanalyst David Winnicott "good enough" (e.g., Winnicott 1960).

This ability is impaired in those with *severe autism,* which is primarily a genetically caused brain derangement (e.g., Kemper & Baumer 1998). And, attentional control problems are always seen in functional psychopathologies such as chronic *anxiety, depression, and psychosis.* Autists and those with serious psychopathology have difficulties intrapsychically and interpersonally.

In normal subjects, concept activation can be inhibited experimentally by means of *transcranial magnetic stimulation* (TMS) at the *left orbital prefrontal cortex* (e.g., Snyder et al. 2004, 2006). This causes the person to be more aware than usual of raw sense data. Hence, they show improved performance on tasks calling for accuracy in describing sense data from all exteroceptive sensory channels (e.g., auditory, visual, etc.). *Autistic savants,* whose conceptual processes are impaired, represent the brain state characteristic of Snyder's subjects whose conceptual processes are inhibited for about a minute after TMS.

26.4 Stress and Decision Making

All organ systems of the body play some role in operations designed to maintain safety and security, and in operations involving appetitive behaviors. But each organ has a *primary function*.

The primary function of the renal system, for example, is to make urine. A primary function of the nervous system and brain is to make decisions. Most generally, deciding involves choosing between performing one of three general types of operations: (1) *approach* in thought or overt movement of the body, toward some object or condition in the mind or the external world, (2) *avoidance* of the object or situation, or (3) *immobilization*.

Since few or perhaps no object or situation in nature might be actually "all good" and certain to cause only pleasure, nor "all bad" and certain to cause pain, all decision making involves some level of stress and conflict regarding the best response to sense data (cf., Lewin 1935). Determining the best response to sensory information depends, in large part, on the validity of the concepts used to interpret it.

Selye (1936) conceptualized biological stress as caused by "noxious agents." The noxiousness of stimuli arising from the body and nervous system itself might be operationalized in terms of the extent to which they signal deviations from evolved or learned standards for physical and mental control variables. Deviations from standards coded in DNA; and, deviations from standards learned socially and remembered by the nervous system cause the body and mind to respond to stress to regulate the body, mind, and overt social behavior.

Both positive and negative discrepancies from standards cause stress. For example, one's blood pressure can be too high or too low to maintain and promote health. Similarly, one might feel "too good" and be vulnerable to overestimating their competence to achieve *extrinsic* and *intrinsically* rewarding goals (e.g., Deci 1971). Or, the person could feel "too bad" and be susceptible to underestimating their chances of success in life. Extreme pessimism is associated with clinical *depression* (e.g., Alloy and Ahrens 1987). And, grandiose optimism is seen in *mania,* as well as creative, fluid states of mind prone to easy distractibility of attentional focus (see Biss et al. 2010).

The process of registering stress in the body and mind can be described in cybernetic terms. Specifically, *test*–operate–*test*–*exit* (*TOTE*) decision-making processes are used by the nervous system. For example, mechanoreceptors in the vasculature respond to stretching of blood vessels by increasing or decreasing neuronal firing rates. These changing sensory signals can cause efferent neuromuscular signals that initiate endocrine, hypothalamic, brain stem, limbic, and neocortical attempts to regulate blood pressure up or down. Baseline, sensory neuron firing rates might be considered *standards* for ideal hemodynamic and other physiological processes including those of the brain (cf., Northoff 2011).

Cognitive control processes can also be understood in cybernetic terms (e.g., Miller et al. 1986; Carver and Scheier 1981). For example, when the mind's eye turns to the self (e.g., after seeing one's image in a mirror), the discrepancy between ones real and ideal standing on some dimension of psychosocial functioning becomes a focus of attention (e.g., Duval and Wicklund 1972; Wicklund 1975). This causes attempts to reduce stress by means of action to reduce the discrepancy or by avoiding self-focus.

Most generally, biological and psychosocial stressors work to initiate information processing to make decisions about how to respond to them. Processing occurs in each of the three anatomically distinct parts of the brain that evolved over time: the old reptilian brain stem, the mammalian limbic system, and the uniquely large human neocortex (e.g., MacLean 1990; Panksepp 1998; Porges 2011).

Something like *TOTE* processes are used probably in all decision making in all parts of the nervous system. Autonomic control processes are very energy efficient compared to conscious processes. From a bioenergetic standpoint, there is no reason to expend the large amounts of glucose needed to control conscious attentional focus if reflexive, autonomic parts of the nervous system can competently reduce stress. Adding rational thinking to reflexive responding creates a tremendous *selective advantage*. But intentional, effortful, conscious thinking is energy intensive (e.g., Galliot et al. 2007). "Don't wake up the boss if you can solve the problem yourself."

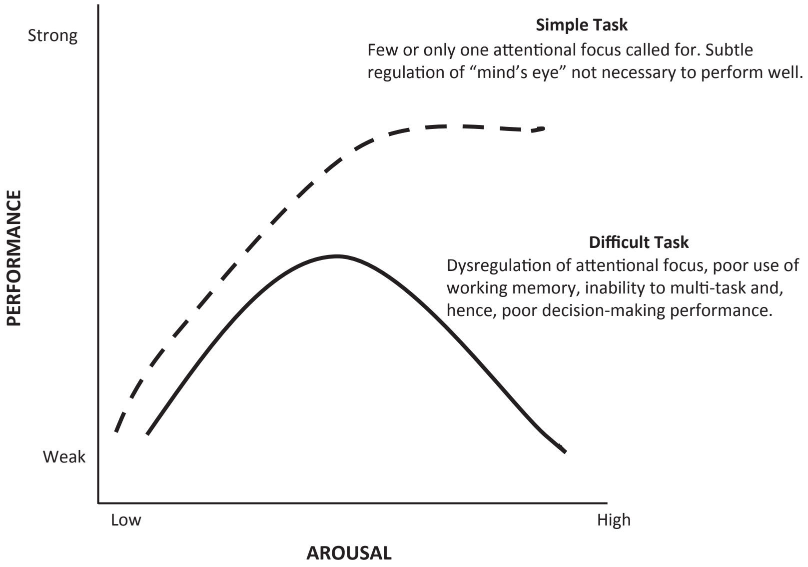

Fig. 26.1 This figure is based on one from Diamond et al (2007), an open access article

26.5 Sympathetic Arousal and Performance

Generally, the person is best able to cope with stressors if regulation of the autonomic nervous system (ANS) can be influenced by the central nervous system, especially the *semantic concepts* residing in the neocortex. From both personal and evolutionary perspectives, it is very desirable in emergencies to be competent to perform both complex cognitive processing, e.g., "thinking of an escape plan;" and, simple, brutish tasks that may be instrumental in executing plans, e.g., "smashing down a locked door." Usually, high sympathetic arousal promotes high performance on simple tasks and reduces performance on complex tasks. For most people, the best cognitive functioning seems to occur in moderate states of arousal (Fig. 26.1). This is the classic finding that arousal and performance of complex tasks are related in an inverted U curve (Yerkes and Dodson 1908, see Fig. 26.1 below).

26.6 Parasympathetic Tone and Performance

Of course, human performance is not dependent solely on sympathetic arousal. Parasympathetic braking of adrenergic arousal is another important part of the equation. Stephen Porges' *polyvagal theory* (2011) represents an insightful understanding of the parasympathetic system. The theory is based on the differentiation of the phylogenetically older, vegetative parts of the vagal system from the newer parts. Older vagal nerves originate in the brain stem *nucleus tractus solitaries* (NTS). They are unmyelinated, and they function, in part, to activate the old reptilian instinct to *freeze* or *become immobile* in response to stress. Phylogenetically newer vagal nerves originate in the brain stem *nucleus ambiguous* (NA). They are myelinated; and, they function, in part, to regulate the action of the heart. In particular, myelinated vagal efferents from the NA can inhibit the intrinsically rapid electrical pacemaking of the heart's sinoatrial node and, thereby, promote *parasympathetic tone* and "social engagement." Porges' primary measure of *parasympathetic tone* is *respiratory sinus arrhythmia* (RSA).

> RSA is a naturally occurring rhythm in the heart rate pattern that oscillates at approximately the frequency of spontaneous breathing…. By quantifying RSA and the relation between RSA and heart rate during various challenges, it is possible to measure the dynamic regulation of the myelinated vagal brake to study the responses of infants and young children to people and to objects (Porges 2011, p. 122).

The ability to express a wide range of RSA indicates that the myelinated vagal tracts from the *NA* to the heart can produce a large array of cardiac arousal levels via "parasympathetic braking" and, hence, a large number of subtle differences in somatic arousal intensity and quality. Porges assumes, I think rightly, that competent control of these states promotes competent social behavior.

Porges (2011) reports a study in which subjects were made anxious by frightening videos. Compared to normal subjects, those diagnosed with *borderline personality disorder* or who had histories of *childhood abuse* were less able to quickly reestablish *good parasympathetic tone* (i.e., High RSA Range) after withdrawal of the frightening stimuli. The obvious implications of such a study are that mental health might be improved by increasing a person's ability to control RSA. Zucker et al. (2009) demonstrated that RSA can be influenced by providing a person with data about his contemporaneous RSA range. Subjects with *posttraumatic anxiety* were shown a visual representation of RSA range variation (biofeedback), and instructed to time their breathing to match the oscillations of the visual representation of RSA. This procedure works to expand RSA range and alter other heart rate variables. And, increased RSA range was associated with decreased anxiety.

RSA affects movements of the face and body, the action of the heart and lungs, and probably brain levels of polypeptide hormones such as oxytocin and vasopressin (e.g., Meyer-Lindenberg et al. 2011). Overall, the polyvagal theory describes the dynamic relations between sympathetic arousal and parasympathetic braking.

According to Porges, the full extent of "the social engagement system of the brain" includes cranial nerves V (trigeminal), VII (facial), IX (glossopharyngeal), X (vagus), and XI (spinal accessory). These nerves control muscular movements in the face, vocal cords, and the spine. These are the "affect making" parts of the body that other creatures can perceive and respond to socially. Three of the five nerves in Porges' "social engagement system" derive from the brain stem (VII, IX, and X).

26.7 Affective Neuroscience

Posture and muscular gestures of the face are especially important to affect theories (e.g., Ekman 1973). We know that configuring the mouth into a smile, for example, can increase the amount of pain a person can tolerate (e.g., Lanzetta and Orr 1986). The discovery of *mirror neurons* has given brain science a hook to explore empathic and related social processes (e.g., Decety and Ickes 2009). But, "face making" and "posture making" neurons have elaborate connections to the neocortical association areas involved in using *semantic concepts* to think.

> The cerebral cortex is the chief controlling entity of the human central nervous system…. The primary fields of the neocortex are the point of departure of neocortical evolution and, as such, they command the most space in the cerebral cortex of lower mammals and early primates…. Myelination represents the final step in brain maturation (Braak and Braak 1996, p. 197).

Is it not safe to assume that cognitive operations in the neocortex are at the top of the hierarchy of the brain and mind control systems in humans and other mammals? It is not merely a metaphor to say, "Cognition is King" or, "Neocortex is King."

Subcortical brain mechanisms and their relations with sensory-motor processes have been the central focus of *affective neuroscience theory* (e.g., Panksepp 1998). Such theories are almost devoid of concepts attempting to describe or explain cognition. For example, Porges (2011) does not describe the neocortical information processes underlying *social cognition* (e.g., Fiske and Taylor 2008). Rather, he has posited a "social engagement system." I have argued that *affect theories* are inadequate to explain the body–mind system because they have no concepts for concepts (Bernstein 2014).

Sylvan Tomkins' affect theory (Tomkins 1962, 1963) tried to bring something like "emotions" or "feelings" back into scientific psychology after the study of mental experiences had been ignored by the behaviorists. He revived interest in consciousness after it had been seemed to be de-emphasized relative to unconscious processes by psychoanalysis. And, he assumed logically that animal life is understood best as always concerned with anticipation and response to pains and pleasures. But according to his student Virginia Demos,

> [Tompkins] thumbed his nose at all behaviorisms in his emphasis on imagery and consciousness, and by putting more weight on consciousness than on the unconscious, he further departed from his Freudian roots. (Demos 1995, p. 2)

But, of course, Hull (1943), Spence (1956), other behaviorists, and the psychoanalysts too have developed experimentally validated concepts to explain the person (e.g., Bernstein 1984; Westen 1999). Can a theoretician merely "thumb his nose" at all that?

Tompkins described nine affects, some are positive or "good" (e.g., joy and excitement), some are negative or "bad" (e.g., anger and disgust), and, one is thought to be "neutral" (surprise). Tompkins theory is the basis for *affective neuroscience theories*. For example, Panksepp (1998) describes seven "primary process emotions" or "primal affects" which he likes to write in capital letters: SEEKING, RAGE, FEAR, LUST, CARE, PANIC, and PLAY. Each "basic affect" is subserved by a more or less discrete system of subcortical brain regions. Most recently, Panksepp and Wright (2012) elevated SEEKING to a superordinate position above the other six primal affects.

> The SEEKING system appears to control appetitive activation—the search, foraging, and investigatory activities—that all animals must exhibit before they are in a position to emit consummatory behaviors (Panksepp 1998, p. 146)…. [M]any brain regions and neurochemical systems are interconnected with the SEEKING system, forming a complex web among coordinated neural networks, facilitating the integration of homeostatic, sensory, autonomic, and learning processes to yield a *coordinated affective presence* that in classical behaviorist terminology has been called an approach motivation system (Panksepp and Wright 2012, p. 11, italics added).

In my view, theory integration can proceed best if we stick to the most general, valid concepts of motivation and cognition. Concepts of approach and avoidance motives are the most important general concepts for describing, predicting, and controlling both cognition and overt behavior. "Basic affects" are not exactly instincts, sensations, motivations, cognitions, or feelings. Rather, they involve movements of the facial muscles and they emanate from the "deeply subcortical [brain]" (Panksepp and Wright 2012, Fig. 26.1). Beyond that, what are they? What is a "coordinated affective presence"? How can any theory without concepts of cognition advance our ability to understand the person? I cannot imagine how any number of affects (or instincts) alone could work singly or in every conceivable combination to produce science or art. Rather, an enormous number of semantic concepts must be differentiated and integrated to produce meaning in the life of the individual and of cultures.

26.8 The Meaning of Concepts

The semantic differential of Osgood et al. (1957) indicates that the meaning of all words (semantic concepts) can be understood generally as having three dimensions: evaluation (good–bad), potency (strong–weak), and activity (mobile–immobile). These are the things one wants to know about sense data representing objects in the world and the mind: (1) Is it good or bad? that is, "Can it cause me pleasure or pain? (2) Is it strong or weak? or, "Can it overpower me?" (3) Can it move? In other words, "Can I escape it if necessary"? Osgood was trying to understanding "the meaning of meaning" at a general level of abstraction. This question has continued to generate interest among social scientists (e.g., Heise 2010).

Decisions to think or act can be made by combining evaluations of objects on "meaning dimensions." Compared to using only one aspect of meaning, use of three aspects should increase the accuracy of expectations of the relative amount of pain or pleasure likely to result from approaching, avoiding, or freezing in response to physical and mental objects (concepts). That is, prediction errors are reduced when more valid predictors are added to the equation.

Now, instincts are based on the *face validity* of the interpretation of the meaning of sensory arrays. *Fixed action patterns* are *released* if objects registered by exteroceptors match some hardwired standard for action such as the shadow of a predator (e.g., Tinbergen 1951). By trial and error, evolution has determined the selective advantages of particular responses to stressors and hardwired them into the nervous system. The important point for us is that the new, big neocortex of individuals alone and together (culture) has learned a few things too. And, in a pinch one wants reason and logic on their side in addition to instinct.

Instinctual decisions are made on the basis of *face validity* (e.g., That moving shadow above may indicate a predator. I better get undercover). But problems can occur if the simplification processes deprive the person of information that might help to define reality more exactly. From the neuroanatomical perspective, the neocortex might be able to learn the nature of one's situation using a deeper model of reality including multiple perspectives that were left out of subcortical decision processes. Taking the information "upstairs" allows the boss to more thoroughly contemplate the situation. *The neocortical executive* has, most often, many degrees of decisional freedom.

26.9 Self-Concepts and Mental Control

Focus on the surface of the self, like focus on the surface of physical objects in the external world leads initially to evaluations of "goodness" and "badness." One tends to avoid self-focus after failure and seek it after meeting or exceeding self-ideals (Wicklund 1975). Since by definition, most people hold self-ideals that are consistent with the normative ideals of their culture, initial reactions to self-focus do not reveal much about a person's uniqueness. Rather, *objective self-awareness theory* (Duval and Wicklund 1972) concerns primarily the sort of self-consciousness associated with things that give most people in any particular culture feelings of shame and pride.

After initial evaluation of items in focal awareness, thinking about concepts one knows a great deal about, such as oneself, is different from other types of thinking. This is because single concepts in expert systems are nodes in relatively large networks. The person is connected to his own brain by billions of neurons. Infants have few semantic concepts and no "expert conceptual systems." Such systems develop with learning. Likewise, an adult who knows nothing of geology, for example, has no system of concepts about rocks. But when a learned geologist sees a bit of granite rock, or the word "granite," thresholds to activate neurons that encode concepts related to "granite" are lowered. This is the process of *spreading activation* discovered in semantic priming experiments by cognitive psychologists (e.g., Collins and Loftus 1975; Anderson 1983; Najmi and Wegner 2008). The psychoanalytic idea of *free association* describes the subjective correlates of *unconstrained spreading activation* of neurons encoding concepts that are in some type of meaningful relationships.

The processes in brain and mind that regulate tendencies to approach pleasure can be differentiated from pain avoidance tendencies (e.g., Miller 1944; Dollard and Miller 1941). In the body, brain, and mind, the sympathetic system drives attempts to achieve more and less urgently needed states (e.g., comfort, warmth, orgasm) and materials (e.g., oxygen, food, water). The myelinated parts of the parasympathetic system and neocortical processing of semantic concepts are involved in dynamic, sophisticated decisions regarding control of appetitive sympathetic tendencies.

Using the myelinated vagus as a "hard, chronic brake" means it cannot realize its functional potential to dynamically control sympathetic arousal. Brain–mind competence is limited by strong mental habits to operate the brake in a crude manner. Freud (1923) assumed that a chronically anxious person is engaged constantly in conscious and unconscious, exhausting efforts to control himself. He wants to approach people, places, ideas, and things that he expects will bring him pleasure. Pathological anxiety usually includes implicit and explicit assumptions that obtaining desired pleasures is sure to cause terrible pain or punishment.

An individual's concepts about reality will conform largely to the normative beliefs of the culture the person lived in during youth. Enormous efforts are made by society and parents to "train" individuals to live in social groups. Each infant is born a wild animal. Social authorities instill strong expectations of pain in most citizens should they perform overtly illegal, or immoral behaviors. But most individuals police themselves. "Bad thoughts" can generate guilt and anxiety and, in turn, inhibit "bad behavior" (e.g., Bernstein 1984). Of course, social agents also *incentivize* individuals by means of anticipated pleasures. There are the rewards of status and money for those who have learned to sublimate or co-opt instinctive drives into economically useful personal and social habits.

26.10 Normal, Very Competent, and Very Incompetent Stress Management

Repeated, automatic, and intentional attempts to resolve problems are a feature of normal brain and mind operations. Most people use at least *trial and error methods* to find an effective solution to problems (Thorndike 1913). Some search in a more programmatic way, guided by previously learned, more or less valid self- and nonself-concepts. One way or another, a majority of people are successful enough at stress control (i.e., conflict resolution) to avoid constant anxiety. But repetitive attempts to apply a futile method to reduce stressful problems are pathological (cf. Freud 1920 on *The Repetition Compulsion*).

So, we could say that the competence of the person is a function of at least two general factors: The validity of the concepts used to contain and explain sensory data and other concepts; and, the competence of decisions about when to activate particular concepts (Bernstein 2011). *Concept activation* here is more or less equivalent to the control of attentional focus.

It is important to differentiate the meaning of the terms *stress* and *anxiety*. *Anxiety* is the result of unresolved *stress*. *Anxiety* can operate to motivate instrumental stress reduction processes. And, at high, chronic levels anxiety may be a psychopathology that works to inhibit competent responding to stressors. This sort of idea has been more or less implicit in a wide range of social, psychological, and biological theories. Most generally, one must measure stress separately from anxiety. *Stress* might be quantified in the cybernetic sense as "size of discrepancy from standards." *Anxiety* is a concern about one's ability to resolve stress. It can cause a sense of urgency that may be useful, or a detriment to the person's ability to think.

The mental control methods of those with *anxiety disorders* must have been effective at reducing anxiety at some point in their history. Hence, the habits would have been *reinforced strongly* and become *dominant habits of thought* (e.g., Hull 1943; Spence 1956). For example, the thinking of all very young children is characterized by a tendency that Freud named *the omnipotence of thought* (1913). That is, infants (and most adults to a degree) overvalue the concepts of things compared to their reality. This results in a form of incompetent thinking due to both lack of education and the motive to push anxiety out of awareness. But it is reinforcing to make such an assumption because, especially in childhood, it is quite effective at reducing anxiety. Accordingly, "wishful thinking" is *reinforced* strongly in youth.

Better habits of thought (i.e., "the better defenses") such as *humor and* subclinical *obsessional and compulsive habits of mind* can promote anxiety control with minimal distortion of reality It helps to not be too gloomy and to be somewhat organized. *Sublimation* involves learning to channel energy from ones foundational self-conflicts into creative work in art, science, business, and all other social activities. *Sublimation* was Freud's attempt to describe the best one could do in response to reality.

"Bad defenses" like *psychotic dissociation* and *paranoia* represent last-ditch strategies to not know something. Persistent, definable, and unresolved conflicts are the source of the worst mental pain and suffering. Such defenses must operate in close cooperation with truth-seeking mechanisms. A system can only defend against knowing something specific if, at some level of mind, it already "knows what not to know."

We all distort reality a bit to avoid anxiety, and we are usually able to get away with it. The ability to execute all cognitive operations, including *defense mechanisms* depends, in part, on different states of the ANS. The ANS determines conditions affecting neocortical competence to regulate stress and, thereby, anxiety and other feelings. Competent anxiety control effected by neocortical information processes depends on an ability to use "good" rather than "bad" conceptual defenses. Decisions to activate concepts are affected by the heart, lungs, brain stem, hypothalamic-pituitary axis (HPA), limbic system, and neocortical information processing.

Helping people to learn habits to activate concepts that are more valid than older invalid, ineffective concepts is the purpose of psychotherapy. Fruitless, repetitive information processing drains energy and gives rise to frustration, aggression, and anxiety. At a certain point, the person gives up the active, repetitive defense against anxiety and becomes depressed (e.g., Seligman 1975). This is due, in part, to sympathetic exhaustion, which involves a drop in levels of sympathomimetic hormones (e.g., glucocorticoids, epinephrine) and adrenergic neurotransmitters (norepinephrine, dopamine). Then, *protein transcription mechanisms* direct increased production of postsynaptic adrenergic receptor sites to catch the increasingly scarce stimulating molecules. This phenomenon, *disuse hypersensitivity* (e.g., Ghose 1975), is part of a complex of causal variables that can result in depression. And, there can be further regression to bipolar illness and psychosis (e.g., Bernstein 2012).

The sympathetic system responds urgently to sensations indicating wants and needs. It activates fast, fixed, reflex-like responses when dangers (e.g., predators) and pleasures (e.g., sex partners) are close in time and space. The newer, myelinated parasympathetic vagal nerves help regulate sympathetic arousal and its correlated subjective sense of urgency.

The *parasympathetic brake* can be applied dynamically, on and off, with varying intensity within the time it takes the heart to beat once (about one second). Roughly speaking, thoughts and feelings can and do change at similar rates (milliseconds to seconds). A high RSA range is caused by signals carried by vagal efferents emanating from the *NA* in the brain stem. Such signals ideally work to increase *parasympathic tone* which, in turn, can increase the person's ability to reflect upon the costs and benefits of decisions made in the brain stem, aided by logic and concepts developed over life.

A dynamically changing heart, sensitive to respiratory processes, increases the brain's agility to activate concepts associated with many different memories and feelings. *High parasympathetic tone* is associated with a calm feeling and curiosity. This promotes consideration of the validity of multiple concepts to explain the meaning of raw sensory data. *High parasympathetic tone* is operationalized as *a wide range of RSA*. Compared to low RSA range, high RSA range indicates that more dynamic changes in the frequency and force of attempts to modify sympathetic arousal are occurring. The key point is that one somehow has the ability to vary the signal rates by means of a more or less intelligent decision-making process. This ability must reside in the neocortex which is elaborately interconnected with subcortical areas by the myelinated white matter sitting between them anatomically.

The ANS can initiate reflexive, instinctive stress responses that *have survival value*. The most primitive response to stress is *immobilization* or *freezing*. This action works, in part, by increasing the difficulty of detection by predators. It is harder to notice an unmoving lizard or opossum in the reeds than a frenetic creature, noisily running for its life. Early in the development of the individual's brain and mind, instinctive decisions about external objects are always based on *face validity*. This is because infants, animals, and people with forms of *autism* have few or no concepts in mind to augment subcortical decisions about the meaning of sensory data, made on the basis of only the exteroceptively sensed attributes of objects. That is, the attributes on the surface of objects.

With development of the neocortex, semantic concepts work to make decisions that can inhibit

Table 26.1 Body-Mind States typical of sympathetic arousal and parasympathetic tone. (This table is from Bernstein (2014). Printed with Permission)

		SYMPATHETIC AROUSAL		
		Low	***Average***	***High***
PARASYMPATHETIC TONE (DYNAMIC BRAKING)	***Low***	**(1)** Vegetative Depression Anhedonia, Hypersomnia, Cognitive & Somatoform Illness	**(2)** Anxious, OCD, Depression Boredom, Panic, Insomnia Cognitive & Somatoform Illness	**(3)** Severe Anxiety, PTSD Bipolar Mania, Psychosis Cognitive & Somatoform Illness
	Average	**(4)** Dysthymia	**(5)** *Statistically Normal*	**(6)** Euthymia
	High	**(7)** Calm, Reserved Disinhibits Cardiac Pacemaker (Wise Old Person)	**(8)** Cognitively & Socially Engaged Successful at Work & Love (Manager/Good Citizen)	**(9)** Competent in Emergencies Agile Response to Stress (Leader/Hero)
Old Vagus (IMMOBILIZATION)	***On-Off***	*Functional:* Playing Dead (e.g., opossum); Metabolic Slowdown in drowned infant *Dysfunctional*: Fatal Parasympathetic Rebound/Bradycardia; Psychotic Catatonia		

or promote overt enactment of instinctual tendencies. People with functional mental illnesses resemble infants, animals, and autists in their incompetence to make and use valid semantic concepts to control body and mind.

26.11 Immobilization

The bottom of Table 26.1 indicates that immobilization reflexes are controlled by the phylogentically older, unmyelinated vagus nerves. As noted above, feigning death may work to increase an animal's chance of survival (e.g., the opossum's prototypical response to threat). The reptilian ability to "shut down" somatic activity is sometimes activated in young infants or children who have drowned, especially in cold water (e.g., Modell et al. 2004). Remarkably, they can be often rescued after 30 min underwater with no brain damage. This is because the immobilization process works to lower metabolic rates and, hence, reduces the brain's usual large demand for oxygen. So, a "freezing" or "shutting down instinct," controlled by neuronal switches, has various functional uses.

But *immobilization* can have pathological and fatal consequences. For example, heart and respiration rates slow markedly after chronic sympathetic arousal are reduced abruptly. This is called *parasympathetic rebound* and it is a normal physiological response to high stress. But if stress has been unremitting for a long period, the rebound can be so great as to cause death. This is *fatal parasympathetic rebound,* observed first by Brady (1958) in *Executive Monkeys* coping with stress. Other dysfunctional results of immobilization include the frozen, catatonic postures assumed by psychotics to ward off ideas emerging from the unconscious.

Decisions to perform instinctive actions such as *immobilization* are "all on or all off decisions." As far as I know, affect theorists assume that something less than complete enactments of more than one *basic affect* can be added together to generate the entire range of human behavior. But when instincts or affects are executing their *primary function,* for example, as a defense against threat, initiation decisions have a *primary process,* zero-sum nature. In contrast, the newer, smart vagus from the *NA* produces signals ranging from low to high ranges of intensity within the time of a heartbeat.

26.12 Parasympathetic Tone and Sympathetic Arousal

Table 26.1 identifies *nine body–mind states* that tend to occur with particular combinations of *sympathetic arousal* and *parasympathetic tone levels.* These are not entirely distinct entities but have connections at various levels of analysis. On the surface, they are recognizable things (*face validity).* They also have some *discriminant validity.* For example, people in some of the conditions can be treated effectively with drugs that do not work for people in other conditions; and, prognoses differ between conditions. The conditions also have *predictive validity*. When we account for the attributes of a particular condition, we can predict with some accuracy what will happen next. These nine categories might be called "clusters of biological and psychological variables"; "prototype states"; or, "illustrative mind–body conditions." In any case, my descriptions of them are based on five starting assumptions:

1. The states can occur if no unadulterated reflex, such as *immobilization,* has been initiated and is controlling the organism.
2. Effective stress regulation depends on the alignment between the more or less competent subsystems including heart and lungs, ANS, brain stem, limbic system, hypothalamic-pituitary axis, and neocortex.
3. Following Porges (2011), I assume that *low levels of RSA range* indicate poor dynamic control (e.g., unresponsive, or ineffectively responsive to information); and, that *high RSA range levels* indicate high competence to respond to changing information about stressors.
4. The *NA,* a brain stem nexus for afferent and efferent myelinated vagal nerves, can exchange information with neocortical conceptual areas.
5. Theoretically, any combinations of sympathetic arousal and parasympathetic tone can exist. In practice, certain combinations are more likely than others.

The *horizontal axis* of Table 26.1 depicts a continuous range of low to high sympathetic arousal. In an oversimplification of sorts, I assume that sympathetic arousal increases in a simple linear fashion, analogous to how fuel is delivered into a car engine by pressing on the accelerator. The *vertical axis* arranges parasympathetic tone from low to high. Range in RSA is an operational measure of parasympathetic tone. A high RSA range indicates the person is capable of inducing a wide range of rates and intensities of heart action within seconds. Low RSA range indicates that rates and intensities are constrained within a narrow, relatively unchanging range.

Combinations of different levels of *parasympathetic tone* and *sympathetic arousal* work, in part, to produce "body–brain–mind states" ranging from pathological to highly competent. If heart and lungs are regulated too rigidly (*low RSA range*), it is hard to think and behave in a sophisticated manner. This is especially so in real and imagined emergencies when sympathetic arousal tends to be high.

Mind–brain and visceral elements are in bidirectional, causal relationships. Calm thoughts can relax the body. And, a body at ease is a comfort to the mind. Ideally, the integrated operating system works to confer knowledge and good feelings to the person, and *evolutionary advantages* to their species. The individual's body, brain, mind, and social world are "all in it together." But *decisional authority* is not distributed equally throughout the body or the social environment. In the newborn mammal, few decisions are made in neocortical areas. With development, the system of concepts about the self and external reality, stored in the neocortex, may become "authorized" to decide how to resolve the person's conflicts.

Many, if not all of the patients I have seen in psychotherapy doubt their own authority to override decisions made by some part of their body, mind, or other people. Most people find it difficult to do anything, including thinking, at *low levels of sympathetic arousal*. Performance on increasingly complex mental tasks improves at moderate or *average levels of sympathetic arousal*; and performance starts to decline at *high sympathetic arousal levels*. But Yerkes-Dodson is only statistically valid. Not all individuals perform worse on complex tasks under high arousal.

For example, more than a few people perform extremely well in emergencies.

26.13 High Competence and Peak Experience

People with *high parasympathetic tone* have somehow learned to regulate heart rate variability (HRV), respiration, and the cognitive operations that depend on well-timed, effective control of *sympathetic arousal*. *Condition 9* (Table 26.1) is a state of *highly responsive parasympathetic braking and high sympathetic arousal*. A racecar driver in such a state, for example, could likely drive very fast on a torturous road and win the race without being injured. They have the energy, and can quickly gather sensory data to make good decisions constantly about their direction (steering) and speed (acceleration and braking).

Decisions about "Where you are going" and "When and how hard to brake" can be made on the basis of instinct and/or learned semantic concepts. To drive safely and fast on a dangerous road depends on the information processing competence of the brain–mind system. The driver must sense quickly (and constantly) distances between objects, and the directions and speeds of objects. Then, he must use concepts to interpret the meaning of the data. Specifically, he needs ideas that have implications for predicting the likely amounts, and kinds of pains and pleasures one might incur if approaching or avoiding a particular point in time and space.

What the driver really needs is a cognitive system that functions as decisively as the old instinctive one; but that has more potential for accurate prediction and control. Of course, if conscious intentional decision-making processes produce responses that are not better than hardwired instincts, why bother thinking? The chief value of neocortical operations involving processing of semantic concepts is not speed. Rather, thinking increases the range of response options beyond those offered by fast, instinctive, subcortical processes. If a person assumes categorically that security and achievement motives are in zero-sum relationships, he or she could only *increase speed or increase control*. Success in love and work involves making good decisions regarding avoidance of injury and approach of pleasure.

Csikzentmihalyi (1990) described *flow states* in which thinking and moving are performed in uniquely competent and pleasurable ways. I assume that such states are related to having fast access to the most valid concepts of nature; and, that access to valid concepts and the ability to use them gets faster as the conceptual system itself becomes more meaningfully organized (Bernstein 2011, Chap. 11). Competent use of concepts is *intrinsically motivating,* I think in the sense that Deci meant (e.g., Deci 1971).

The task of seamlessly integrating instinctive somatic reflexes with inferential decision making to create a *state of flow* is similar or the same as what happens in *Condition 9*. The highly aroused person under threat from a lion is able to differentiate thinking from acting. They can assess relevant self-attributes (e.g., strength, speed, past experience) and situational variables (e.g., lion's strength, speed, and the distance to a protected place). This information leads to consideration of decisional options, and predictions of each option's chance of success. Then, the best option is chosen and enacted.

One needs durable, strong habits of mind to maintain *parasympathetic tone* when under threat. This is because *high sympathetic arousal* works to potentiate instinctive immobilization, flight, or fight behavior. The arousal of such tendencies occurs in mind too. Thinking is usually strongly influenced by the emergency signals coming from subcortical regions of the brain. The instincts have proven useful over evolutionary history. But *fixed action patterns* cannot account for any idiosyncratic aspects of one's current emergency. This is when one needs active concept using and creating neocortical responses.

Ideally, the special competencies of the sympathetically aroused mind and body can be controlled by operations involving the myelinated vagus from the *nucleus ambiguous*. High parasympathetic tone, produced in large part by the right sort of breathing and heart rate variability, promotes the creation and use in the neocortex of valid concepts to interpret the causes of stress.

Sensation of threatening or attractive objects in the world or the brain–mind release adrenergic hormones (e.g., epinephrine) and neurotransmitters (e.g., norepinephrine, dopamine). These chemicals speed reaction time, increase visual acuity, muscular strength, and endurance. *Endogenous opiates* are also released under stress and raise pain thresholds. The combination of adrenergic stimulants and opiates is highly pleasurable and enhances the pleasures of thinking about objects compared to merely sensing them (e.g., Biederman and Vessel 2006).

26.14 Better Than Well

People with high parasympathetic control will experience chronic or more changeable levels of sympathetic arousal. *Condition 7* involves high parasympathetic tone and low levels of sympathetic arousal. As people age, adrenergic hormones and neurotransmitter levels tend to fall and with them, energy levels. But, if the person is not suffering from some dementias or other brain damage, the lessons learned about parasympathetic braking remain functional. Older, otherwise intact people can ideally use energy very efficiently and effectively. The intrinsic rate of the cardiac pacemaker, unrestricted by parasympathetic braking, is very fast. It makes sense then for everyone, especially older or sick people with low energy to "coast downhill," using as little vagal braking as needed to optimize energy usage.

Because everyone loses energy with advancing age, I use adrenergic stimulants in older patients as a cognitive enhancer and antidepressant (e.g., Methylphenidate). In about half of these patients executive functioning, mood, and energy are markedly improved (see Amen 2008). Most of the other patients have no clear positive reaction, and a small proportion can regress into psychotic states. I assume that the good responders have *high parasympathetic tone.* They have learned and can activate valid semantic concepts that explain something about the causes or meaning of visceral sense data. These are "wise old people" who can be considered "better than well." Poor responders have habits to use less valid ideas to explain reality, and impoverished social relationships. This is consistent with Porges' assumption that *high parasympathetic tone* potentiates overt "social engagement" behavior.

But I want to emphasize the *cognitive causes and effects* of *parasympathetic tone*. Poor responders become less competent when the press of *sympathetic arousal* increases. The neurology of activating semantic concepts is not so different from moving a muscle. *Dominant habits* of thought, helpful or harmful, increase more as sympathetic arousal increases than do tendencies to express weaker habits (e.g., Hull 1943; Spence 1956). So, if a person has strong habits to do stupid things, giving them adrenergic stimulants can work to degrade, rather than enhance cognitive and social functioning.

Another type of "better than well" person has *high parasympathetic tone* and *average sympathetic arousal levels (Condition 8)*. They tend to be successful socially and at work because they have above-average habits to use valid concepts. But their energy or drive is not outstanding. Incentives for pursuing very high aspirations are mediocre. Biologically speaking, endogenous levels of adrenergic neurotransmitters, especially dopamine, are statistically average. Attempts to perform complex conceptual tasks are driven and controlled by the pleasures underwritten by dopamine and opiates (see Biederman and Vessel 2006). Without above-average levels of circulating sympathomimetic molecules, one is unlikely to experience, and subsequently anticipate, feeling the most sublime pleasures from resolving complex conceptual and social tasks.

Accordingly, someone in *Condition 8* is more likely to pursue and be successful in situations calling for using specific, detailed concepts concerning the salient costs and benefits of social transactions. Transactional expertise works to maintain social stability. The motivation to stimulate and lead social, organizational, and conceptual change, and tolerate greater risk, is more characteristic of those in *Condition 9*. Compared to managers, entrepreneurial leaders are more incentivized to resolve complex conceptual and social conflicts and take more risks (Stewart and

Roth 2001). This is consistent with the idea that leadership is based on a capacity to have strong feelings and high aspirations, and an ability to communicate the concepts underlying their goals to followers (e.g., Freud 1921; Burns 1978).

26.15 Statistically Normal

By definition, most people, most of the time, have *average levels of sympathetic arousal and average levels of parasympathetic tone* (*Condition 5*). It is generally recognized that *parasympathetic tone* is a more important determinant of mental and physical health than *sympathetic arousal levels* (e.g., Harvey et al. 2010; Nugent et al. 2011). Because *parasympathetic tone* supports general health and durability, changes in sympathetic arousal occurring with average sympathetic tone, usually produces mental and physical states that are "within normal limits."

When average control combines with average sympathetic arousal, you get an average state of mind (*Condition 5*). *Average parasympathetic tone* with *low sympathetic arousal* may result in dysthymia, a gloomy feeling that falls short of full-blown clinical depression *(Condition 4)***.** When a person with average autonomic, conceptual, and social competence is in a state of *high sympathetic arousal,* they will feel mostly positive, happy, or *euthymic (Condition 6)*. This sort of "normal happiness" can edge into a more intense happy feeling or *hypomania***.** The assumption that most people like to feel jolly and competent to cope with life is consistent with the increasing, widespread usage of sympathomimetic psychostimulants (e.g., Smith and Farrah 2011; Swanson et al. 2011) and glutamate agonists like modafinil.

26.16 Psychopathology

In medical terms, a *functional psychopathology* is one without apparent organic or structural cause. But we know that every mental event occurs because something has happened in the brain. The brain is an organic entity and it has physical structure. A person experiences some of the activity of their brain consciously, but most of it never enters awareness.

Six valid disease concepts can be used to describe most functional psychopathology: *anxiety, cognitive, somatoform, depression, bipolar, and psychotic* (Bernstein 2011, 2012, 2014). Each of the six can be recognized by words used in everyday speech *(face validity).* We can specify predisposing conditions and "likely course" in each case *(predictive validity)*. And, characteristic changes in metabolic processing rates in different parts of the brain are associated with each disorder. Also, different neurotransmitter systems are implicated in each syndrome *(discriminant validity).*

Each of the six can be characterized, in part, by specific of biological processes and by dominant habits used by the person to interpret reality. That is, they have characteristic somatic, conceptual, and feeling attributes. For example, anxiety is associated with magnified estimates of danger, increased basal ganglion blood flow, and low parasympathetic tone (Porges 2011). Depression is associated with guilt feelings (Freud 1923), changes in the hippocampus (Massey and Bashir 2007), and in neurotransmitter receptor systems (e.g., Boyle et al. 2004). I use the term functional to describe symptoms of psychopathology that are the most potentially reversible by learning. They are problems caused mostly by software that might be rewritten. Software problems are different in degree from damages to the macro-anatomical structures of the brain. Hardware problems can be due to flawed interconnectivity of neurons as seen in mental retardation, schizophrenia, or autism; and, by injuries or diseases like stroke, cancer, and Alzheimer's dementia.

A person can compensate for hardware defects by writing new software. For example, after a stroke that disables certain functions such as movement of an arm, patients can learn to use brain regions unaffected by the stroke to regain lost function (e.g., Krakauer 2005). Software change involves micro-anatomical change, such as the up and down regulation of the postsynaptic receptors for particular neurotransmitters (e.g., Gonzales-Forero 2004). Such processes are best altered when psychotropic drugs are combined with habit-altering training.

> Antidepressant drugs and psychotherapy combined are more effective in treating mood disorders than either treatment alone…. Combining extinction training with chronic fluoxetine, but neither treatment alone, induced an enduring loss of conditioned fear memory in adult animals. Fluoxetine treatment increased synaptic plasticity, converted the fear memory circuitry to a more immature state, and acted through local brain-derived neurotrophic factor. Fluoxetine-induced plasticity may allow fear erasure by extinction-guided remodeling of the memory circuitry (Karpova et al. 2011, p. 1731).

In behaviorist terms, learning involves changes in *habit hierarchies* (e.g., Hull 1943; Spence 1956). That is, "What are the person's *dominant habits* to use particular concepts to interpret the meaning of sense data?" And, "What less dominant habits, involving activation of better explanations for things, might exist, unused in mind?" Both normal development and change aided by psychotherapy involve increasing the strength of more effective habits so they become *dominant habits*.

Most generally, patients should have access to information about bodily conditions (e.g., bio- or neurofeedback), as they are exploring their subjective experience of mind with a therapist. This makes treating mental problems less of a hit or miss affair. Taking into account contemporaneous events in body, brain and mind allows clinicians and patients to more complete understand and resolve conflicts. Ideally, clinicians should use talk combined with biofeedback (e.g., Porges 2011), neurofeedback (e.g., Thomas 2012), and drugs that increase neural plasticity. The availability of computers in cell phones will make data about the conditions of the body (e.g. RSA) available to everyone.

26.17 Executive Function

The term *executive functions* describes processes involving decision making, attentional control, management of items in memory, planning and other things. The ability to regulate attention is the apex of human information processing competence. Attentional control is at the end of a causal chain of innumerable biological, psychological, and social developmental variables (c.f., Banich 2009).

A very small number of young children may have so called "attention deficits" due to delays in neocortical development. *But the most important cause of attentional dysregulation in both children and adults is anxiety*. Ignorance of this has caused useless debates about whether adults can have *attention deficit disorder* and whether they should be treated with stimulants. Anxiety in children and adults can be treated with tranquillizers and/or stimulants. Stimulants include adrenergic reuptake inhibitors (e.g., amphetamines). Glutamate agonists are not sympathomimetic but are stimulatory and can increase alertness.

A central assumption I am making is that the *validity of the concept used to contain and explain a sensation or other concepts determines the intensity of pleasure.* Pains in body and mind might increase in the short run when explained with valid causes. But soon afterwards, anxiety, guilt and somatic pain usually decrease when interpreted correctly (cf. Bion 1962).

Sympathetic arousal levels are correlated with stress. Unresolved stress leads to *anxiety*. Statistically, the ability to think competently is related to anxiety in a curvilinear manner (Yerkes-Dodson Law). The most common psychopathologies involve the deleterious effects of anxiety on cognition. Cognitive incompetence is a cause and an effect of inability to tell the difference between feelings of pain stemming from damage to the tissues of the body, and pain stemming from unpleasant thoughts. This leads to *somatoform disorders* like *hypochondria* and *pain syndromes* such as *fibromyalgia.* In such cases there is usually no gross tissue damage in the body (See, Sarno 1991).

The brain's capacity for pleasure is so great that nature and societies have to have means of regulating the drive to approach pleasure. In mental illness, pleasure is often regulated with pain. It is not an accident that guilt about masturbation is universal, at least at early stages of development. Feeling guilty or ashamed are cognitive correlates of parasympathetic braking (e.g., Schore 2003; Siegel 2012). Freud understood brilliantly the relations between cognition, feeling, and self-regulation: "Masturbation represents the executive agency to the whole of infantile sexuality and is, therefore, able to take over the sense of guilt attaching to it" (Freud 1905, p. 189).

26.18 Cognitive and Somatoform Disorders

I include both *cognitive and somatoform* disorders in each of the three *low parasympathetic tone situations* in Table 26.1 *(Conditions1, 2, and 3)*. This is because being able to differentiate sensations, concepts, and feelings that originate in the external world from those arising in the body and the mind are fundamental mental competencies. Incompetence at making these distinctions underlies serious psychopathology, and represents perhaps the most frustrating, important barrier to the individual's successfulness at love and work. Studies of *misattribution of arousal* of the causes of one's subjective experience are very good, operational examples of this problem.

The negative effect of *low parasympathetic tone* on cognitive competence occurs at all levels of *sympathetic arousal*. But the degree of arousal influences the nature of the negative effects. Table 26.1 illustrates how variations in *sympathetic arousal* operate to produce different symptoms when *parasympathetic control is low* (*Conditions 1, 2, and 3*).

In *Condition 1,* there is *low parasympathetic tone* and *low sympathetic arousal*. This state is unlike *Condition 7* where we have assumed that the person can make efficient and effective use of low energy. This could be made possible by means of timely, smart control of the intrinsically energetic sinoatrial cardiac pacemaker. In contrast, *Condition 1* involves poor control of low energy. People in this state have *vegetative depressions* with symptoms of sadness, anhedonia, hypersomnia, low energy and weight gain or loss. Vegetative symptoms usually develop after a period of chronic unresolved stress and anxiety. Chronic, unresolved stress causes sympathomimetic, adrenergic neurotransmitters to fall to low levels.

The result is low energy, depressed mood, and declines in *executive functioning* including dysregulation of attentional focus and memory retrieval processes. *Anhedonia*, the inability to enjoy the appetitive, gustatory pleasures of life, often occurs in *Condition 1***.** Most importantly, *anhedonia* involves a loss of mental competence and, in turn, a reduction in the felt pleasures of thinking. Patients with these symptoms usually do best when given stimulating drugs that increase levels of dopamine and norepinephrine in the synapse. These include bupropion, atomoxetine, and amphetamines. Also, glutamate agonists such as Modofinil can be helpful.

Condition 2 represents *low parasympathetic tone* plus *average sympathetic arousal*. This is a more aroused state than *Condition 1*. But control systems are no better. Defenses against poorly regulated stress and anxiety involve energetic obsessions and compulsions, boredom and insomnia. These conditions are often helped by serotonin reuptake inhibitors. Adrenergic stimulants can be added to improve cognition and mood; and gamma-aminobutyric acid (GABA) modifiers, such as like benzodiazepines (and alcohol) reduce felt anxiety.

Condition 3 includes the most severe psychopathologies. A *system with high, poorly controlled energy is in a most vulnerable state.* Overall, mood regulation is poor and feelings can go from very elated to very depressed. These shifts may be more or less rapid. The person may be so afraid of being in this condition that they regress to using primitive defenses including psychotic delusions, especially paranoid delusions. Paranoia is a particularly useful operation for a very aroused person needing to get some control. This is because the task of cognition is greatly simplified by the paranoid assumption that a single malevolent force is the cause of everything. This sort of belief can "glue the mind together," albeit at the cost of being able to know reality and function effectively in the world.

26.19 Misattribution of Sympathetic Arousal

One phenomenon that occurs in all psychopathology, with somewhat different features, is *misattribution of sympathetic arousal.* The psychopharmacology of parasympathetic tone is not too well understood. Maybe the neuropeptides are most important, but cholinergic agents, especially muscarinic agonists, might have beneficial effects (e.g., Olshansky et al. 2008). The best treatments for a person in *Condition 1, 2, or 3* are those that promote learning how to regulate cognitions, especially pain attributions.

Misattribution of arousal was studied first by Schachter and Singer (1962). Their *two-part theory of emotion* was that "having an emotion" depended on two variables: sympathetic arousal and an explanation or attribution about the cause of the arousal. I use the term *feeling* for what they call emotion. Schachter and Singer (1962); Dutton and Aron (1974); Zillmann (1983), and many others have confirmed that a *feeling* results when one uses a concept to interpret the meaning or the cause of a sensation in the body. This is also a psychoanalytic assumption (e.g., Brenner 2006; p. 24). The concepts a person uses can be manipulated in a laboratory, and they are influenced by parents, teachers, politicians, doctors, salesmen, friends, lovers, characters in books, actors on stage and screen, and just about everyone else.

Somatoform disorders represent, in part, conceptual incompetence involving attributions of pain. Pain can come from damaged tissue in the body and from thoughts and memories. Somatoform patients largely discount unpleasant thoughts themselves as causes of pain. MRI and other imagining techniques find tissue injury in these patients that is more or less normal for their age. For example, everyone develops some degree of "spinal degeneration" with aging. But the usual aches and pains of aging seem particularly severe in *fibromyalgia* patients. These patients, who almost always have histories of sexual or other serious trauma in childhood, tend to attribute all their pain to damage in the back or neck.

Most *somatoform illnesses* present first at middle age when adrenergic potency starts to drop. Common symptoms include back and neck pain, social avoidance, sleep problems, and depression. For example, I treated a man with chronic headaches, neck, and back pain. He sought medical treatments including opiates, surgeries, and physical therapies. It is not that he had no damage to his head and neck tissues. But the physical therapies were never quite effective. Analysis revealed that he had various mental habits and memories of trauma that evoked mental pains including anxiety and sadness. I made a concentrated effort to have him always consider mental causes and physical causes of pain. This reduced the subjective sense of the severity of head and backaches, and he was able to discontinue his use of opiates (see Pennebaker 1989).

In attribution terms, when two possible causes for an effect are considered (e.g., tissue damage and psychic pain), the person *discounts* the size or importance of any single cause (Kelly 1967). Merely considering that remembered or new thoughts can cause mental pain can work to reduce somatic pain. This is consistent with a central assumption in my work: Learning and using multiple valid *semantic concepts* to explain *sensations* increases control of *feelings, other concepts,* and *overt muscular behavior*.

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Index

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