

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

Mattie Tops, Caroline Schlinkert, Mandy Tjew-A-Sin,
Dalya Samur and Sander L. Koole

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.

M. Tops (✉) · C. Schlinkert · M. Tjew-A-Sin ·
D. Samur · S. L. Koole
Department of Clinical Psychology,
VU University Amsterdam, van der Boechorststraat 1,
1081, Amsterdam, The Netherlands
e-mail: m.tops@vu.nl

C. Schlinkert
e-mail: c.schlinkert@vu.nl

M. Tjew-A-Sin
e-mail: m.m.tjew-a-sin@vu.nl

D. Samur
e-mail: d.samur@vu.nl

S. L. Koole
e-mail: s.l.koole@vu.nl

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

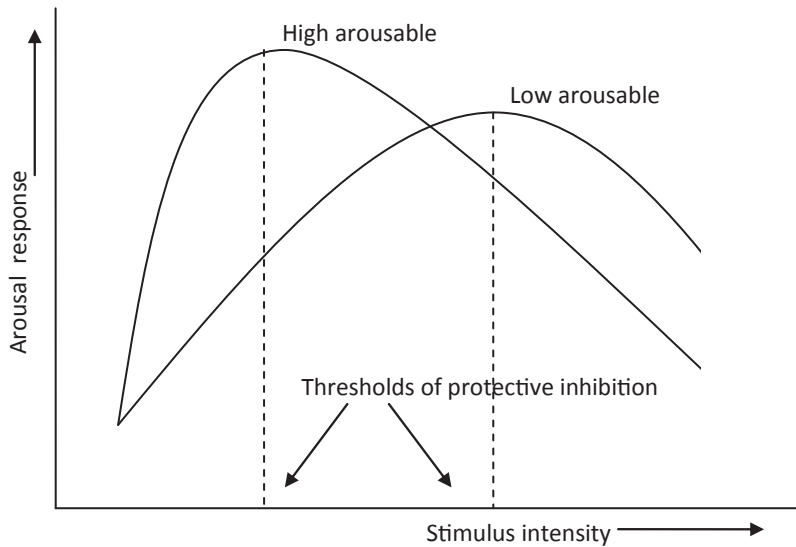


Fig. 6.1 Theoretical curves illustrating results from the protective inhibition (PI) paradigm. In the PI paradigm, participants were exposed to a succession of discrete stimuli increasing in intensity. Initially, arousal responses increased as stimulus intensity increased; however,

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.

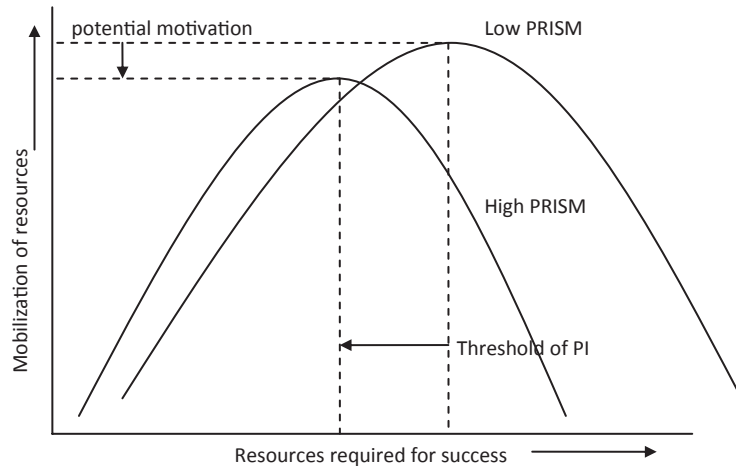
For this reason, and because reactive control reduces predictive homeostatic regulation of the internal milieu, such cognitive control requires the momentary tracking of physiological costs and resources and is experienced as effortful (Tops et al. 2013). The experience of effort is hence an adaptive 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



High control	— Threat to control	— Uncontrollability
High (or low) demands/high resources (e.g., self-esteem)	— High demands/less resources	— High demands/low resources
Social inclusion	— Threat of exclusion	— Social exclusion/rejection

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 (Frieze 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 activa-

tion 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., Wardeenaar 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.

Acknowledgments This research was supported by a Veni grant of the Netherlands Organization for Scientific Research (NWO) (451-07-013) awarded to Mattie Tops, a Mosaic grant of the NWO awarded to Mandy Tjew-A-Sin (017-009-120), and a Consolidator Grant of the European Research Council (ERC-2011-StG_20101124) awarded to Sander Koole.

References

- Ackerman, P. L. (1987). Individual differences in skill learning: An integration of psychometric and information processing perspectives. *Psychological Bulletin*, *102*, 3–27. doi:10.1037/0033-2909.102.1.3.
- Allport, L. E., Butcher, K. S., Baird, T. A., MacGregor, I., Desmond, P. M., Tress, B. M., et al. (2004). Insular cortical ischemia is independently associated with acute stress hyperglycemia. *Stroke*, *33*, 1886–1891. doi:10.1161/01.STR.0000133687.33868.71.
- Arnsten, A. F. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Review Neuroscience*, *10*(6), 410–422. doi:10.1038/nrn2648.
- Baumeister, R. F., Bratslavsky, E., Muraven, M., & Tice, D. M. (1998). Ego depletion: Is the active self a limited resource? *Journal of Personality and Social Psychology*, *74*, 1252–1265. doi:10.1037/0022-3514.74.5.1252.
- Bentson, G. G., Boysen, S. T., & Cacioppo, J. T. (1992). Cardiac orienting and defensive responses: Potential origins in autonomic space. In B. A. Campbell, H. Hayne, & R. Richardson (Eds.), *Attention and information processing in infants and adults: Perspectives from human and animal research* (pp. 163–200). Hillsdale: Lawrence Erlbaum.

- Boksem, M. A. S., & Tops, M. (2008). Mental fatigue: Costs and benefits. *Brain Research Reviews*, *59*, 125–139. doi:10.1016/j.brainresrev.2008.07.001.
- Booij, S. H., Bouma, E. M., de Jonge, P., Ormel, J., & Oldehinkel, A. J. (2013). Chronicity of depressive problems and the cortisol response to psychosocial stress in adolescents: The TRAILS study. *Psychoneuroendocrinology*, *38*(5), 659–666. doi:10.1016/j.psyneuen.2012.08.004.
- Brehm, J. W., & Self, E. A. (1989). The intensity of motivation. *Annual Review of Psychology*, *40*, 109–131. doi:10.1146/annurev.ps.40.020189.000545.
- Cardoso, C., Ellenbogen, M. A., Serravalle, L., & Linnen, A. M. (2013). Stress-induced negative mood moderates the relation between oxytocin administration and trust: Evidence for the tend-and-befriend response to stress? *Psychoneuroendocrinology*, *38*(11), 2800–2804. doi:10.1016/j.psyneuen.2013.05.006.
- Carmichael, S. T., & Price, J. L. (1995). Sensory and premotor connections of the orbital and medial prefrontal cortex of macaque monkeys. *Journal of Computational Neurology*, *363*, 642–664. doi:10.1002/cne.903630409.
- Chiao, J. Y., Harada, T., Oby, E. R., Li, Z., Parrish, T., & Bridge, D. J. (2009). Neural representations of social status hierarchy in human inferior parietal cortex. *Neuropsychologia*, *47*(2), 354–363. doi:10.1016/j.neuropsychologia.2008.09.023.
- Chida, Y., & Steptoe, A. (2009). Cortisol awakening response and psychosocial factors: A systematic review and meta-analysis. *Biological Psychology*, *80*(3), 265–278. doi:10.1016/j.biopsycho.2008.10.004.
- Coan, J. A., Schaefer, H. S., & Davidson, R. J. (2006). Lending a hand: Social regulation of the neural response to threat. *Psychological Science*, *17*, 1032–1039. doi:10.1111/j.1467-9280.2006.01832.x.
- Craig, A. D. (2003). Interoception: The sense of the physiological condition of the body. *Current Opinion in Neurobiology*, *13*, 500–505. doi:10.1016/S0959-4388(03)00090-4.
- Craig, A. D. (2008). Interoception and emotion: A neuroanatomical perspective. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.), *Handbook of emotions* (3rd ed., pp. 272–288). New York: Guilford.
- Craig, A. D. (2009). How do you feel—now? The anterior insula and human awareness. *Nature Neuroscience*, *10*, 59–70. doi:10.1038/nrn2555.
- Craig, A. D. (2013). An interoceptive neuroanatomical perspective on feelings, energy, and effort. *Behavioral and Brain Sciences*, *36*(6), 685–686; discussion 707–726. doi:10.1017/S0140525x13001489.
- Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, *7*, 189–195. doi:10.1038/nn1176.
- Damasio, A. (1999). *The feeling of what happens*. New York: Harcourt Brace.
- de Graaf, J. B., Gallea, C., Pailhous, J., Anton, J.-L., Roth, M., & Bonnard, M. (2004). Awareness of muscular force during movement production: An fMRI study. *NeuroImage*, *21*, 1357–1367. doi:10.1016/j.neuroimage.2003.11.009.
- de Rover, M., Brown, S. B., Boot, N., Hajcak, G., van Noorden, M. S., van der Wee, N. J., et al. (2012). Beta receptor-mediated modulation of the late positive potential in humans. *Psychopharmacology*, *219*(4), 971–979. doi:10.1007/s00213-011-2426-x.
- DeWall, C. N., & Baumeister, R. F. (2006). Alone but feeling no pain: Effects of social exclusion on physical pain tolerance and pain threshold, affective forecasting, and interpersonal empathy. *Journal of Personality and Social Psychology*, *91*(1), 1–15. doi:10.1037/0022-3514.91.1.1.
- DeWall, C. N., Twenge, J. M., Koole, S. L., Baumeister, R. F., Marquez, A., & Reid, M. W. (2011). Automatic emotion regulation after social exclusion: Tuning to positivity. *Emotion*, *11*, 623–636. doi:10.1037/a0023534.
- Eckert, M. A., Menon, V., Walczak, A., Ahlstrom, J., Denslow, S., Horwitz, A., et al. (2009). At the heart of the ventral attention system: The right anterior insula. *Human Brain Mapping*, *30*(8), 2530–2541. doi:10.1002/hbm.20688.
- Engel, G. L., & Schmale, A. H. (1972). *Conservation withdrawal: a primary regulatory process for organic homeostasis*. In Ciba Foundation Symposium 8: Physiology, emotions and psychosomatic illness (pp. 57–95). New York: Elsevier.
- Engert, V., Efanov, S. I., Dedovic, K., Duchesne, A., Dagher, A., & Pruessner, J. C. (2010). Perceived early-life maternal care and the cortisol response to repeated psychosocial stress. *Journal of Psychiatry and Neuroscience*, *35*(6), 370–377. doi:10.1503/jpn.100022.
- Eysenck, H. J. (1970). *The structure of human personality* (3rd ed.). London: Methuen.
- Fisk, A. D., & Schneider, W. (1983). Category and word search: Generalizing search principles to complex processing. *Journal of Experimental Psychology: Learning Memory Cognition*, *9*, 177–195. doi:10.1037/0278-7393.9.2.177.
- Friese, M., Binder, J., Luechinger, R., Boesiger, P., & Rasch, B. (2013). Suppressing emotions impairs subsequent stroop performance and reduces prefrontal brain activation. *PLoS One*, *8*(4), e60385. doi:10.1371/journal.pone.0060385.
- Gendolla, G. H. E., & Wright, R. A. (2009). Effort. In D. Sander & K. R. Scherer (Eds.), *The Oxford companion to emotion and the affective sciences* (pp. 134–135). New York: Oxford University Press.
- Grant, A. M., & Schwartz, B. (2011). Too much of a good thing: The challenge and opportunity of the inverted U. *Perspectives on Psychological Science*, *6*(1), 61–76. doi:10.1177/1745691610393523.
- Hagger, M. S., Wood, C., Stiff, C., & Chatzisarantis, N. L. (2010). Ego depletion and the strength model of self-control: A meta-analysis. *Psychological Bulletin*, *136*(4), 495–525. doi:10.1037/a0019486.
- Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experi-*

- mental Psychology General*, 108, 356–388. doi:10.1037/0096-3445.108.3.356.
- Hedborg, K., Anderberg, U. M., & Muhr, C. (2011). Stress in migraine: Personality-dependent vulnerability, life events, and gender are of significance. *Upsala Journal of Medical Sciences*, 116(3), 187–199. doi:10.3109/03009734.2011.573883.
- Herbert, B. M., Ulbrich, P., & Chandry, R. (2007). Interoceptive sensitivity and physical effort: Implications for the self-control of physical load in everyday life. *Psychophysiology*, 44(2), 194–202. doi:10.1111/j.1469-8986.2007.00493.x.
- Hilty, L., Jäncke, L., Luechinger, R., Boutellier, U., & Lutz, K. (2011). Limitation of physical performance in a muscle fatiguing handgrip exercise is mediated by thalamo-insular activity. *Human Brain Mapping*, 32(12), 2151–2160. doi:10.1002/hbm.21177.
- Inzlicht, M., & Schmeichel, B. J. (2012). What is ego depletion? Toward a mechanistic revision of the resource model of self-control. *Perspectives in Psychological Science*, 7, 450–463. doi:10.1177/1745691612454134.
- Jansma, J. M., Ramsey, N. F., de Zwart, J. A., van Gelderen, P., & Duyn, J. H. (2007). fMRI study of effort and information processing in a working memory task. *Human Brain Mapping*, 28(5), 431–440. doi:10.1002/hbm.20297.
- Koole, S. L., Tops, M., Strübin, S., Bouw, J., Schneider, I. K., & Jostmann, N. B. (2014). The Ego Fixation hypothesis: Involuntary persistence of self-control. In J. P. Forgas & E. Harmon-Jones (Eds.), *The control within: Motivation and its regulation* (pp. 95–112). New York: Psychology.
- Landys, M. M., Ramenofsky, M., & Wingfield, J. C. (2006). Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *General and Comparative Endocrinology*, 148, 132–149. doi:10.1016/j.ygcen.2006.02.013.
- Leary, M. R., Haupt, A. L., Strausser, K. S., & Chokel, J. T. (1998). Calibrating the sociometer: The relationship between interpersonal appraisals and state self-esteem. *Journal of Personality and Social Psychology*, 74, 1290–1299. doi:10.1037/0022-3514.74.5.1290.
- Levin, M. (1953). Aggression, guilt and cataplexy. *A.M.A. Archives of Neurology and Psychiatry*, 69, 224–235. doi:10.1001/archneurpsyc.1953.02320260082006.
- Levin, M. (1961). Sleep, cataplexy, and fatigue as manifestations of Pavlovian inhibition. *American Journal of Psychotherapy*, 15, 122–137.
- Light, S. N., Heller, A. S., Johnstone, T., Kolden, G. G., Peterson, M. J., Kalin, N. H., et al. (2011). Reduced right ventrolateral prefrontal cortex activity while inhibiting positive affect is associated with improvement in hedonic capacity after 8 weeks of antidepressant treatment in major depressive disorder. *Biological Psychiatry*, 70(10), 962–968. doi:10.1016/j.biopsych.2011.06.031.
- MacKinnon, D. P., Krull, J. L., & Lockwood, C. M. (2000). Equivalence of the mediation, confounding and suppression effect. *Prevention Science*, 1, 173–181. doi:10.1023/A:1026595011371.
- Maltzman, I., & Raskin, D. C. (1965). Effects of individual differences in the orienting reflex on conditioning and complex processes. *Journal of Experimental Research in Personality*, 1(1), 1–16.
- Maresh, E. L., Beckes, L., & Coan, J. A. (2013). The social regulation of threat-related attentional disengagement in highly anxious individuals. *Frontiers in Human Neuroscience*, 7, 515. doi:10.3389/fnhum.2013.00515.
- Marsh, A. A., Blair, K. S., Jones, M. M., Soliman, N., & Blair, R. J. (2009). Dominance and submission: The ventrolateral prefrontal cortex and responses to status cues. *Journal of Cognitive Neuroscience*, 21(4), 713–724. doi:10.1162/jocn.2009.21052.
- Mehrabian, A. (1995). Theory and evidence bearing on a scale of trait arousability. *Current Psychology*, 14(1), 3–28. doi:10.1007/BF02686870.
- Moore-Ede, M. C. (1986). Physiology of the circadian timing system: predictive versus reactive homeostasis. *American Journal of Physiology*, 250(5 Pt 2), R737–R752.
- Morgan, W. P. (1994). Psychological components of effort sense. *Medicine and Science in Sports and Exercise*, 26(9), 1071–1077.
- Morris, W. N. (1999). The mood system. In D. Kahneman, E. Diener, & N. Schwarz (Eds.), *Well-being: The foundations of hedonic psychology* (pp. 169–189). New York: Russell Sage.
- Nebylitsyn, V. D. (1972). *Fundamental properties of the human nervous system*. New York: Plenum.
- Nebylitsyn, V. D., & Gray, J. A. (Eds.). (1972). *Biological bases of individual behavior*. New York: Academic.
- Oswald, I. (1962). *Sleeping and waking: Physiology and psychology*. Amsterdam: Elsevier.
- Otto, T., Zijlstra, F. R., & Goebel, R. (2014). Neural correlates of mental effort evaluation—involvement of structures related to self-awareness. *Social Cognitive and Affective Neuroscience*, in press. doi:10.1093/scan/nss136.
- Paulus, M. P., & Stein, M. B. (2006). An insular view of anxiety. *Biological Psychiatry*, 60(4), 383–387. doi:10.1016/j.biopsych.2006.03.042.
- Pavlov, I. P. (1955). *Selected works*. Translated by S. Belsky. Moscow: Foreign Languages Publishing House.
- Romero, L. M., Dickens, M. J., & Cyr, N. E. (2009). The Reactive Scope Model—a new model integrating homeostasis, allostasis, and stress. *Hormones and Behavior*, 55(3), 375–389. doi:10.1016/j.yhbeh.2008.12.009.
- Sacks, O. W. (1985). *Migraine*. Berkeley and Los Angeles, CA: University of California Press, first published in 1970, revised in 1985.
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, 308(5722), 648–652. doi:10.1126/science.1106477.
- Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and

- preparative actions. *Endocrine Reviews*, 21(1), 55–89. doi:10.1210/er.21.1.55.
- Seery, M. D., Leo, R. J., Lupien, S. P., Kondrak, C. L., & Almonte, J. L. (2013). An upside to adversity?: Moderate cumulative lifetime adversity is associated with resilient responses in the face of controlled stressors. *Psychological Science*, 24(7), 1181–1189. doi:10.1177/0956797612469210.
- Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychological Review*, 84, 127–190. doi:10.1037/0033-295X.84.2.127.
- Sokolov, E. N. (1960). Neuronal models and the orienting reflex. In M. A. B. Brazier (Ed.), *The central nervous system and behavior* (pp. 187–276). New York: Josiah Macy Jr. Foundation.
- Sokolov, E. N. (1963). *Perception and the conditioned reflex*. New York: Macmillan.
- Spitz, R. A., Emde, R. N., & Metcalf, D. R. (1970). Further prototypes of ego formation: A working paper from a research project on early development. *Psychoanalytic Study of the Child*, 25, 417–441.
- Tennes, K., Emde, R., Kisley, A., & Metcalf, D. (1972). The stimulus barrier in early infancy: An exploration of some of the formulations of John Benjamin. In R. Holt & E. Peterfreund (Eds.), *Psychoanalysis and contemporary science* (pp. 206–234). New York: MacMillan.
- Thayer, R. E. (1989). *The biopsychology of mood and arousal*. New York: Oxford.
- Tops, M., & Boksem, M. A. S. (2008). Cortisol, energy mobilization and chronic fatigue. *Neuropraxis*, 12(4), 126–132. doi:10.1007/BF03077133.
- Tops, M., & Boksem, M. A. S. (2012). “What’s that?” “What went wrong?” Positive and negative surprise and the rostral-ventral to caudal-dorsal functional gradient in the brain. *Frontiers in Psychology*, 3(21), 1–5. doi:10.3389/fpsyg.2012.00021.
- Tops, M., Boksem, M. A. S., Wester, A. E., Lorist, M. M., & Meijman, T. F. (2006). Task engagement and the relationships between the error-related negativity, agreeableness, behavioral shame proneness and cortisol. *Psychoneuroendocrinology*, 31(7), 847–858. doi:10.1016/j.psyneuen.2006.04.001.
- Tops, M., Riese, H., Oldehinkel, A. J., Rijdsdijk, F. V., & Ormel, J. (2008). Rejection sensitivity relates to hypocortisolism and depressed mood state in young women. *Psychoneuroendocrinology*, 33, 551–559. doi:10.1016/j.psyneuen.2008.01.011.
- Tops, M., Russo, S., Boksem, M. A., & Tucker, D. M. (2009). Serotonin: Modulator of a drive to withdraw. *Brain and Cognition*, 71, 427–436. doi:10.1016/j.bandc.2009.03.009.
- Tops, M., Boksem, M. A. S., & Koole, S. L. (2013). Subjective effort derives from a neurological monitor of performance costs and physiological resources. *Behavioral and Brain Sciences*, 36(6), 703–704. doi:10.1016/j.pbb.2013.07.015.
- Tops, M., Huffmeijer, R., Linting, M., Grewen, K. M., Light, K. C., Koole, S. L., et al. (2013). The role of oxytocin in familiarization-habituation responses to social novelty. *Frontiers in Psychology*, 4, 761. doi:10.3389/fpsyg.2013.00761.
- Tucker, D. M., Luu, P., Frishkoff, G., Quiring, J., & Poulsen, C. (2003). Frontolimbic response to negative feedback in clinical depression. *Journal of Abnormal Psychology*, 112(4), 667–678. doi:10.1037/0021-843X.112.4.667.
- Twenge, J. M., Catanese, K. R., & Baumeister, R. F. (2003). Social exclusion and the deconstructed state: Time perception, meaninglessness, lethargy, lack of emotion, and self-awareness. *Journal of Personality and Social Psychology*, 85(3), 409–423. doi:10.1037/0022-3514.85.3.409.
- Veen, G., van Vliet, I. M., DeRijk, R. H., Giltay, E. J., van Pelt, J., & Zitman, F. G. (2011). Basal cortisol levels in relation to dimensions and DSM-IV categories of depression and anxiety. *Psychiatry Research*, 185(1–2), 121–128. doi:10.1016/j.psychres.2009.07.013.
- Wardenaar, K. J., Vreeburg, S. A., van Veen, T., Giltay, E. J., Veen, G., Penninx, B. W., et al. (2011). Dimensions of depression and anxiety and the hypothalamo-pituitary-adrenal axis. *Biological Psychiatry*, 69(4), 366–373. doi:10.1016/j.biopsych.2010.09.005.
- Waters, E., Matas, L., & Sroufe, L. A. (1975). Infants’ reactions to an approaching stranger: Description, validation, and functional significance of wariness. *Child Development*, 46(2), 348–356.
- Weik, U., Maroof, P., Zöller, C., & Deinzer, R. (2010). Pre-experience of social exclusion suppresses cortisol response to psychosocial stress in women but not in men. *Hormones and Behavior*, 58(5), 891–897. doi:10.1016/j.yhbeh.2010.08.018.
- Williamson, J. W., McColl, R., Mathews, D., Ginsburg, M., & Mitchell, J. H. (1999). Activation of the insular cortex is affected by the intensity of exercise. *Journal of Applied Physiology*, 87, 1213–1219.
- Williamson, J. W., McColl, R., & Mathews, D. (2003). Evidence for central command activation of the human insular cortex during exercise. *Journal of Applied Physiology*, 94, 1726–1734. doi:10.1152/jappphysiol.01152.2002.
- Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of Comparative Neurology and Psychology*, 18, 159–182. doi:10.1002/cne.920180503.
- Zuckerman, M. (1979). *Sensation seeking: Beyond the optimal level of arousal*. Hillsdale: Lawrence Erlbaum.