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Mindy F. Levin *Editor*

Progress in Motor Control

Skill Learning, Performance, Health, and Injury

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This volume is dedicated to Dr. John P. Scholz, (1950–2013), scholar, colleague, teacher, mentor and friend. Forever in our hearts.

Preface

This volume and all the previous volumes of the Progress in Motor Control series are united by a common theme: understanding the basic principles and mechanisms underlying the control and coordination of voluntary movement and relating these findings to gain insights into the impact of pathology and injury on the sensorimotor control system. This volume contains contributions by scientists invited to participate in the meeting of the Ninth Progress in Motor Control, held in Montreal, Quebec, Canada in July 2013. Progress in Motor Control international meetings are held bi-annually and are the official scientific meetings of the International Society of Motor Control (ISMC; www.i-s-m-c.org). At the 2013 meeting, there were 28 invited presentations organized into 6 symposia, and a special pre-Congress symposium on advances in cerebral palsy research organized by Annette Majnemer and Carol L. Richards. During the meeting, the Society bestowed its highest recognition, The Bernstein Award, to Dr. Gregory Orlovsky for his outstanding contribution to the understanding of the organization of posture and locomotion.

The mission of the ISMC and the Progress in Motor Control conference series is to promote basic and applied research that furthers our knowledge of the understanding of the control of movements in biological systems. An equally important goal of the Society is to promote knowledge transfer and exchange between basic and applied scientists, educators, and clinicians. Motor control scientists come from diverse backgrounds, including bioengineering, biomechanics, biophysics, genetics, kinesiology, neuropsychology, neuroscience, rehabilitation, speech and language, and sports sciences. A relatively new addition to this multidisciplinary field, represented in the current volume, is the area of the performing arts, including dance, music, and circus arts.

The current volume is divided into four parts. Part I, "Sensorimotor Integration" includes 6 chapters. Chapter 1 presents an integrated view of motor control based on referent variables organized into a hierarchical system. The view is supported by evidence of how multiple motor elements, such as segment positions and finger forces, produce feed-forward, anticipatory synergy adjustments. Chapter 2 continues on this theme and presents the notion of referent control, which describes how movement is produced due to the difference between the referent position of the body segments set by the nervous system and the actual position of the body segments due to its interaction with the physical environment. The concept is supported by empirical evidence of changes in corticospinal excitability during voluntary and involuntary movement. The concept is also extended to provide a new explanation of position sense that is not dependent on notions of 'sense of effort' or 'efference copy'. Chapter 3 describes some of the properties of a basic element of the sensorimotor system: motoneuronal firing behavior. This in-depth chapter describes persistent inward currents and their neuromodulatory systems that are matched to the basic motor behaviors of posture, voluntary movement, and locomotion. Chapter 4 continues on the theme of locomotion with a description of the regulation of limb stiffness during locomotor tasks. Using a decerebrated cat model, the authors extend their previous studies to show how pattern generation, endpoint stiffness, and proprioceptive feedback are modulated in a task-specific way during upslope and downslope walking. The role of the vestibular system and neck proprioceptors on the modulation of these properties is discussed to explain the regulation of whole-body locomotion. The role of sub-cortical systems in the control of voluntary limb movement in humans is further elaborated in Chap. 5. Using rapid unexpected target jumps during upper limb reaching movement and lower limb stepping, the authors show that corrective movements occur at very short latencies consistent with a sub-cortical visuomotor mechanism. Finally, Chap. 6 returns to the notion of perception discussed in Chap. 2. The authors propose a multisensory binding model of the perception of the location of body segments and question the role of motor simulation in this process.

Part II of the volume deals with the concept of variability in motor control. All three chapters in this part provide evidence to support the view that kinematic variability is not simply an undesirable manifestation of the noise within the system. On the contrary, they suggest that variability is a necessary and desirable consequence of purposeful control strategies. Chapter 7 is a review of the Uncontrolled Manifold Model (UCM), by two of its original formulators. The UCM enables researchers to classify the variability of a redundant number of kinematic degrees of freedom with respect to their contribution or non-contribution tothe motor goal, and provides a means by which motor equivalence and self-motion during movement can be interpreted. Chapter 8 presents a methodological approach to study complex skills that have extrinsic redundancy and dynamic characteristics. The authors provide examples of how humans find stable solutions to the redundancy problem so that movements are minimally affected by unexpected perturbations. The third chapter in this part, Chap. 9, also uses a computational approach to provide an explanation of how redundancy influences the structure and variability of repetitive movements, using goal equivalent manifolds. Based on this theoretical approach, the authors suggest that the nervous system uses a minimum intervention principle to produce movement that minimizes variables at the level of the task goal.

Part III includes three chapters on the performing arts devoted to dance (Chap. 10), music production (Chap. 11), and circus performance (Chap. 12). Chapter 10 extends the concept of action-perception via mirror neurons to action-observation learning of whole-body movements amongst professional dancers. Chapter 11 explores the highly specialized training of musicians in multi-sensory and emotional domains. Musician-specific injuries in the motor domain such as overuse injuries and dystonias, as well as those linked to psychological mechanisms are invoked as contributing to such injuries. This new classification, which takes into account both motor and psychological mechanisms may help define prevention and treatment interventions. Chapter 12, written by a professional artist and a medical doctor specializing in prevention and treatment of performance-related injuries, reviews the specific skills needed by highly specialized circus arts performers in an entirely new domain for the field of motor control and learning, thereby providing important insights into the care of these athletes.

Part IV of this volume includes three chapters about motor control approaches to the understanding of musculoskeletal and neurological injury and recovery. Chapter 13 reviews musculoskeletal disorders of the neck and shoulder region, especially those related to occupational injuries after fatigue. The concepts of variability and motor abundance are discussed as ways for the system to restore function in chronic musculoskeletal disorders. Chapter 14 presents evidence of disorders of motoneuronal threshold control, a concept based on the equilibrium-point theory of motor control, as a primary mechanism underlying disorders of movement in patients with acquired brain injury such as stroke. Evidence supporting the role of the corticospinal tract in modulated motoneuronal thresholds is discussed. This concept may provide a link between the observations of spasticity and disordered motor control that has important implications for rehabilitation. Finally, Chap. 15 discusses the sensorimotor contributions to balance and locomotor deficits in people with multiple sclerosis. The chapter presents novel methods for quantifying stability and adaptability of posture and gait and discusses how these methods may inform the development of new treatments for people with neurological dysfunction.

The chapters in this volume present state-of-the art methodologies and insights into motor control concepts that are essential for the understanding of skilled movement and motor learning in healthy individuals and in those with musculoskeletal and neurological deficits. The chapters are written for the informed reader who has some background in movement production, measurement methods, skilled performance and/or rehabilitation. The volume will be a valuable reference for students and professionals in both basic and applied areas of motor control such as neurophysiology, biophysics, biomechanics and bioengineering, neuropsychology, kinesiology, sports science, motor disorders, rehabilitation and the performing arts.

Montreal Mindy F. Levin

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Chapter 1
Motor Control: On the Way to Physics of Living Systems

Mark L. Latash

1.1 Motor Control as a Subfield of *Physics of Living Systems*

Two approaches to the problem of the neural control of movement have dominated the field recently. According to the first approach, the central nervous system (CNS) performs computations in an attempt to predict the complex interactions both within the body and between the body and the environment. Specific examples of such computations have been addressed as "internal models" (reviewed in Kawato 1999; Shadmehr and Wise 2005). The recent developments within the field of internal models have been based on classical studies in the control theory developed for inanimate objects directly applied to problems of motor control.

The alternative approach considers the CNS not as a computational system but as a physical one (reviewed in Kugler and Turvey 1987; Latash 2010, 2012). Under the word "physical," I imply the totality of mechanical, chemical, and physiological processes that obey laws of nature. Some of these laws may be unknown to us at this time, particularly those related to such notions as intentionality, specific for biological objects. While the established laws of physics of the inanimate nature are expressed using mathematical equations, the existence of these equations does not assume that planets, particles, neural structures, and other objects of study solve these equations or perform any related computations. For example, no physicist would assume that there is a structure on the Sun that computes all the forces that have to be applied to the planets and other celestial objects within the solar system. Such an assumption is, unfortunately, only all too common with respect to the brain: Within the computational approach, the neural controller is frequently assumed to solve mathematical equations. Within the physical approach, the term "neural controller" is used in a different meaning, to represent decision-making processes with currently unknown physics. *Physics of living systems* is a very poorly developed field

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of science. A major with this name was created in the Moscow Institute of Physics and Technology (MIPT), the *alma mater* of the author, over 50 years ago. This was, however, not a reflection of existence of this new subfield of physics, but rather a promise that this subfield would be developed in future. The purpose of this chapter is to try to persuade the reader that motor control may in fact be the most promising area of research of biological systems to make *physics of living systems* a reality.

Studies of voluntary movements are very attractive for a physicist. Humans and animals are usually very good at producing well-coordinated movements. One can set tasks relatively easily and record all the relevant mechanical variables relatively objectively (in comparison, for example, to studies of such brain functions as thoughts, emotions, memory, etc.). The mathematical apparatus of classical mechanics is also of a great help, although its application to biological objects is never easy. Most classical mechanical characteristics of moving objects (such as their mass-inertial characteristics, parameters that define their elastic and damping properties, etc.) change in the course of a movement. These characteristics also change in response to an externally applied perturbation making commonly used system identification techniques marginally useful. That is why, sometimes, I like to address the fields of motor control and biomechanics as "physics of unobservable objects."

1.2 Equilibrium-point Hypothesis and Control With Referent Configurations

Arguably, the first physical approach to the problems of motor control was introduced by another alumnus of *physics of living systems* in MIPT, Anatol Feldman (1966). He developed the equilibrium-point (EP) hypothesis that views the neural control of a muscle as a process of defining an input parameter, associated with the threshold (λ) for activation of the alpha-motoneuronal pool of that muscle (Feldman 1986). Further, the interaction of the muscle and all its reflex loops with the external load, results in reaching an EP of that whole system characterized by certain values of muscle length and force (and electrical activity, EMG). This simplified scheme is illustrated in Fig. 1.1.

Within this simple scheme, two kinds of movements are possible. First, a change in the external load (from L_1 to L_2 in Fig. 1.1a) leads to a change in the EP along the tonic stretch reflex characteristic. Such a movement may be called "involuntary" because no change in the parameter λ specified by the CNS is assumed to take place. Note that activation patterns of many neurons within the CNS change during involuntary movements due to the action of reflex loops; such movements are obviously associated with changes in muscle activation level and force. A voluntary movement happens when the parameter λ changes (from λ_1 to λ_2 in Fig. 1.1b). Mechanical effects of such a change in λ depend on the external load: In isometric conditions, a change in force takes place, while in isotonic conditions, the muscle moves (compare $EP_{2,1}$ and $EP_{2,2}$ in Fig. 1.1b).

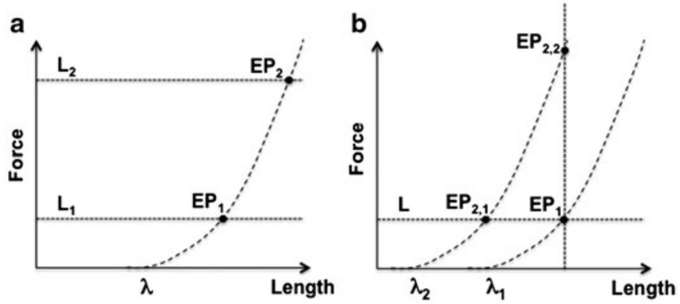

Fig. 1.1 An illustration of involuntary and voluntary movements within the equilibrium-point hypothesis. **a** A change in the external load from L_1 to L_2 leads to a shift in the equilibrium point (*EP*) of the system along the characteristic of the tonic stretch reflex shown by the *dashed line* from EP_1 to EP_2. This leads to a change in muscle length, muscle force, (and activation level, not illustrated). **b** A change in the threshold of the tonic stretch reflex (λ) from λ_1 to λ_2 may lead to different consequences depending on the external load. In isotonic condition, a movement takes place (EP_1 to $EP_{2,1}$), while in isometric conditions, muscle force increases (EP_1 to $EP_{2,2}$)

Generalization of the control with tonic stretch reflex thresholds to a two-muscle system acting at a joint was relatively straightforward (Feldman 1980; Feldman and Latash 1982). The development of the EP hypothesis to multi-muscle systems that participate in all natural movements resulted in the referent configuration (RC) hypothesis (Feldman and Levin 1995; Feldman 2009). According to this hypothesis, the controller specifies neural parameters (associated with subthreshold depolarization of neuronal pools) resulting in a referent body configuration defined as a configuration, at which all muscles show zero activation levels and are at their thresholds for activation via the tonic stretch reflex loops. Such configurations may be unattainable leading to nonzero muscle activations because of both anatomical and external factors. In addition, nonzero muscle activations at the RC may be due to a coactivation command (Feldman 1980, 1986). The notion of RC can be generalized to location of the body in the environment, as shown in studies of locomotion (Feldman et al. 2011).

Let me emphasize a couple of important features of the EP hypothesis that make it a truly physical hypothesis (these features are also parts of the RC hypothesis). First, it does not try to deduce properties of the whole system from properties of its elements such as individual neurons, peripheral receptors, and reflex loops. Instead, it considers motor behavior as an emergent result of interactions among all elements (muscle + receptors + feedback loops + neuronal machinery + external force field) affected by a single parameter (λ) generated by a hierarchically higher controller. Second, it appreciates that a controller dealing with a system evolving in time (a dynamic system) can only define parameters of this system but not its output variables. So, this approach refutes all control schemes based on prescribing time patterns of muscle forces or activation levels (cf. Gordon and Ghez 1987; Gottlieb et al. 1989; Scheidt and Ghez 2007; Shadmehr and Mussa-Ivaldi 1994).

1.3 Equifinality and its Violations: Mass–Spring Analogy and its Demise

One of the features of the original, simplified version of the EP hypothesis was its rather direct association with mass–spring models. The muscle seemed to be adequately represented as a nonlinear spring with modifiable zero length (reviewed in Feldman 1986). This analogy led to predictions of equifinality of movements in cases of unexpected transient perturbations acting in the course of a movement, if the subject of this experiment does not react to the perturbation. Indeed, a mass on a spring (with some kind of a dissipative element, a damper) is expected to come to an equilibrium, which depends only on parameters of this system and external force at the final state, but not on possible transient force changes. Phenomena of equifinality have indeed been reported in several studies with transient changes in the external forces (Bizzi et al. 1976; Kelso and Holt 1980; Schmidt and McGown 1980; Latash and Gottlieb 1990). However, violations of equifinality have also been reported giving rise to doubts about the EP hypothesis as a whole (Lackner and DiZio 1994; DiZio and Lackner 1995; Hinder and Milner 2003).

In particular, when a person sits in a chair aligned with the vertical axis of a rotating centrifuge, any arm movement is associated with the Coriolis force that acts only during the voluntary movement but not at the final steady state. Experiments in such conditions (performed in darkness to remembered visual targets) showed, however, reproducible deviations of the arm end-state coordinates from the target (Lackner and DiZio 1994; DiZio and Lackner 1995), that is, violations of equifinality. Another study used a torque motor to generate external torques proportional to the rotational velocity magnitude and acting to increase the velocity (Hinder and Milner 2003). In other words, the torque motor simulated motion in a medium with (physically impossible!) negative viscosity. In this experiment, the motor torque was applied during the movement but not when velocity became zero. After the subjects learned to move in such an unusual, destabilizing force field, the force field was turned off, and the subjects showed consistent undershoots of the target.

These observations have been discussed in detail within the framework of the EP hypothesis (Feldman and Latash 2005). In particular, it was necessary to dispel the simplified view on the EP control and refute the mass–spring analogy as too simple and leading to wrong expectations about the system's behavior. This analogy was used originally to illustrate the phenomenon of equifinality that could be expected within the EP hypothesis under certain, but not all, conditions. In particular, the EP hypothesis was sometimes viewed in an oversimplified way: The input into the motoneuronal pool was supposed to be defined exclusively by descending signals related to the task (Fig. 1.2a). There are other inputs that can change threshold of the tonic stretch reflex, in particular those originating from proprioceptors in other muscles. In addition, muscle spindle endings are sensitive not only to muscle length but also velocity, which makes λ dependent on actual movement velocity. There are also history effects on λ changes. So, descending signals define only a fraction of actual λ changes as reflected by the equation in Fig. 1.2b.

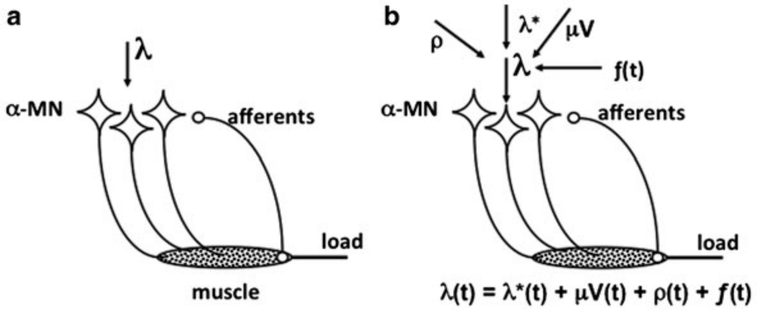

Fig. 1.2 In the simplified version of the equilibrium-point (*EP*) hypothesis (**a**), the input into a motoneuronal pool (λ) is defined exclusively by the brain. In a more recent version, this input depends on the contribution from the brain (λ^*) and also on other inputs such as those produced by sensory receptors in other muscles (ρ), related to velocity sensitivity of muscle spindle endings (μV), and history effects (*f(t))*

Note that these apparent complicating factors are not questioning the main principle of muscle control, although they potentially make movements not as accurate as they could otherwise be. Indeed the central input into the motoneuronal pool defines only a portion of signals leading to λ shifts and, as such, does not predetermine the motor outcome. Since other contributors to λ shifts may be not perfectly predictable, movements may be expected to show errors partly due to the varying contributions of the three additional terms in the right side of the equation in Fig. 1.2. This mode of control may be called "reasonably sloppy". It requires corrections based on sensory feedback signals as postulated by Bernstein (1967).

1.4 Redundancy and Abundance

At any level of analysis of the system for movement production, all natural movements involve more elements than necessary. In other words, the number of constraints associated with typical tasks is larger than the number of variables produced by the elements (elemental variables). This leads to one of the central problems of motor control, the problem of motor redundancy (Bernstein 1947, 1967): How does the CNS facilitate specific movement patterns from an infinite set? Examples of this problem are: (1) How to select joint rotations leading to desired coordinates of the endpoint in space? (2) How to select muscle forces leading to a desired resultant joint moment of force? (3) How to select digit forces leading to a desired resultant force applied to the hand-held object? (4) How to select a particular pattern of recruitment of alpha-motoneurons to match a desired level of muscle activation? and so on.

Most approaches to this problem have followed the tradition set by Bernstein that the main problem of motor control is that of elimination of redundant degrees of freedom (DOF; Bernstein 1967). In particular, optimization methods have been broadly used to find unique solutions for this problem (reviewed in Seif-Naraghi and Winters 1990; Prilutsky and Zatsiorsky 2002). Recently, the problem of motor redundancy has been revisited and reformulated as bliss of motor abundance (Gelfand and Latash 1998; Latash 2012). The principle of abundance states that the CNS uses all the available DOFs and arranges task-related stability properties in different directions within the redundant space of those elemental variables. The different stability properties are reflected in the structure of variance across repetitive trials (Scholz and Schöner 1999; Scholz et al. 2000; Latash et al. 2001) as well as in reactions to perturbations (Yang et al. 2007; Mattos et al. 2011, 2013).

The two approaches seem incompatible since the former generates a single solution while the latter generates families of solutions equally able to solve the task. Recently, a way to reconcile the two approaches has been suggested (Park et al. 2010). The principle of abundance generates families of solutions—clouds of data points at each phase of the action, while the centers of those clouds may be defined based on an optimization principle.

1.5 Synergies and the Uncontrolled Manifold Hypothesis

The term "synergy" has been used in the field of movement studies for at least 100 years (Hughlings Jackson 1899; Babinski 1899). Most commonly, this term implied something like "coordinated action of several elements" or "several elements that change their outputs in parallel" (Ivanenko et al. 2004, 2005; Ting and Macpherson 2005; Tresch et al. 2006). Recently, an explicit, operational definition for this term has been offered focused on stability of actions of redundant systems. Synergies have been defined as neural organizations that make across-trials variance within the space of elemental variables relatively small along directions that change task-related performance variables and relatively large along orthogonal directions (reviewed in Latash et al. 2007; Latash 2008). This definition is intimately linked to the principle of abundance because it assumes that the neural control of natural actions is associated with defining task-related stability properties in different directions within the space of the elemental variables.

The suggested definition also provides direct links between the notion of synergies and the concept of the uncontrolled manifold (UCM; Schöner 1995; Scholz and Schöner 1999). The UCM hypothesis assumes that variance is structured within the redundant space of elemental variables to provide desired stability properties of potentially important performance variables. For any performance variable, there is a subspace within which this variable does not change; this subspace is the UCM for that variable. If this performance variable is stabilized by covaried (across repetitive trials) adjustments of elemental variables, variance within the UCM (V_{UCM}) is expected to be larger than that orthogonal to the UCM (V_{ORT}), if both are quantified per dimension in the corresponding subspaces.

Clearly, the two notions, synergy and UCM, are intimately linked. Quantitative analysis of synergies has been developed using the framework of the UCM

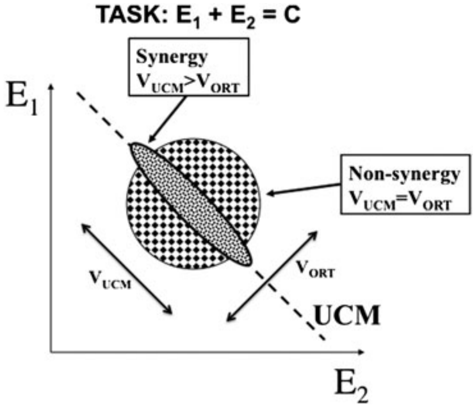

Fig. 1.3 An illustration of a task $E_1 + E_2 = C$. Two data distributions are illustrated. One of them is spherical and has about equal amounts of variance in the direction that does not affect $E_1 + E_2$ (UCM) and orthogonal to that direction. The second distribution is elongated along the UCM. Most of its variance has no effect on $E_1 + E_2$. Synergy is defined operationally as $V_{UCM} > V_{ORT}$

hypothesis. In particular, indices of synergy have been used reflecting the ratio of V_{UCM} to V_{ORT} and the normalized difference between V_{UCM} and V_{ORT} (ΔV). Figure 1.3 illustrates two data distributions for a task of producing a constant sum of two elemental variables, E_1 and E_2. One of the distributions is elongated along the UCM for the task-related variable (dashed, slanted line), and for this distribution $V_{UCM} > V_{ORT}$. This allows claiming that CNS actions organized variations in the E_1 and E_2 to stabilize their sum against spontaneous changes in the initial conditions associated with repetitive tasks. This is not the case for the spherical data distribution ($V_{UCM} = V_{ORT}$). Note that accuracy of performance is defined by V_{ORT} only; so, it is possible to perform accurately without a synergy (a tiny spherical cloud of data points, stereotypical performance) and to be sloppy with a synergy (a large data cloud elongated along the UCM).

The notions of synergies and UCM do not imply any computations within the CNS, although data distributions expected from the UCM hypothesis can be obtained using computational methods such as optimal feedback control (Todorov and Jordan 2002). Synergies and corresponding variance structure may be expected from purely physical/physiological mechanisms such as those offered in two recent schemes incorporating the idea of control with referent configurations and the idea of hierarchical control of natural actions (Martin et al. 2009; Latash 2010). One of these ideas explicitly assumes the existence of two types of parameters specified by the hypothetical controller (a neural structure with the currently unknown physics). One group of parameters defines target values (trajectories) of important, task-related performance variables. The other group defines stability properties of those variables. Two predictions follow from this general scheme. First, one can perform actions of different magnitude and direction using the same synergies (same ΔV indices). Second, one can change stability properties of an action without changing the value (pattern) of associated performance variable. While the first prediction is intuitively clear (e.g., Danna-dos-Santos et al. 2007), the second one is less obvious. It predicts the existence of previously unknown phenomena, anticipatory synergy adjustments (ASAs).

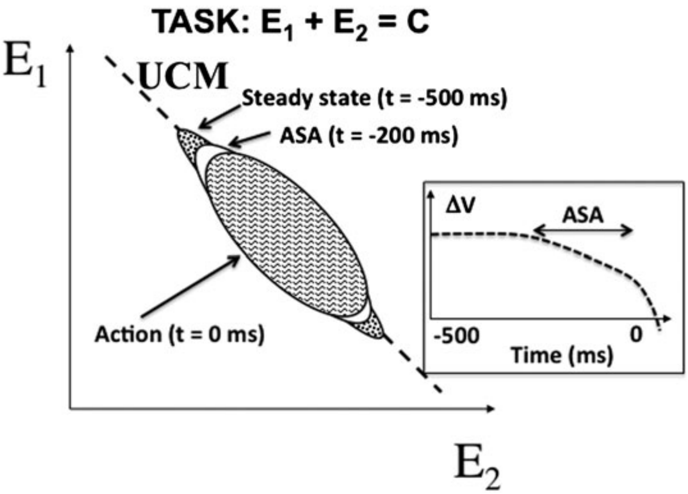

Fig. 1.4 An illustration of anticipatory synergy adjustment (*ASA*) for the task $E_1 + E_2 = C$. At steady state, most variance is along the UCM corresponding to a strong synergy stabilizing ($E_1 + E_2$). Prior to a self-paced quick change in ($E_1 + E_2$), V_{ORT} starts to increase, while V_{UCM} may show a parallel decrease. This process continues until movement initiation (time zero). The inset shows a change in the synergy index during this process

1.6 Feed-forward Control of Synergies: Anticipatory Synergy Adjustments

Stability of actions is one of the important features of motor control, particularly given the poorly predictable external conditions for most everyday movements and the continuously changing state of the body (for a critical review see Hasan 2005). However, there is a trade-off between stability and ability to change the action quickly. That is why, the ability of the CNS to modify stability of a performance variable without changing the action is important for preparation to a quick change in that variable when it becomes necessary. Consider a goalkeeper standing quietly in the goals while the ball is on the opposite half of the field. The goalkeeper's posture is stable and shows little sway. Now consider the same goalkeeper waiting for a penalty kick. Quite frequently, large body sway can be seen with the naked eye, increasing as the opponent runs towards the ball. An ability to adjust synergies in preparation to an action in an unknown direction has recently been documented (Zhou et al. 2013).

The phenomenon of ASAs represents attenuation of synergies stabilizing a performance variable when a change in that variable is planned. Figure 1.4 illustrates ASAs using the earlier example of the task $E_1 + E_2 = C$ (as in Fig. 1.3). If a quick change in C is planned, a gradual increase in V_{ORT} (sometimes associated with a drop in V_{UCM}) is seen during the steady-state C production, 200–300 ms prior to the actual change in C (Olafsdottir et al. 2005; Shim et al. 2005). Three ellipses of data distributions are shown in Fig. 1.4 illustrating the time development of ASAs. The changes in the two-variance components lead to a drop in the synergy index (ΔV, the inset in Fig. 1.4) documented in a variety of multi-finger pressing task, multi-digit prehensile tasks, and multi-muscle postural tasks (Shim et al. 2006; Klous et al. 2011; Zhou et al. 2013).

Other aspects of feed-forward control have been studied extensively, such as anticipatory postural adjustment (APAs, reviewed in Massion 1992) and grip force adjustments in preparation to changes in the load forces during prehensile tasks (Johansson and Westling 1988). Such populations as healthy elderly and patients with neurological disorders show an impaired ability to generate APAs and grip force adjustments (Woollacott and Manchester 1993; Novak et al. 2007; Muratori et al. 2008; Albert et al. 2010). The same groups of people show reduced and delayed ASAs (Olafsdottir et al. 2007; Park et al. 2012, 2013) suggesting that different aspects of feed-forward control may rely on similar neurophysiological mechanisms.

1.7 Synergies Within a Hierarchical Control Scheme

The idea of hierarchically organized control of movement is very old. Arguably, the first hierarchy considered in the field of movement studies was that of the brain (upper level) and the spinal cord (lower level). Note that the notion of hierarchical control does not refute exchange of information across the levels of the hierarchy in both directions. It implies, however, that higher levels are not as strongly driven by information from the lower levels. In terms of the RC hypothesis, one can claim that actual state of the system is driven by changes in the RC (and other factors such as external forces) while RC may also not be 100 % immune to effects from changes in the actual state of the system. Such effects have been modeled as back coupling within a recent theoretical scheme developed by Schöner and his colleagues (Martin et al. 2009).

While RC was originally defined as the body configuration when all muscles are at their thresholds for activation, it has also been long accepted that the neural controller does not micromanage at the individual muscle level (“the brain knows nothing about muscles, it knows only movements,” Hughlings Jackson 1899) but likely unites muscles into relatively stable groups (addressed as “modes” or “synergies,”d’Avella et al. 2003; Krishnamoorthy et al. 2003; Ivanenko et al. 2005; Ting and Macpherson 2005). Such stable groups may reflect certain RC combinations that are used as the basis for creation of more specific, task-related RC shifts. At the level of joint mechanics, basic RCs may be reflected in sets of eigenmovements introduced for whole-body actions (Alexandrov et al. 2001).

The scheme uniting the ideas of hierarchical control, control with RCs, and synergies has been proposed recently (Latash 2010). Within this scheme, at the higher level of the hierarchy, only a handful of task-related variables define the top RC. Further, a chain of few-to-many transformations leads to RCs at lower, effector-specific levels (e.g., limb-specific, digit-specific, joint-specific, and muscle-specific). Each of the transformations is organized in a synergic way, that is, it leads to variable RCs

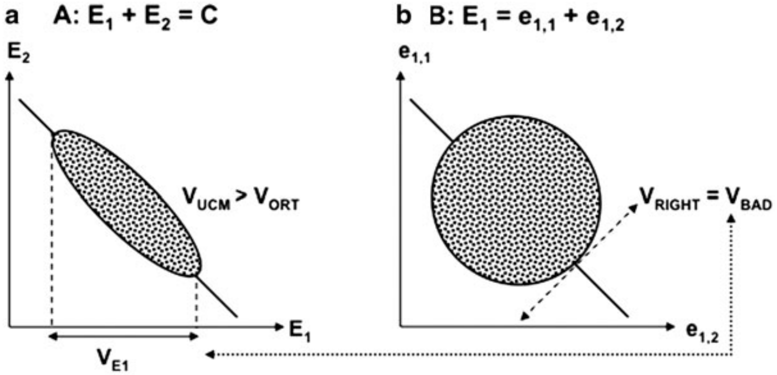

Fig. 1.5 An illustration of a trade-off between two levels of a hypothetical hierarchy. In the task $E_1 + E_2 = C$ (**a**), each E variable is produced by two contributors, for example $E_1 = e_{1,1} + e_{1,2}$ (**b**). There is a synergy stabilizing ($E_1 + E_2$) ($V_{\mathrm{UCM}} > V_{\mathrm{ORT}}$). Variance of each element is defined by V_{UCM}: $V_{\mathrm{E1}} = V_{\mathrm{UCM}} \bullet \cos(45°)$. At the lower level (**b**) V_{E1} defines V_{ORT}. So, high V_{UCM} in panel A is beneficial for a synergy at that level, but it produces high V_{ORT} at the lower level, which hurts synergies

at the lower level compatible with stable RC at the higher level. This scheme results in a few nontrivial, testable predictions. For example, it predicts a trade-off between synergies at different levels of the hierarchy (Gorniak et al. 2007; Latash et al. 2010).

Indeed, consider Fig. 1.5 illustrating a task similar to the one described earlier ($E_1 + E_2 = C$; see Fig. 1.3) but assuming that each E variable is produced by two contributors, for example $E_1 = e_{1,1} + e_{1,2}$. Assume also that, at the upper level of this hypothetical hierarchy, there is a synergy reflected in covariation between E_1 and E_2 reducing variance of ($E_1 + E_2$) ($V_{\mathrm{UCM}} > V_{\mathrm{ORT}}$, Fig. 1.5a). The ellipse of data points in Fig. 1.5a can be projected on the two E-axes, and the length of each projection is going to be defined by the long axis of the ellipse (for example, $V_{\mathrm{E1}} = V_{\mathrm{UCM}} \bullet \cos(45°)$). Now let us turn to the two contributors to E_1, $e_{1,1}$ and $e_{1,2}$. In that space, V_{E1} defines V_{ORT}. The comparison of the two panels suggests that high V_{UCM} at the upper level of the hierarchy is beneficial for a synergy at that level, but it produces high V_{ORT} at the lower level, which hurts synergies. It is possible to have synergies at both levels as demonstrated by studies of static prehension; however, only some of the performance variables show synergies at both levels, while others fail to do so (Gorniak et al. 2009).

In addition, the scheme suggests that transient perturbations applied to such a system may not change the top level RCs resulting in equifinality of the action (assuming that the subject is not reacting to the perturbation) while intermediate RCs may show variations compatible with the top RC (violations of equifinality at the level of elements). These predictions have been tested in a few recent experiments including the study of arm–trunk coordination during reaching (Ma and Feldman 1995).

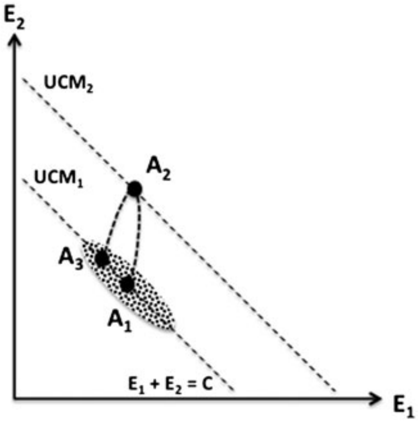

Fig. 1.6 A perturbation applied during the task $E_1 + E_2 = C$ is likely to show a large deviation of the system along the UCM because of the lower stability in that direction (A_1 to A_2). After the perturbation is removed, the system returns to a different point A_3 on the UCM for the task. There is equifinality with respect to the task-related variable ($E_1 + E_2$) but not at the level of elements

1.8 Equifinality in a Redundant System

As mentioned earlier, within the EP-(RC) hypothesis, movement and force production are different peripheral outcomes of basically the same neural control process. This allows testing the hypothesis formulated at the end of the previous section using two types of tasks: A force-production task with transient positional perturbations, and a positional task with transient force perturbations. The general idea is illustrated in Fig. 1.6 using the same minimalistic task, $E_1 + E_2 = C$. Imagine that this redundant system shows relatively low stability along the UCM for this task and relatively high stability in the orthogonal direction. Now imagine that in one particular trial, the system is in steady state at point A_1 on the UCM. A perturbation is likely to show deviations of the system both along the UCM and orthogonal to it, for example to point A_2. The deviation along the UCM is expected to be larger because of the lower stability in that direction (cf. Mattos et al. 2011, 2013). If now a perturbation is removed, the system returns to a state compatible with the original value of ($E_1 + E_2$) (defined by the referent value for that variable and external steady-state forces). However, it does not have to return to A_1 because this secondary perturbation is expected to lead to another deviation along the UCM, which is not attracted strongly to A_1. Assume that it ends at point A_3. This illustration suggests that transient perturbations that lead to equifinality with respect to the task-related variable may be associated with significant variance (violations of equifinality) at the lower hierarchical level.

In one of the recent studies (Zhou et al. 2014), the subjects were asked to hold a handle in a static position against a baseline force generated by a robot. Then the robot applied a short-lasting change in the total force while the subjects were instructed “not to intervene voluntarily” (let the robot move your arm). When the force changed, the handle moved to a new position (and orientation); when the force returned to the baseline level, the handle returned close to the initial position/orientation, which is an example of equifinality. However, final positions after the perturbation were associated with large variability at the level of joint rotations. Most of this variability was within the UCM for the endpoint location (and orientation). In other words, transient perturbations resulted in relative equifinality at the level of task variables, which was achieved by using variable joint configurations, as predicted by Fig. 1.6.

In another study (Wilhelm et al. 2013), the subjects were asked to produce constant level of total force while pressing with four fingers on four force sensors. Then, the visual feedback was turned off and one of the sensors was lifted using the "inverse piano" apparatus (Martin et al. 2011). This manipulation resulted in an increase in the force of the lifted finger and a drop in the forces of the other three fingers (similar to the results by Martin et al. 2011). Total force increased. When the perturbed finger was lowered to its initial position, total force was close to that observed in similar trials without perturbations. In all trials the total force dropped gradually, which is common after turning off visual feedback (Slifkin et al. 2000; Vaillancourt and Russell 2002). There were, however, significant variations in the force distribution among the fingers. In other words, equifinality was observed at the task level but not at the level of elemental variables.

1.9 What Now? Let Me Tell You What Now

The good news is that we have a working hypothesis on how coordinated natural movements are produced by the CNS based on laws of nature. We also have a reasonably well-developed associated computational apparatus that allows estimating quantitatively relevant variables that describe not only patterns of performance variables but also their characteristics related to action stability. This computational apparatus describes a physical/physiological system but does not assume that somewhere within the system such computations (or any computations) are performed.

The not-so-good news is that the available knowledge is miniscule, fragmented, and not always reliable. In particular, mapping of the models onto neurophysiological structures and mechanisms is all but missing. Even behavioral properties of the system are known unreliably, not much is known about such crucial features of movements as their stability. While the overall picture remains mosaic, recent works offer a coherent physical approach to putting pieces together (Martin et al. 2009; Latash 2010; Feldman 2011). Unfortunately, large efforts are still wasted on studies that are not driven by a clear theoretical scheme compatible with the known physics and physiology.

While a coherent, comprehensive theory of motor control is not here yet, there are already elements of progress in applying elements of the theory to clinical problems. Among those are, for example, the analysis of spasticity as a disorder in the control of the threshold of the tonic stretch reflex (Jobin and Levin 2000), the analysis of changes in motor synergies in stroke, Parkinson's disease and cerebellar disorders (Reisman and Scholz 2003; Park et al. 2012, 2013), the analysis of changes in the structure of motor variance with specialized practice in persons with atypical development (Scholz et al. 2003), young and older persons (Olafsdottir et al. 2008; Wu et al. 2012, 2013). The developed tools are sensitive to aging, fatigue, training, and neurological disorders; in some cases, they even show sensitivity to subclinical states of neurological patients (Park et al. 2012).

Among questions that are in an urgent need for research are: Is there back coupling between actual and referent trajectories? What factors define stability at different levels of a hypothetical control hierarchy (cf. Gorniak et al. 2009)? Is there a distribution of responsibilities among brain structures, for example are subcortical loops more likely to define stability properties of actions (cf. Reisman and Scholz 2003; Park et al. 2013)? What are the neurophysiological mechanisms that define stability of performance (cf. Latash et al. 2005)? What is the role of information from peripheral receptors versus back coupling within the CNS in defining synergies?

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Chapter 2
Motor Control and Position Sense: Action-Perception Coupling

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2.1 Introduction

This chapter focuses on the relationship between motor control and position sense (PS) defined as the ability of humans to recognize the position of body segments under different conditions. Studies showed that afferent signals from proprioceptive and cutaneous and, to a lesser degree, articular receptors satisfactorily reflect passive changes in the position of body segments (Matthews 1972; Edin and Johansson 1995). In contrast, afferent signals deliver ambiguous positional information during intentional motor actions. For example, the activity of a major contributor to PS—muscle spindle afferents—increases with increasing isometric muscle torque (Vallbo 1974) whereas the arm position at which the torque is produced is perceived as unchanged. During slow intentional finger motion in isotonic conditions, discharges of spindle afferents virtually remain constant (Hulliger et al. 1982) and thus do not reflect the perceived changes in the finger position. These and other examples, justified the conclusion that afferent signals are somehow integrated with central control signals underlying motor actions to form PS (von Holst 1954; McCloskey 1981; Feldman and Latash 1982a; Proske and Gandevia 2012). The nature of this integration in PS remains unclear. This situation results, in particular, from controversies in the understanding of how motor actions are controlled.

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This chapter reviews major hypotheses on how motor actions are controlled and the respective views on how PS is formed. Data will be described that permit choosing between alternative hypotheses of motor control. This approach may help advance the understanding of how control signals underlying motor actions contribute to PS in different conditions as well as of kinesthetic illusions, including the phantom limb phenomenon—the feeling that the amputated limb is present.

2.2 Alternative Views of Motor Control

Historically, a departure point in thinking about neural control of actions was based on the fact that motor actions obey and therefore are described in terms of the laws of mechanics. Many outstanding scholars in the field of action and perception, including von Holst (1954) combined this fact with the unconditional assumption that control levels of the nervous system are directly involved in the specification of variables characterizing the motor outcome in terms of movement kinematics, muscle forces and electromyogram (EMG) activity commonly called motor commands. One problem associated with this assumption was recognized by Von Holst (1954). He noticed that direct specification of motor commands to muscles to make intentional motion from a stable posture would be met with the resistance of posture-stabilizing reflexes (the posture-movement problem). To solve the problem, he suggested that neural control centers use a copy of pre-programmed motor commands—efference copy (EC)—to suppress movement-related afferent signals (reafference) and thus prevent resistance of postural reflexes to movement. The EC concept introduced by von Holst (1954) replaced similar concepts expressed under different names since the nineteenth century (Bridgeman 2007). Except for some researchers (e.g. Gibson 1968), the solution for the posture-movement problem and the EC concept has been accepted by the majority of researchers in the field without any critical analysis. It became a key concept in theories of motor control, including those that postulated the use of internal neural models for computations and specification of the motor outcome (e.g. Bays and Wolpert 2007).

A recent analysis (Feldman and Latash 2005; Feldman 2009, 2011) has revealed some drawbacks of the solution of the posture-movement problem offered by von Holst (1954). Physically, by suppressing reafference or, in modern terminology, position- and velocity-dependent feedback, would make the initial position unstable. This proposal does not explain how stability of the final posture is regained. Before the motion, postural mechanisms were tuned to stabilize the initial posture and, once restored at the final posture, would react to the accumulated deviation from the initial posture and drive the arm back to it. This prediction of von Holst's proposal conflicts with consistent findings that arm motion ends at a stable posture without any tendency to return to the initial posture. His proposal also conflicts with physiological data that postural reflexes are not suppressed but are reset to a new position when self-initiated motion is made, thus transferring stability to the final posture (Asatryan and Feldman 1965; Adamovich et al. 1997; Feldman 2011).

The resetting mechanism represents an empirically based solution to the posture-movement problem that does not rely on the idea of preprogramming of motor commands to muscles and the EC concept (Feldman 2011). When postural reflexes are reset (re-addressed) to a new posture, the initial posture becomes deviated from the new posture, and the same posture-stabilizing mechanisms that would resist self-initiated motion, now drive the body segments to the new position to which stability is transferred. In other words, by shifting the threshold position at which posture-stabilizing mechanisms are centered, the nervous system converts postural reflexes from a movement-resisting to a movement-producing mechanism.

EC-based theories of motor control have further been questioned by recent findings that descending systems in humans, particularly the corticospinal system, do not carry information about motor commands (EMG, forces) to muscles (Raptis et al. 2010; Sangani et al. 2011; Ilmane et al. 2013). Instead, these systems specify spatial thresholds at which neuromuscular structures (including reflexes and intrinsic muscle properties) begin to act, thus confirming the hypotheses that motor control is not based on preprogramming of the motor outcome and EC. These thresholds define a certain position, *R,* of body segments at which the activity of muscles is minimized. Thereby, any deviation from this position is opposed by reflexes. The *R* is also called the *referent position* since it plays the role of the origin of the spatial frame of reference in which the muscles and reflexes are constrained to work (Feldman 2011). These studies confirmed the earlier demonstration that central shifts in the referent position of body segments underlie intentional arm movements in humans (Asatryan and Feldman 1965), an empirical finding underlying the equilibrium-point hypothesis (for recent review see Feldman 2011).

2.2.1 Alternative Views on the Role of Central Control Processes Underlying Motor Actions in Position Sense

The alternative theories of motor control motivated different answers to the question of how PS is formed. One answer is based on the dominant view that the brain is directly involved in preprogramming of the desired motor output, including EMG patterns and muscle forces. It suggests that a copy of motor commands, i.e., EC, is somehow integrated with afferent signals to form PS (Proske and Gandevia 2012). It has also been assumed that EC underlies the sense of effort and therefore this sense and PS are interrelated. Evaluations of PS before and after ischemic deafferentation of the arm have been considered as supporting evidence of a contribution of sense of effort to PS (Proske and Gandevia 2012). This proposal, however, conflicts with results of the study by Allen et al. (2007) showing that under normal conditions, PS is load- and effort-independent.

Threshold position control is an alternative to the EC-based view not only about how motor actions are controlled but also about how they are perceived. Specifically, as the threshold position for muscle activation, the *R* carries essential positional information and as such, it can be used to form PS. The PS rule based on the *R* concept was previously proposed by Feldman and Latash (1982a) and recently updated (Feldman 2009, 2011; Feldman et al. 2013). Specifically, to determine the actual position, Q, of body segments, the nervous system can use already available information about the referent position, R, and combine it with sensory information related to the *deviation*, P, of the actual position of body segments from the referent position:

$$Q = R + P \tag{2.1}$$

This formula describes a natural, physical relationship between variables Q, R, and P, as illustrated in Fig. 2.1a for a single joint interacting with a load. To clarify, suppose that a referent position R, is centrally set, say, for wrist flexor muscles. A load counteracting these muscles will stretch them beyond the threshold, R. The muscle activity and torque will increase until muscle and load torques become balanced at some actual position, Q. To perceive this position, it is sufficient to know its deviation, P, from R, as defined by formula 1.

By applying this formula to PS, we need to assume that proprioceptive, cutaneous, and articular afferents do not convey direct information about the actual position, Q, of body segments but instead signal the deviation, P, of the actual position of the body segments from the referent position. In other words, it is assumed that PS has central (R) and afferent (P) components that are integrated at some level of the brain to perceive the actual position of body segments. The R is the control variable underlying motor actions and the P is the afferent outcome conveyed by ascending pathways to the brain. The PS rule thus represents *an explicit expression of action–perception coupling in kinesthesia* (see also Ostry et al. 2010).

2.2.2 Explanations of Position Sense Based on the PS Rule

The PS rule provides an explanation of PS in different motor tasks as well as of kinesthetic illusions and the phantom limb phenomenon (Feldman 2009; Feldman et al. 2013)—the sense that the amputated limb is still present. In particular, the PS rule suggests that passive changes in position that do not involve changing in the central PS component are perceived from changes in afferent signals, P, from muscle spindles and cutaneous receptors. In contrast, all active (self-initiated) changes in position are associated with changes in the central component, R, and PS will result from combined changes in both PS components. The relative contribution of these components to PS may be different depending on the motor task. Consider several examples.

Figure 2.1 shows not only how the PS rule is derived (A) but also how it works under different conditions. The thick solid curve in each panel is the muscle-reflex characteristic (torque versus joint angle) for a given R. The thin solid curve is the characteristic following a shift in the R. Dashed lines are load (L) characteristics. Subscripts i and f refer to initial and final values of variables, respectively, and filled dots are the initial and open dots are final equilibrium points of the system.

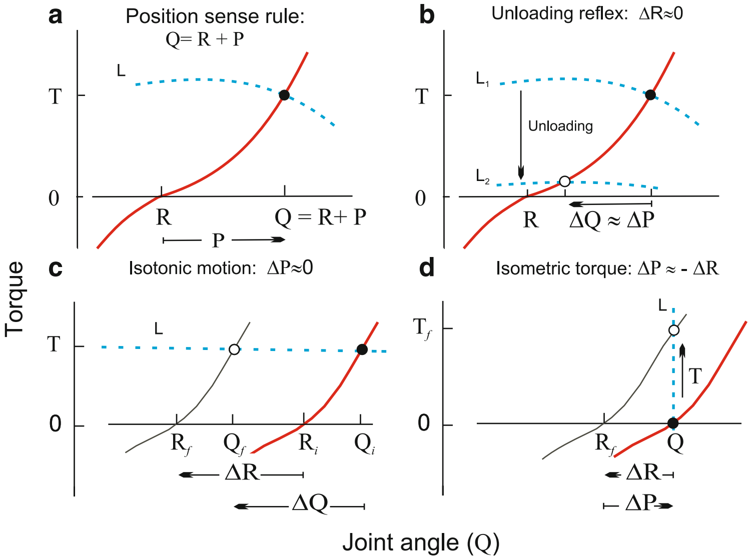

Fig. 2.1 The position sense rule: its derivation and application to different motor tasks. **a** PS rule for a single joint interacting with a load. When a referent joint angle (R) is set by descending systems, the activity of muscles and the net joint torque (T) increases with deviation of the joint angle from the R position (*solid curve*). The load (L) stretches the muscles (flexors in this example) until the system reaches an equilibrium point (*filled circle; point of intersection of the two curves*), i.e., the combination of the joint angle and muscle torque that balances the load (*dashed curve*) at some position, Q. To identify this position, it is sufficient to know the deviation, P, of the joint from its referent position: $Q = R + P$. It is assumed that this deviation is transmitted by ascending afferent pathways and converges with the referent joint angle at some central level where position sense is formed. **b–d** PS in different motor tasks. **b** during the unloading reflex elicited by a sudden change in the load, the same R is maintained. Changes in the joint angle, ΔQ, are perceived from changes in the *afferent* PS component, $\Delta Q \approx \Delta P$. **c** During slow isotonic motion, changes in the joint angle are predominantly perceived from changes in the *central* PS component, $\Delta Q \approx \Delta R$. **d** During isometric torque production, changes in the two PS components are equal but opposite, such that the joint angle is perceived as unchanged, $\Delta Q = 0$. Thick solid curve in each panel is the muscle-reflex characteristic (torque versus joint angle) for a given R; *thin solid curve* is the characteristic following a shift in the R; *dashed lines* are load (L) characteristics; subscripts i and f refer to initial and final values of variables, respectively; *filled dots* are the initial and *open dots* are the final equilibrium points of the system. (Reproduced with permission from Feldman et al. 2013)

During the unloading reflex (B) elicited by a sudden change in the load of say, preloaded elbow flexors, the same R is maintained (see Ilmane et al. 2013) and the arm moves to another position at which the residual load and muscle torques are balanced. According to the PS rule, changes in the joint angle, ΔQ, in the unloading reflex are perceived from changes in the *afferent* PS component alone, $\Delta Q \approx \Delta P$, since in this case, $\Delta R \approx 0$.

In contrast, during slow isotonic motion (Fig. 2.1c), the afferent PS component remains virtually constant, which is consistent with data by Hulliger et al. (1982) on the absence of position-related changes in muscle spindle afferents during isotonic finger motion. Thus, in isotonic conditions, changes in the joint angle are predominantly perceived from changes in the *central* PS component, $\Delta Q \approx \Delta R$.

During isometric torque production, the position (Q) of the joint remains unchanged but the deviation of this position increases when the threshold position, R, decreases (Fig. 2.1d). As a result, the activity of muscles and isometric torque increases. This process is associated with increasing proprioceptive signals (Vallbo 1974). The changes in the two PS components are equal but opposite such that the joint angle is perceived as unchanged, $\Delta Q = 0$.

The alternative, EC-based PS hypothesis is not sufficiently specific to explain all these cases. In particular, EC and sense of effort are virtually the same at different positions under isotonic conditions (Fig. 2.1c) and hardly contribute to PS. It is unclear how afferent signals can be used to identify the changes in position in isotonic conditions. Muscle spindle afferents in this condition do not signal changes in position (Hulliger et al. 1982). However, the contribution of cutaneous afferents to PS in isotonic conditions cannot be rule out. To our knowledge, positional sensitivity of these afferents has been demonstrated during *passive changes* of different joint angles (e.g., Edin and Johansson 1995). Cutaneous and proprioceptive afferent influences usually converge on common interneurons (Jankowska 1992; Hultborn 2006) and it is likely that during *active isotonic movements,* cutaneous, like spindle afferents, convey ambiguous positional information.

The unloading reflex and isometric torque production are associated with changes in effort. The EC or effort-based hypotheses are also not specific enough to explain why the sense of effort can contribute to the sensation of changes in position during the unloading reflex and to the sensation of the absence of changes in position during isometric torque generation. The sense of effort is primarily associated with muscle torques and the EC- or effort-based hypotheses do not provide clues as to how it can affect PS that is formed in the positional domain.

2.3 Testing Alternative Hypotheses on PS

The prediction of the effort-based hypothesis of PS was tested by asking subjects to produce changes in elbow position against different isotonic loads. According to the Weber–Fechner law (Weber 1834; Fechner 1860), the sense of effort and the error in identification of the changes in the load are scaled with the magnitude of the load. Therefore, if dependent on the sense of effort, PS would reflect such properties of the law. It appeared that PS is load-independent (Feldman et al. 2013; Fig. 2.2), confirming previous findings by Allen et al. (2007). These findings conflict with the effort-based PS hypothesis, but are consistent with the PS rule that is based on experimental findings that control signals underlying motor actions do not carry information about motor commands or sense of effort.

In the unloading reflex (Figs. 2.1b, 2.3), the changes in the wrist position were correlated with the amount of unloading and thus with the sense of effort. However, the precision with which subjects reproduced the positional changes for different

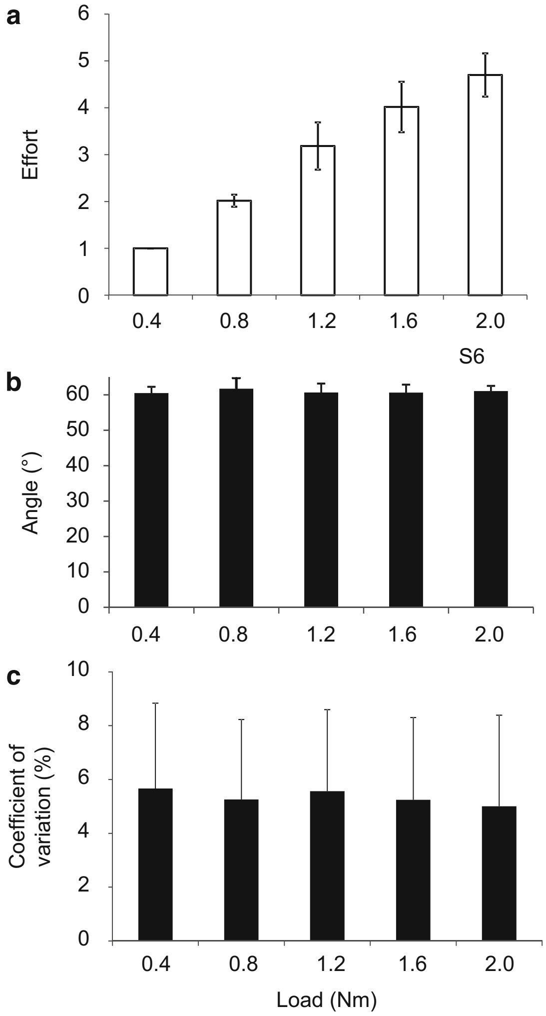

Fig. 2.2 The sense of position is independent of the sense of effort. **a** Different loads counteracting elbow flexor muscles were associated with different efforts identified with numbers 1–5 (group data). **b** With eyes closed, the subject (*S6*) reproduced the same elbow angle regardless of the load. **c** The precision of the reproduction (coefficient of variation) was also load-independent in this and other 11 subjects. (Reproduced with permission from Feldman et al. 2013)

amounts of unloading was load-independent (Feldman et al. 2013). This finding also conflicts with the assumption that PS depends on the sense of effort since if the PS were effort-dependent, the precision of the perceived changes in the wrist position would be scaled with the load according to the Weber–Fechner law (Weber 1834; Fechner 1860).

Consider findings that have been regarded as evidence that PS depends on the sense of effort (Gandevia et al. 2006; Smith et al. 2009; Walsh et al. 2010). In these studies, PS at the wrist was measured before and after the arm was paralyzed by an anesthetic or by ischemia produced by a blood pressure cuff. Before paralysis, subjects accurately detected the position of the wrist when it was passively rotated. After paralysis, subjects were unable to indicate the position of the hand at rest.

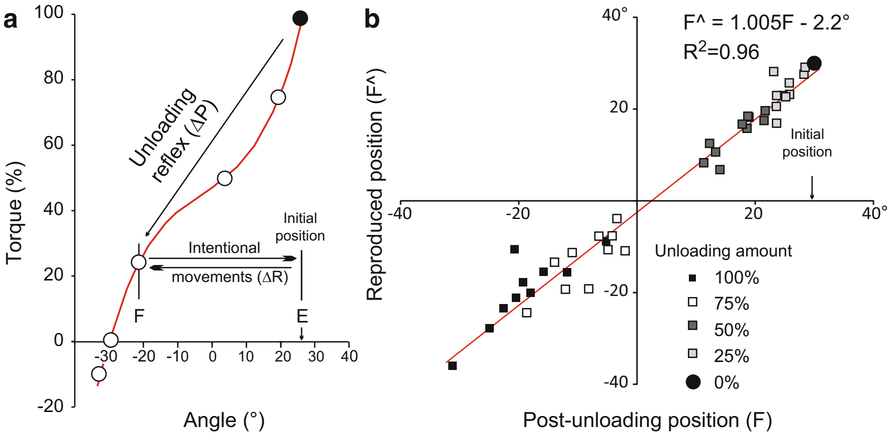

Fig. 2.3 Converting changes in the afferent component of position sense into intentional motion. **a** The mean initial (*filled circle*) and final (*open circles*) wrist equilibrium points resulting from different levels of unloading of wrist flexors from an initial position (*E*) in a representative subject, in the absence of vision. After unloading, the subject intentionally moved the wrist from the post-unloading position (*F*) to the initial, pre-unloading position and back to the memorized post-unloading position ($F^\wedge$). According to previous analysis (Ilmane et al. 2013), motion resulting from unloading was predominantly perceived from changes (ΔP) in the afferent component of position sense whereas intentional movements from position *F* to the pre-unloading and back to the post-unloading position, $F^\wedge$, required respective changes ($\Delta \text{R} \approx \Delta \text{P}$) in the referent position. The test was made for a different amount of unloading (100, 75, 50, and 25 % of the initial load; 0 % is for trials in which unloading was not produced). **b** A plot of position $F^\wedge$ versus *F* for different amounts of unloading. The slope of the regression line between positions $F^\wedge$ and *F* was close to 1 in this and other 9 subjects. (Reproduced with permission from Feldman et al. (2013)

Efforts to move the hand during paralysis produced large illusions of hand motion. From these observations, the authors suggested that PS depends on the sense of effort.

Alternatively, these observations can be explained in terms of the PS rule. During passive movements or relaxation, the *R* is shifted outside of the biomechanical range of the joint (Levin and Feldman 1994). As a result, PS during muscle relaxation is mainly based on changes in the afferent PS component. Naturally, when afferent feedback is blocked, subjects are unable to perceive the changes in wrist position, as observed by Gandevia et al. (2006). Based on the PS rule, the illusion of motion of the hand during paralysis can be explained in the following way. In the absence of afferent feedback, the position of body segments can still be sensed based on the central PS component, *R*. In experiments by Walsh et al. (2010), subjects learned to produce different efforts before paralysis. They thus learned to scale the *R* shifts with effort (cf. Fig. 2.1d). Indeed, when subjects reproduced these *R* shifts during paralysis, they perceived illusory movements correlated with the sense of effort. Since correlation between the two senses was preconditioned by the experimental protocol, results of the above studies cannot be considered as evidence for a dependency of PS on the sense of effort. This conclusion is also supported by the obvious dissociation between the two senses in isotonic, isometric, and reflex unloading conditions (Fig. 2.1b–2.1d).

Experiments were also conducted to test specific predictions of PS rule. According to the PS rule, the central and afferent components are equally important to position sense. The relative contribution of the two components to PS depends on the condition. In particular, it has been shown that descending influences on motoneurons of wrist muscles and thus the referent position, *R,* are similar at the pre- and post-unloading positions (Ilmane et al. 2013; Fig. 2.3). This means that changes in position elicited by unloading are predominantly perceived from a change in the afferent PS component, *P:* $\Delta Q = \Delta P$. In contrast, descending influences are modified when the wrist is intentionally moved to another position, suggesting that intentional changes in position in isotonic conditions are predominantly perceived from the change in the referent position, *R*. We tested the hypothesis that the nervous system is able to transform afferent information about changes in the wrist position resulting from unloading into the *R* command to make *intentional* isotonic movement of the same extent as that resulting from unloading (Fig. 2.3). Preloaded wrist flexors were fully or partially unloaded, and subjects were required to reproduce the involuntary wrist excursions by intentionally moving the wrist, in the absence of vision. Subjects had no difficulty in performing the required transformation of the *P* into the *R* component of PS. Indeed, such a sensorimotor transformation was facilitated by the parity in the dimensions of the two PS components as well as by the fact that the central PS component also underlies intentional motor actions. The finding of a strong correlation between voluntary and involuntary changes in the wrist position (Fig. 2.3) seems obvious, but only in the context of the PS rule. The initial and final positions in the unloading reflex were associated with different tonic EMG levels (or ECs), different senses of effort and different afferent feedback whereas these aspects, including afferent feedback (Hulliger et al. 1982), were hardly distinguishable at wrist positions established before and after intentional motion in isotonic conditions. In other words, the effort- or EC-based PS theory is not helpful in the explanation of PS. Indeed, intuitively, we take for granted that our sense of position is adequate regardless of what we do, but the PS rule shows that this intuition is physiologically justified in the context of the PS rule, rather than in the context of effort- or EC-based theory.

2.4 Kinesthetic Illusions

Usually, vibration of a muscle tendon elicits the illusion of muscle lengthening (extension of the elbow joint if vibration is applied to elbow flexors; Matthews 1972) in the absence of physical motion. If vibration is prolonged, the illusion can be reversed (Roll et al. 1989, 1980; Feldman and Latash 1982b). In terms of the PS rule, these illusions result from influences of vibration predominantly on the afferent and central PS components, respectively.

Physical changes in position are apparently coupled with appropriate awareness about these changes. The integration of the two components may just be a first step in the formation of PS and it does not address the challenging question of how subjects become consciously aware of physical or illusory changes in position. Normally, subjects are well aware of the position of body segments but this awareness may become inadequate during artificial stimulation (e.g. tendon vibration or electrical stimulation of the brain). The illusion of motion elicited by tendon vibration is an example of such inadequacy. Another example was observed in a patient undergoing brain surgery (Desmurget et al. 2009). Electrical stimulation of inferior parietal areas (Brodmann areas 39 and 40), elicited the sensation of arm movement although no movement was made. The authors concluded that activation of these areas reflected the intention to move even in the absence of motion. One can add that under normal conditions, activation of these areas might be combined with opening of pathways that transform the intention to move into changes in the referent position of the appropriate body segments. The resulting motor action (a movement or, if movement is prevented, isometric torque generation) is recognized by combining afferent feedback with the referent command, as implied by the PS rule.

No motion illusions have been observed in two studies (Desmurget et al. 2009; Feldman et al. 2013). In one, electrical stimulation of the premotor area (the dorsal sector of Brodmann area 6) in patients undergoing brain surgery triggered limb movements but patients denied that they had moved (Desmurget et al. 2009). One can suggest that the physical motion was elicited by changes in the *R* command without simultaneous influence of this command on the PS. In the other study (Feldman et al. 2013), no motion illusion has been observed during long-term tonic vibrations of elbow flexors in the absence of vision when subjects were unaware of any physical motion of the arm elicited by the vibration (Fig. 2.4).

It appeared that the no-motion illusion elicited by vibration is preserved when the arm moves against different isotonic loads. The critical angle at which subjects start perceiving physical motion does not depend on the magnitude of the load, further confirming that PS does not depend on the sense of effort.

2.5 Phantom Limb Phenomenon

The phantom limb phenomenon was considered as supporting the assumption that PS depends on the sense of effort (Proske and Gandevia 2012). However, a phantom limb can be sensed in the absence of any physical or mental effort. The phantom limb phenomenon can be explained without the assumption that it relies on the sense of effort. According to the PS rule, when afferent sensitivity is deficient or absent, the amputated limb can still be sensed as being present based on the central PS component, *R*. Because of the absence or deficiency of the afferent PS component, however, the shape of the phantom limb can be abnormal (e.g., twisted phantom elbow or knee joint) and associated with pain or other abnormal sensations.

Although *R* may be controlled independently of the current position, the transformation (“re-calibration”) of electrochemical descending influences into a spatial (positional) variable *R* would be impossible in the absence of position-dependent afferent feedback to α-motoneurons (for details see Fig. 2.4 in Feldman 2009). Therefore, in the absence of such feedback, the association of descending influences with

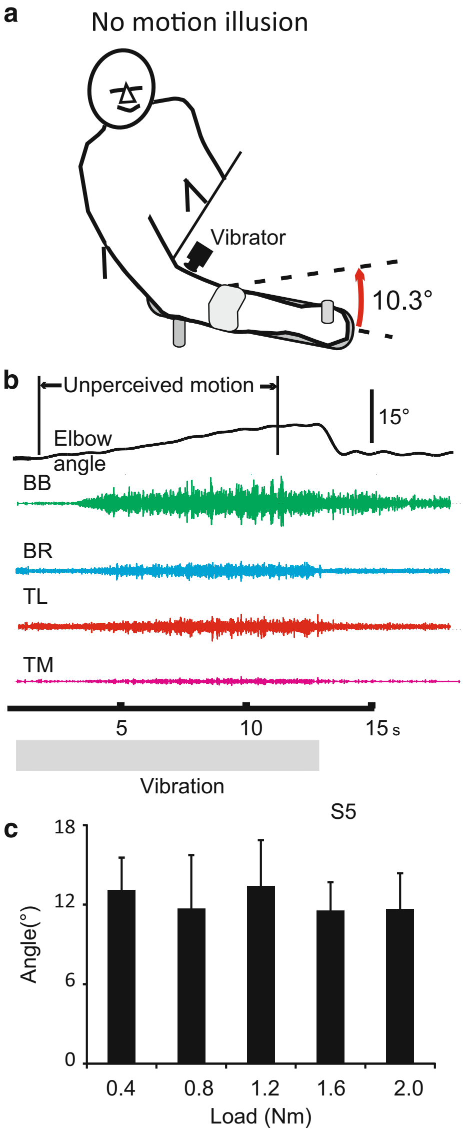

Fig. 2.4 No-motion illusion and its independency of the sense of effort. **a** Experimental setup. **b** Tonic vibration of the biceps tendon (frequency 100 Hz, amplitude 3 mm) elicited activation of elbow flexors (*BB, BR*) and extensors (*TL, TM*), resulting in elbow flexion. This subject (and other 9 subjects) was not aware of this motion (no-motion illusion) until the change in the joint angle began to exceed 10.3°. **c** The mean (± SD) change in the elbow joint angle after which the subject began to feel the motion, for different loads counterbalanced by elbow flexor muscles. (Reproduced with permission from Feldman et al. 2013)

spatial variables, like the *R*, gradually decays. This explains why phantom limb sensation in amputees eventually disappears and why chronically deafferented subjects do not have phantom limb sensations (Paillard 1991). The absence of referent control in deafferented humans may result in the loss of the body scheme and other sensorimotor deficits (Paillard 1991).

2.6 Further Implications and Future Directions

The notion that somatosensory feedback conveys information about deviation of the actual position of body segments from a centrally specified referent position may be applicable to ascending somatosensory pathways as well as to neurons of dorsal and ventral spinocerebellar tracts and propriospinal neurons having recurrent projections to the cerebellum (Arshavsky et al. 1972, 1978; Alstermark et al. 2007). According to the PS rule, this would be helpful in continuously monitoring changes in the actual position of body segments to decide whether it is necessary to correct the ongoing movement or switch to another pattern of referent shift in response to destabilizing external perturbations, environmental events, or internal intentions. Indeed, this is not the only function of ascending pathways. In particular, together with other proprioceptive afferents, tendon organ afferents may transmit information about muscle forces to form the sense of effort associated with the ongoing action.

Another implication of the present results is that they constrain the choice between different theories of action–perception coupling. Previous studies (Raptis et al. 2010; Sangani et al. 2011; Ilmane et al. 2013) have questioned the long held assumption (von Holst 1954) that the brain preprograms motor commands to muscles or efference copy (EC). Descending systems, particularly the corticospinal system, have been shown to not be involved in direct specification of motor commands to muscles. The same conclusion refers to theories of motor control based on the idea of internal models in which EC is a core concept (e.g., Bays and Wolpert 2007). Results obtained in our recent studies have also shown that PS is independent of motor commands and the sense of effort, thus rejecting EC- or effort-based theories of PS.

Some emerging theories of action and perception have not integrated the notion of referent position control. The sensory prediction theory (SPT) suggests that the brain predicts the proprioceptive consequences of the intended movement and that these predictions are delivered to motoneurons via descending pathways (Adams et al. 2013). Motoneurons are activated or not depending on the difference ("predictive error") between the predicted and the actual proprioceptive feedback. The SPT is reminiscent of a similar theory proposed several decades ago by Powers (1973) with the complementary assumption that the predictive error is eliminated by the neuromuscular system that works as a linear closed-loop servo-controller. To be functional, such a controller would have to have a physiologically unrealistic high gain, like in the servo-control hypothesis by Merton (Merton 1953; see also criticisms of the Powers' theory by Fowler and Turvey 1978). In any case, by assuming that the nervous system preprograms the sensory consequences of the motor outcome, SPTs do not help explain how PS is formed since these sensory consequences carry ambiguous information about positions of body segments (see Introduction). In addition, SPT seems to misrepresent how motor actions are controlled. Consider, for example, isometric torque production. In terms of SPTs, this is achieved by preprogramming of the sensory signals ("afference copy") associated with the required torque resulting from activation of motoneurons that function depending on the error in prediction of these signals. After several trials, the sensory signals associated with the required torque could be identified correctly and reproduced with a minimal error. Then, paradoxically, motoneurons that function depending on this error would barely be activated to generate the required torque. Therefore, not only PS but also motor control is inexplicable in the framework of SPTs.

Previous studies (Raptis et al. 2010; Ilmane et al. 2013) have shown that isotonic wrist movements are accomplished by shifting the referent wrist position, R. Results of these studies were interpreted based on the assumption that changes in the afferent PS component in isotonic conditions were minimal and therefore the difference in the initial and final wrist angles in these conditions was predominantly perceived from the difference in the central PS component. Future experiments are necessary to test whether this conclusion can be generalized to isotonic positions at other joints, including the elbow joint. The contribution of cutaneous afferents to PS in isotonic conditions cannot be rule out. To our knowledge, positional sensitivity of these afferents was demonstrated during *passive changes* of different joint angles (e.g., Edin and Johansson 1995). Cutaneous and proprioceptive afferent influences usually converge on common interneurons (Jankowska 1992) and it is likely that during *active movements,* cutaneous, like spindle afferents, convey ambiguous position information, which can also be tested in future studies.

The nature of information conveyed by ascending pathways to the cerebellum and other brain areas remains unclear. Based on our present findings, future studies can address the question of whether these pathways carry information about the deviation of the actual position of body segments from their referent position, rather than information about efference copy, as usually assumed.

2.7 Conclusions

There are several demonstrations that the corticospinal and other descending systems specify the referent position, R, of body segments at which motor commands can emerge without preprogramming. It is assumed that the referent position not only underlies motor actions but also represents a component of position sense. In other words, motor actions and position sense are controlled jointly, by setting and resetting of the referent position of body segments. Thereby, feedback from proprioceptive, cutaneous, and articular afferents delivers information about the deviation (P) of the body segments from the referent position. Taken together, the central and afferent components of position sense provide adequate information about the actual position (Q) of body segments, as defined by the PS rule: $Q = R + P$. This rule is helpful in the explanation of PS in many motor tasks as well as of kinesthetic illusions, including the phantom limb phenomenon. Three suggestions derived from the PS rule were confirmed by showing that: (1) changes in the afferent PS component resulting from unloading can be converted to changes in the referent position to produce intentional motor actions, (2) PS is independent of motor commands or sense of effort, (3) subjects may be unaware of arm motion elicited by continuous tendon vibration (no-motion illusion). Several theories of action and perception are rejected based on the present results and previous findings of how motor actions are controlled and perceived. Such are theories that assume direct preprogramming of the motor or/and sensory outcome by the brain based on internal models. Our study thus advances the understanding of how motor actions are controlled and perceived.

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Chapter 3
Reconfiguration of the Electrical Properties of Motoneurons to Match the Diverse Demands of Motor Behavior

C. J. Heckman and Michael D. Johnson

3.1 Introduction

During the past 25 or so years, our studies, as well as those of many colleagues, have revealed ever-greater complexity in the input–output properties of motoneurons. It is thus no longer tenable to consider motoneurons to be simple "threshold and fire" followers of motor commands. This complexity is puzzling though—why is such a wide range of motoneuron input–output states needed to implement motor behaviors? The guiding concept for our ongoing work is that this multiplicity of motoneuron states is in fact an adaptation to match the great diversity of the normal movement repertoire.

We propose the following correspondences between motoneuron states and motor behaviors: For posture, motoneurons may act as integrators to provide memory of brief inputs; for a wide range of voluntary movements, motoneurons may act as variable gain amplifiers; and for repetitive movements driven by central pattern generators, motoneurons may act as oscillators. Admittedly, these correspondences are overly simplified, but they potentially provide clear guides for further studies of this fundamental issue. The first two states are highly dependent on neuromodulatory input from the brainstem, mediated via actions of serotonin (5HT) and norepinephrine (NE) while the oscillatory state appears to depend primarily on glutamatergic *N*-methyl-D-aspartate (NMDA) inputs, adding a whole new dimension to motoneuronal behavior. The data supporting these correspondences are presented in the following sections, after a brief review of the fundamental role of neuromodulation.

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3.2 Motoneuron Input–Output Processing Is Profoundly Influenced by Brainstem Neuromodulatory Systems

Neuromodulation is the foundation of the diversity of motoneuronal states. The two most powerful neuromodulatory inputs to motoneurons are mediated by axons descending from the brainstem and releasing either 5HT or NE. Unlike ionotropic inputs, which open ion channels to generate excitatory postsynaptic potentials (EPSPs) or inhibitory postsynaptic potentials (IPSPs), neuromodulatory inputs use G protein-coupled receptors to activate signal transduction pathways (Hille 2001). The effects of 5HT and NE on motoneuron excitability are extraordinary (Hultborn 2002; Heckman and Enoka 2012). Recruitment thresholds are greatly reduced by depolarization of the rest potential and hyperpolarization of the spike voltage threshold. Rate modulation is transformed due to facilitation of persistent inward currents (PICs) mediated by voltage-sensitive Na and Ca channels. PICs are a primary focus of this proposal. Undoubtedly, motoneurons are subject to neuromodulation by other neurotransmitters in addition to 5HT and NE (e.g., Svirskis and Hounsgaard 1998). The dopaminergic input from the brainstem to the cord increases motoneuronal excitability, but has yet only been studied in neonatal preparations (Garraway and Hochman 2001; Zhu et al. 2007). It is likely weaker than the 5HT and NE systems. Cervical motoneurons in the cat have over 1500 synapses containing 5HT and over 1200 synapses containing NE and these synapses cover their extensive dendritic trees (Montague et al. 2013). Local spinal circuits are known to induce neuromodulatory effects on motoneurons as well. Cholinergic interneurons projecting to C-terminals on motoneurons also reduce the afterhyperpolarization (AHP) (Zagoraiou et al. 2009) and possibly this is the source of the reduced AHP that occurs during the scratch reflex in spinalized animals (Power et al. 2010). In contrast, 5HT and NE have very little effect on the AHP in the adult (Lee and Heckman 1999; Li et al. 2007). Spinal circuits also lower spike voltage threshold (Power et al. 2010). In this review, our focus is on neuromodulation by 5HT and NE for two reasons: their effects on motoneurons are remarkably powerful and reasonably well understood. Further states of motoneurons will likely become apparent as our understanding of the full diversity of neuromodulatory inputs increases.

3.2.1 Neuromodulatory Inputs are an Essential Component of Normal Motor Commands

Numerous studies indicate that the brainstem neuromodulatory input is essential for a wide range of motor behaviors (Heckman and Enoka 2012). To summarize: (1) There exists steady neuromodulatory drive from the brainstem to the cord during the waking state, which is increased during sustained motor output (Aston-Jones et al. 2001; Jacobs et al. 2002). (2) Motoneurons lacking this neuromodulatory drive are severely hypoexcitable (Hounsgaard et al. 1988; Miller et al. 1996). Excitability is so low that even simultaneous, intense activation of all known inputs is far from sufficient to produce the maximal motoneuronal output required for high forces (Powers and Binder 2001; Cushing et al. 2005). (3) Motor unit firing patterns in humans during slow increases in force closely resemble the firing patterns generated by equally slow activation of cat motoneurons with moderate to large amplitude PICs (Hornby et al. 2002; Heckman and Enoka 2012). In summary, normal motor behavior cannot be achieved without a strong neuromodulatory input to motoneurons. This input has a profound impact on motoneuron input–output processing, i.e., on its "state."

3.2.2 The PIC and Bistable Behavior as a Pattern Generator for Postural Control

Bistable behavior reflects the inherent tendency of PICs to prolong inputs. Figure 3.1 shows an example of how the PIC transforms a synaptic current. The PIC converts a brief excitatory current (green trace) into a prolonged "tail" current that persists for many seconds (red trace; inward, depolarizing current is upward). The sustained PIC tail current is the basis of *self-sustained firing,* which requires little or no tonic input from descending or sensory systems. Recordings of electromyogram (EMG) and force in response to brief inputs have documented prolonged motoneuronal output lasting minutes (Hounsgaard et al. 1988; unpublished data, Heckman lab). Bistable behavior has long been thought to be important for posture (Hounsgaard et al. 1988). Consistent with this role, PICs with low-voltage thresholds and long-lasting tail currents only exist in type S motoneurons that innervate fatigue resistant muscle fibers, while PICs in type F motoneurons have much higher thresholds and faster decays (Lee and Heckman 1998a, 1998a). This PIC "tuning" makes good functional sense: Type F motoneurons do not participate in the low forces needed for steady posture and their extremely low fatigue resistance seems well matched to a more rapidly decaying PIC. The match between PIC properties and the fatigue resistance of motor units was a key insight leading to our concept that different motoneuronal states match different motor behaviors. In a sense, bistable behavior can be considered a pattern generator for the steady forces required for posture. Remarkably, this pattern generator is intrinsic to motoneurons themselves.

3.2.3 Does the Bistable State Provide Integration or Memory of Transient Inputs?

Figure 3.1 suggests that a bistable motoneuron is not an integrator in the strict mathematical sense—the prolonged current is less than the initial current during the pulse. This history-dependent behavior, however, does have a strong memory-like aspect to it. For posture, the key functional issue is how a motoneuron in the self-sustained

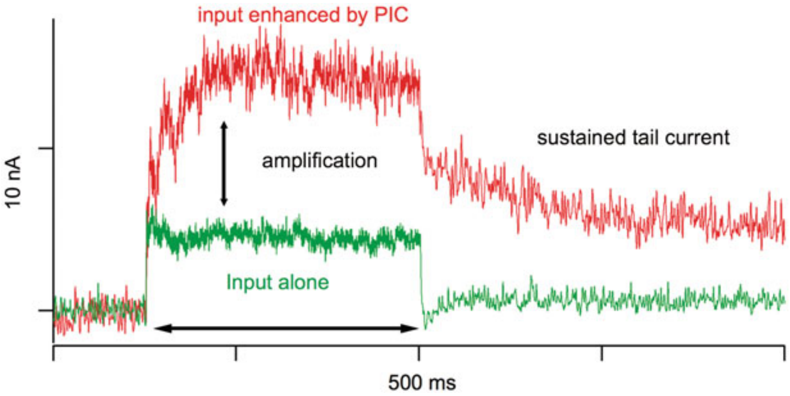

Fig. 3.1 Amplification and prolongation of synaptic input by persistent inward current. Intracellular recording of a medial gastrocnemius motoneuron in the decerebrate cat preparation. The synaptic current was generated by vibration of the Achilles tendon to steadily activate muscle spindle Ia afferents for ∼ 0.75 s. The cell was voltage clamped using the switching single electrode technique. The *green* trace shows the current generated by the steady Ia input when the cell was voltage clamped to a very hyperpolarized level, preventing this input from activating the motoneuron's persistent inward current. The *red* trace shows the effect of the very same input when the cell was clamped near its threshold for firing. Because the clamp is only effective at the soma, the Ia input activated the PIC in dendritic regions. As a result, the input was both strongly amplified and prolonged—the tail current persisted for many seconds (not shown). (Data from Lee and Heckman 1996)

firing state responds to further transients for postural corrections. Previous studies of the effects of PICs on synaptic inputs have been done using a combination of synaptic and injected currents (e.g., Bennett et al. 1998; Lee and Heckman 2000) and have ignored how the cell behaves when primarily driven by the PIC to produce self-sustained firing. Further studies are needed to define the behavior of the motoneuron in the postural state. If the response during self-sustained firing to further transients is prolonged, then the motoneuron is indeed acting much like an integrator or memory device. If not, then bistable behavior may provide a steady background that nonetheless allows for transient corrections.

3.2.4 PIC Amplification as the Basis for Gain Control of Motor Output via the Brainstem

Figure 3.1 shows that the PIC not only prolongs input but also greatly enhances it (note the large increase in current while the input is active). This enhancement is generally thought to provide input amplification (Lee and Heckman 2000; Prather et al. 2001; Hultborn et al. 2003) and this amplification is essential in increasing the gain of motoneurons sufficiently so that they can be activated effectively by descending and sensory inputs (see above). PICs are highly sensitive to inhibitory inputs (Kuo et al. 2003; Bui et al. 2008b) and so motor commands can easily decouple PIC amplification from PIC prolongation by using inhibition to turn off the PIC when it is not needed. The amplitude of the PIC is proportional to the level of neuromodulatory input (Lee and Heckman 2000). Thus, brainstem neuromodulatory control of PICs potentially provides motor commands with a mechanism to control the input–output gain of motoneurons. We have speculated that a low motoneuronal gain is advantageous for low-force, high-precision tasks but that gain should be progressively increased as the force requirements of the task increase (Johnson and Heckman 2010). Matching of motoneuronal gain to the widely varying forces of voluntary motor tasks would constitute a clear example of the diversity of motoneuronal behavior matching the diversity of motor behaviors, but this match has yet to be clearly demonstrated.

3.2.5 Does Synaptic Inhibition of PICs Afford a Local, Highly Specific Gain Control of Motoneurons?

Inhibitory synaptic input hyperpolarizes motoneurons, thereby increasing their threshold for activation and opposing the depolarization from excitatory inputs. Probably, most considerations of the role of inhibition in motor control assume this fundamental model. Yet the effect of inhibition on the PIC suggests that it may also alter motoneuron gain, because we have shown that inhibition can reduce the amplitude of the PIC in a proportional manner (Kuo et al. 2003). Thus, inhibitory input may provide a gain control mechanism that opposes the gain control from the brainstem. The brainstem system is remarkably diffuse—in fact some of these axons give off branches along the entire length of the cord (Holstege and Kuypers 1987). In contrast, there are several highly focused sources of spinal inhibition—e.g., reciprocal inhibition, recurrent inhibition, and low threshold cutaneous inhibition (Baldissera et al. 1981; Jankowska 2001). A previous suggestion that recurrent inhibition may provide gain control (Hultborn et al. 1979) faltered because of its relatively small ionotropic currents (Lindsay and Binder 1991), but the effect of inhibition on the PIC potentially provides a much larger impact on gain (Bui et al. 2008a). If inhibitory inputs can reduce gain by reducing PIC amplitude, then local spinal circuits would have the capacity for a focused, specific control of motoneuron gain (Heckman et al. 2008; Johnson and Heckman 2010).

3.2.6 Is the Oscillatory Motoneuron State Linked to CPGs for Repetitive Behaviors?

NMDA receptors are ionotropic but their behavior is unique in that they are voltage-sensitive because depolarization relieves the Mg2+ block of the channel (Hille 2001). The resulting synaptic currents behave much like a PIC and can generate large plateau potentials. Unlike PICs, however, the NMDA plateau potential is self-terminating, probably because of activation of an outward current (Manuel et al. 2012; Wang et al. 2013). The resulting NMDA-mediated oscillations have been consistently demonstrated in neonatal interneurons and motoneurons (Harris-Warrick 2011). These oscillations are intrinsic to the cell, in that they persist in the presence of tetrodotoxin (TTX) to block all inputs (Hochman et al. 1994; MacLean et al. 1997). We have recently demonstrated that the response of motoneurons to NMDA does not fade with maturation. Instead, adult rodent motoneurons exhibit very strong intrinsic oscillations in response to bath administration of NMDA—exactly like the neonatal results (Manuel et al. 2012). Thus, NMDA-mediated input may place the adult motoneuron in an entirely new, oscillatory state. The actual input system that provides the NMDA input to spinal motoneurons is unknown, but a recent study in phrenic motoneurons (Enriquez Denton et al. 2012) supports the concept that spinal central pattern generators (CPGs) for repetitive behaviors are a major source. If NMDA mediated oscillations in spinal motoneurons are in fact driven from CPGs, then this previously unknown "oscillation" state would match the electrical behavior of the motoneuron to the demands of repetitive motor tasks like scratch and locomotion.

3.3 Summary

Thus far, considerable data indicate that the electrical properties of motoneurons are reconfigured by the interactions between neuromodulation, inhibition, and NMDA-mediated inputs. We present here the hypothesis that these different states are required to match the properties of motoneurons to the extreme diversity of the normal movement repertoire. Considerable further work is required to establish this hypothesis more firmly but it appears to make good functional sense.

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Chapter 4
The Regulation of Limb Stiffness in the Context of Locomotor Tasks

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4.1 Moving in the Real World: Requirements for Muscular Activation and Limb Mechanics During Ramp Walking

Humans and other animals encounter varieties of terrain during terrestrial locomotion, including irregular and sloped surfaces. To navigate the natural terrain and its transitions, the motor system must be capable of adjusting to new physical requirements and making these adjustments quickly. In the case of sloped surfaces, alterations in muscular activation are necessary to deal with the change in orientation with respect to the gravity vector, and also with changes in the mechanical interaction of the limbs and the support surface. Furthermore, changes in the mechanical properties of the limbs are likely to be involved given that muscular function changes with slope. Walking up a slope requires predominantly propulsive action with reinforcement of force and stiffness, while walking down a slope requires some limb muscles to operate in an eccentric mode (Maas et al. 2010) in which they provide a braking action (Cham and Redfern 2002; Gregor et al. 2006; Lay et al. 2006; Prilutsky et al. 2011) with moderate stiffness.

This chapter provides a brief review of recent studies focused on these two aspects of motor control, namely, the manner in which patterns of muscular action and limb mechanics are modulated for slope walking. In these investigations, we used quadrupedal animal subjects. Since locomotion on sloped surfaces requires a substantial reorientation of the quadrupedal body, we presumed that this comparative approach would be helpful in discovering the underlying principles of control. As discussed below, it turned out that these principles are readily applicable to bipedal

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locomotion. The account presented here concerns the physical requirements and corresponding motor adaptations necessary for locomotion on sloped surfaces. Here we provide evidence that the spinal cord changes state[1] for different motor behaviors, including modifications in pattern-generating circuits as well as proprioceptive circuits that regulate limb mechanics. A discussion of the manner in which humans manage *transitions* in slope can be found in a recent publication (Gottschall and Nichols 2011). Since transitions in slope constitute a major contributor to injury in older individuals (Ashley et al. 1977; Tinetti et al. 1995; Polcyn et al. 1998), it is important to understand both the differences in central neural states during walking on different slopes and the manner and speed of the transitions between these states.

The relationships among limb mechanics, muscular activation patterns, and neural control during locomotion have been studied extensively in the cat (Fowler et al. 1993; Gregor et al. 2006; Maas et al. 2007; Prilutsky et al. 2011). During level walking, the hind limb swings forward, briefly yields for weight acceptance upon paw contact, then extends to provide propulsion for the next step during the subsequent stance phase (Goslow et al. 1973). During upslope walking, there is little or no yield at stance onset (Carlson-Kuhta et al. 1998; Nichols et al. 1999; Abelew et al. 2000; Gregor et al. 2006), and there is an additional requirement for limb propulsion during subsequent stance due to a reorientation of the body with respect to the gravity vector. During downslope walking, the reorientation of the body with respect to gravity tends to pitch the animal forward, requiring braking at the hip rather than propulsion. Furthermore, the distal joints undergo more substantial yield as they participate in braking (Nichols et al. 1999; Abelew et al. 2000; Gregor et al. 2006).

In a classical series of articles, Dr. Judith Smith and her colleagues described the patterns of muscular activation in felines corresponding to these and other motor tasks (Carlson-Kuhta et al. 1998; Smith et al. 1998) and the implications of these patterns for the organization of pattern-generating networks in the spinal cord. These results were later extended to include kinetic measurements (Gregor et al. 2006). Examples of key findings are as follows. During level walking, the hip extensor/knee flexor (anterior biceps femoris—aBF) subserves propulsion, and the ankle extensor (lateral gastrocnemius—LG) provides compliance during the initial yield and propulsion during the later phase of stance. The hip flexor (iliopsoas—ILIO) protracts the limb during swing and is silent during stance. During upslope walking, LG and aBF are recruited to a greater extent to provide additional propulsion, but maintain the same pattern as observed during level walking. The rectus femoris muscle (RF), a hip flexor and knee extensor, is recruited in late stance to contribute to propulsion. During downslope walking, braking at the hip is mediated by a reversal in the recruitment patterns of aBF and ILIO during stance, such that ILIO is recruited but not aBF (the "downslope" pattern). In addition, RF is also recruited early in stance and its activity late in stance is amplified, presumably to contribute to braking at the hip.

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[1] The term "state" refers to a given organization of synaptic interactions and active neuronal pathways. For example, during locomotion, pathways mediating excitatory force feedback become active, altering the state of the spinal cord.

The ankle extensor LG is recruited less during downslope walking, especially during initial stance. Changes in body configuration were also recorded in these studies. The animals tended to maintain their heads relatively level, such that the head would be pitched downward for walking upslope and upward for walking downslope, so that body orientation and neck angle changed systematically with slope.

4.2 Central Pattern-Generating Circuits are Modulated by a Body Orientation Signal for Walking on Sloped Surfaces

It occurred to us that a signal coding the orientation of the animal's body might be responsible for mediating the altered patterns of activity for downslope walking in addition to possible contributions from cutaneous and proprioceptive input from the limbs. There is a substantial body of literature from the laboratories of Ottavio Pompeiano and Victor Wilson revealing the presence of such an orientation signal in the vestibular nuclei that reaches both the cerebellum and the spinal cord (Suzuki et al. 1985; Manzoni et al. 2004). This signal is obtained by integration of vestibular and afferent input from muscle spindles in the muscles of the neck (Fig. 4.1, left panel). A signal corresponding to head orientation is detected by the otolith organs in the vestibular apparatus. Muscle spindle receptors in the small muscles linking the cervical vertebrae detect the configuration of the neck and thereby can supply information concerning the spatial relationship of the head with respect to the body (Lindsay et al. 1976). These two signals are combined in the vestibular nuclei to provide an estimate of body orientation. These results were originally interpreted in the context of the problem posed by von Holst and Mittelstaedt (1950), that proprioceptive inputs resulting from voluntary movement could interfere with the movement. These authors considered the "interaction of several afferences," in which two different sensory systems could interact to influence the ongoing movement rather than a given sensory system interacting with an efference copy signal. In this case, voluntary movements of the head would affect both vestibular and neck afferent input in opposite directions resulting in no change in the body orientation signal (von Holst and Mittelstaedt 1950; Boyle and Pompeiano 1981). Only by a change in the pitch angle of the body would a change in the corresponding signal be generated. This mechanism, a combination of "tonic neck" and "tonic labyrinthine" pathways, was originally conceived as part of a postural support system (Magnus and de Kleijn 1912; von Holst and Mittelstaedt 1950). We hypothesized (Gottschall and Nichols 2007, 2011) that this signal representing body orientation might be utilized to modify the pattern formation component of the central pattern-generating networks (Lafreniere-Roula and McCrea 2005) as well. It was this hypothesis that motivated our further studies.

To independently control head and body position, we employed the premammillary decerebrate cat preparation. Under deep surgical anesthesia, the cortices, basal ganglia, and a substantial portion of the thalamus were removed, with preservation of the subthalamic nucleus (Grillner and Shik 1973). The head of the animal was

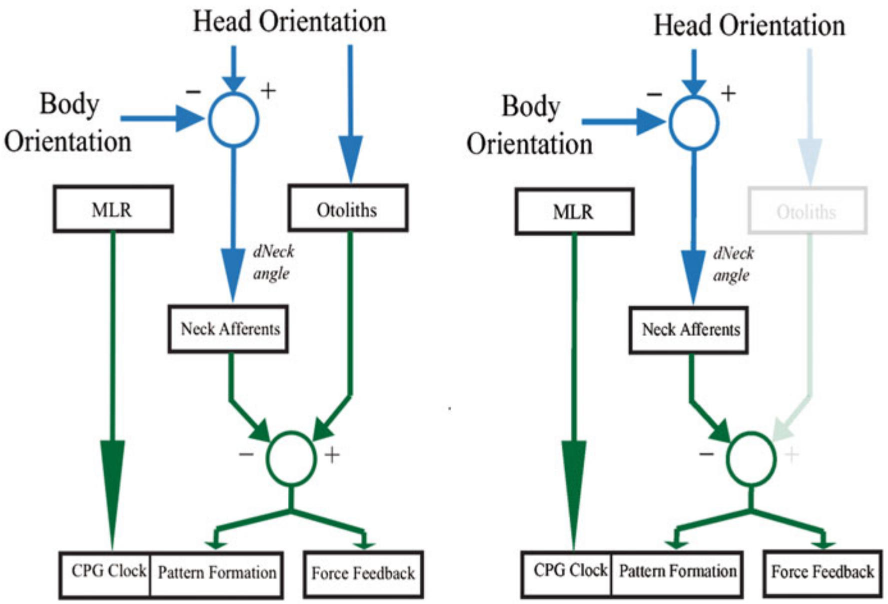

Fig. 4.1 The *left panel* shows a conceptual model providing the origin of a body orientation signal. Physical interactions are shown in *blue*. The orientation of the head is detected by the otolith organs. Proprioceptors in the neck muscles detect neck angle, which is determined by the difference between head and body orientations. The neck angle and head orientation are recombined through neural pathways to provide an estimate of body orientation, which is distributed to pattern-generating networks in the spinal cord as well as proprioceptive circuits. Movements of the head alone result in cancellation of the two signals. The *right panel* depicts the result of destruction of the vestibular apparatus. In this case, movements of the head alone lead to modulation of pattern generation and proprioceptive feedback. *MLR* the mesencephalic locomotor region

fixed in a stereotaxic apparatus mounted on the treadmill. The angle of the head with respect to the treadmill surface could be adjusted by adjusting the angle of the stereotaxic frame. Electromyographic (EMG) electrodes were implanted in selected muscles to measure muscular activation. When anesthesia was withdrawn, this preparation exhibited well-coordinated stepping on a moving treadmill. The patterns of EMG activity were in substantial agreement with the patterns observed previously (Carlson-Kuhta et al. 1998; Smith et al. 1998; Gregor et al. 2006). During level walking, LG and the posterior biceps femoris muscle (pBF, which contributes to hip extensor as does aBF) were recruited during stance, and ILIO was recruited during swing. When we changed the pitch angle of the treadmill (and therefore body orientation) to correspond to downslope walking, we observed the downslope pattern, namely activation of ILIO but not pBF during stance (Gottschall and Nichols 2007). It should be noted that, since the head was fixed in the stereotaxic frame, altering the pitch angle of the treadmill resulted in a change in the angle of the body and head with respect to gravity, but preserved the angle of the head with respect to the body. Therefore, the main sensory influence was on the vestibular apparatus with little or

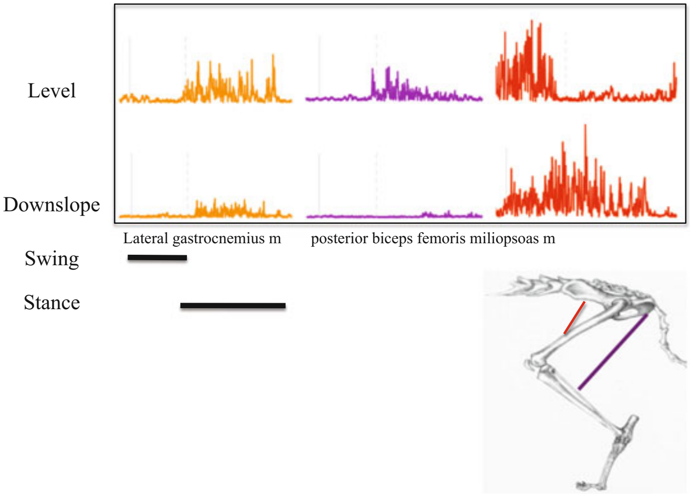

Fig. 4.2 Evidence that a body orientation signal regulates the pattern-generating networks in the spinal cord. Electromyographic activity of three selected muscles in the step following tilting of the head up are shown, for level walking (*upper traces*) and for walking down a slope (*lower traces*). The anatomical sketch indicates the approximate locations of the posterior biceps and iliopsoas (*ILIO*) muscles. Note that the hamstrings muscle posterior biceps was not activated during stance in the downslope condition, and the hip flexor ILIO became active during stance. The change in pattern corresponded to a switch from propulsion to braking between the two tasks. Although an alteration in head position alone should evoke no change in muscular patterns since body orientation is constant, the change occurred because neck afferent input is more rapid than vestibular input. This pattern of activity reverted back to the level walking state within two to three steps as vestibular and neck afferent feedback finally cancelled. After destruction of the vestibular system, the change in pattern remained in effect as long as the head was tilted (data not shown)

no effect on neck angle (see Fig. 4.1). In addition, the recruitment of LG was reduced, in agreement with previous findings (Gregor et al. 2006). These changes took place over two to three steps. In the next experiment, we left the treadmill level and changed the pitch of the head by altering the angle of the stereotaxic frame. Under these conditions, both vestibular and neck afferent inputs would be affected. According to the "interaction of several afferences" (von Holst and Mittelstaedt 1950), we should have seen no change in the pattern of muscular activity, since the vestibular and the neck afferent signals should have cancelled, corresponding to a voluntary head movement. However, when we changed the pitch of the head upward, we observed a transient change in muscular activation as appropriate to downslope walking (Fig. 4.2), but a return to the pattern observed for level walking after a few steps. Combining the results of the two manipulations, we reasoned that the afferent feedback from muscle spindle receptors in the neck musculature had a relatively rapid effect on the pattern formation network, while the vestibular input had a more delayed effect. The expected cancellation of the two signals after tilt of the head alone did occur, but only after a delay determined by the lag time of vestibular processing.

To test this hypothesis directly, we performed an additional set of experiments in which the vestibular apparatus of the animal preparations was disrupted surgically (Fig. 4.1, right panel; Gottschall and Nichols 2011). In these cases, changing the pitch angle of the head alone resulted in ongoing changes in activation patterns of ILIO and pBF. When the head was tilted up, muscular activation switched to the downslope pattern and remained in that state as long as the head was tilted up. Since the vestibular signal was no longer present to counterbalance the neck afferent signal, the pattern formation network was influenced by neck afferents alone (refer to Fig. 4.1). In summary, we had provided strong evidence that the modulation of central pattern-generating networks for slope walking is mediated by a body orientation signal derived from vestibular and neck afferent feedback.

An additional observation from the experiments described above was that the kinematics of locomotion were not visibly altered when head pitch was altered. This suggests that signals from muscle spindle receptors were not likely to change across the three conditions, nor were signals from cutaneous receptors. It is likely, however, that force feedback from Golgi tendon organs might have changed systematically with changes in muscular activation, but not enough to alter limb kinematics. In any case, it appeared that a body orientation signal derived from vestibular and neck afferent feedback had a profound effect on the pattern formation networks in the spinal cord.

Changes in body orientation are not as marked for human bipedal locomotion as for quadrupeds, but the changes in muscular function during slope walking are similar. That is, muscles are used in an eccentric or braking mode to a greater extent during downslope locomotion than during level or upslope walking (Cham and Redfern 2002; Lay et al. 2006). In addition, changes in trunk orientation have also been observed, at least for upslope walking (Prentice et al. 2004). Although the changes in trunk orientation of the cat are more dramatic than in the bipedal human, these data suggest that the evidence from the experiments reported here are relevant to human slope walking. It should also be noted that proprioceptive feedback from within the limb could contribute to the regulation of muscular patterns during walking on various surfaces. The mechanism we describe here appears to account for much of the adjustment of motor patterns in the cat, but this issue remains to be explored in the human. Indeed, EMG data were also reminiscent of the patterns of activity observed in the cat (Lay et al. 2007). Activity of the biceps femoris (BF) muscle was observed through a substantial portion of the stance phase during upslope walking, but was absent during level and downslope walking. Apparently this muscle was recruited when substantial propulsive force was needed. Although activity of ILIO was not measured in these studies, RF, which has a hip flexor action, showed an additional burst of activity during stance that was absent for both upslope and level conditions. The patterns of activity of this muscle were somewhat different between human and cat, but in both cases, the increased duration of its activity was likely to result in a contribution to braking action at the hip during downslope walking (Smith et al. 1998; Lay et al. 2007). It cannot be excluded that cutaneous and proprioceptive feedback contribute to the regulation of the pattern formation network in either cat or human, but the results discussed here indicate that the vestibular system and neck afferents contribute importantly to this regulation.

Electrophysiological studies in the cat indicate that three descending systems may contribute to the transmission of the body orientation signal to the spinal cord, namely, the propriospinal, vestibulospinal, and reticulospinal systems (Srivastava et al. 1984; Brink et al. 1985; Marchand et al. 1987). Since it had been shown that the body orientation signal can be recorded in cells of the vestibular nuclei, the vestibulospinal system is the most likely candidate for the effects observed in our studies, but contributions from the other two systems cannot be excluded. Our observations that changes in muscular activation patterns in response to manipulations of the body orientation signal without concomitant changes in kinematics, indicate the importance of extrinsic feedback to the limb in the regulation of locomotion across motor tasks. It should be noted that alterations in activation patterns of muscles in the feline forelimb were also found during locomotion on different slopes (Smith et al. 1998). Evaluation of the sensory mechanisms underlying changes in forelimb muscular activity can be accomplished using the methods described here, and these studies are planned for the future. Furthermore, the potential role of proprioceptive inputs from within the limb remains to be explored.

4.3 Endpoint Stiffness Is Also Modulated Appropriately by the Body Orientation Signal

In addition to reconfiguration of central pattern-generating networks for slope walking, changes in the mechanical properties of the limbs are also necessary. During upslope walking, the antigravity muscles are used primarily for propulsion and undergo predominantly active shortening. Under these conditions, reinforcement of force output is important, and excitatory force feedback may contribute substantially to this reinforcement (Duysens and Pearson 1980; Duysens et al. 2000; Donelan and Pearson 2004; Donelan et al. 2009). Translated into mechanical terms, this reinforcement would be measured as an increase in stiffness. During downslope walking, high stiffness would not be appropriate given that the musculature is utilized for braking, or eccentric mode where moderate stiffness would be more appropriate to absorb the energy resulting from negative work. We reasoned that the same signals that regulate pattern formation networks might also regulate limb stiffness through modulation of proprioceptive pathways.

In more recent experiments, we have measured limb stiffness in the decerebrate preparation in the level and downslope states. In this case, we employed the conventional intercollicular decerebrate cat, since active locomotion was not required. In this preparation, the brainstem is transected through the superior colliculi. Interruption of the pathways from the subthalamic nucleus precludes spontaneous locomotion that is characteristic of the premammillary preparation. Limb stiffness was measured by connecting the pads of both hind paws to force–moment sensors mounted on multiaxis robotic arms and by stabilizing the pelvis of the animal. In this way, we could

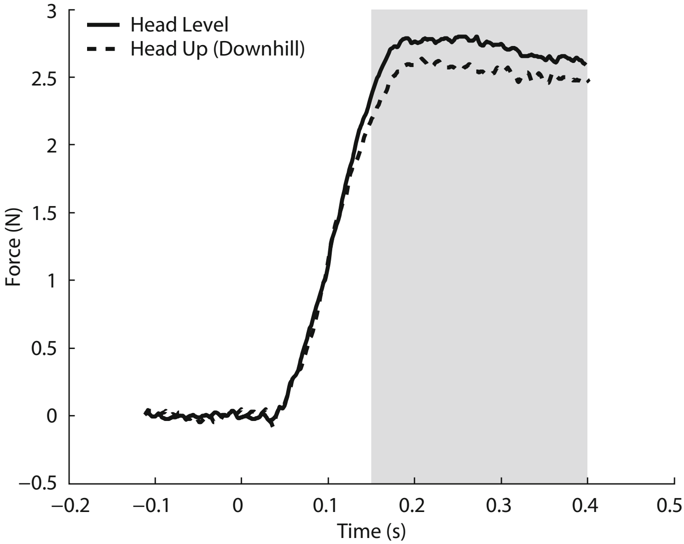

Fig. 4.3 Demonstration that stiffness measured at the endpoint of the limb is reduced for the spinal state corresponding to walking down a slope (head tilt up following labyrinthectomy). Traces represent force trajectories in response to 2 cm perturbations of the limb imposed by a robotic arm along the long axis of the limb in the direction of limb compression. A large number of responses were collected over a range of background forces, and the means for the two conditions (*head level and head up*) are shown. The main effect of condition is statistically significant in the shaded region

measure forces in all three directions in response to motions of the robotic arm. As in the previous experiments described above, the two states were produced by altering head pitch following destruction of the vestibular system. Measurements were obtained from each limb individually, since we desired to isolate the contribution of sensory pathways within the limb. Figure 4.3 illustrates the force trajectory for the limb when subjected to a ramp-and-hold perturbation delivered along the long axis of the limb for the two states. The magnitude of the force is smaller in the downslope state, in confirmation of our hypothesis. Each trajectory is the average of a large number of individual responses obtained over a range of background forces, so the result is a main effect of head position. Even more recently, we have measured stiffness in different directions and confirmed that tilting the head-up results in a lower stiffness in multiple directions (Tuthill and Nichols 2012). Endpoint stiffness of a limb is usually expressed as an ellipsoidal field, with the major axis directed approximately along the long axis of the limb. In our recent results, both major and minor axes were reduced in magnitude in the downslope condition. These results were obtained during static force production in intercollicular decerebrate preparations, so the associated pathways apparently operate independently of locomotion.

4.4 Modulation of Stiffness Is Mediated by Changes in Intermuscular Force Feedback

The observation of modulation of endpoint stiffness provided an opportunity to test the hypothesis that muscular and therefore limb stiffness is regulated by the integration of force and length feedback in the spinal cord. The hypothesis was originally proposed for the regulation of stiffness in individual muscles (Houk 1972). Excitatory length feedback from muscle spindle receptors converging with inhibitory force feedback (Granit 1950) from Golgi tendon organs at the level of the motoneuron theoretically would result in the regulation of stiffness. Increased gain of autogenic (self) length feedback would lead to increased stiffness, while increased autogenic force feedback would result in the decrease in stiffness. Both pathways would compensate for muscular fatigue and other nonlinear or nonstationary properties of muscle. Evidence was subsequently obtained that stiffness is indeed regulated, since certain nonlinear properties are compensated in the presence of autogenic feedback (Nichols and Houk 1976; Huyghues-Despointes et al. 2003). Later research, however, showed that the observed stiffness regulation was most likely mediated by length feedback alone (Houk et al. 1981) for two reasons. First, little evidence was obtained for substantial autogenic force feedback under the same conditions. Second, the response properties of muscle spindle receptors are appropriate for compensation. For example, muscle spindles are more sensitive to increases in length than decreases, and muscular stiffness is greater for shortening than lengthening. The two asymmetries are complementary, so the result is that the stiffness exhibited by the muscle-reflex system is more symmetrical for shortening and lengthening.

This evidence did not support the original hypothesis that length and force feedback around an individual muscle regulates the stiffness of that muscle, and as well left the functional role of inhibitory force feedback poorly understood. A new version of this hypothesis became apparent when we reviewed the research of Eccles and coworkers (Eccles et al. 1957). In that study, the distribution of di- and trisynaptic pathways from group Ib afferents, presumably from Golgi tendon organs, was mapped in the feline spinal cord. These studies revealed extensive intermuscular linkages between the antigravity muscles of the hind limb. In a series of papers we confirmed and extended these findings, and also showed that the pathways in question were force dependent (Bonasera and Nichols 1994, 1996; Wilmink and Nichols 2003). Furthermore, we showed that these inhibitory pathways were active during locomotion and polarized such that force feedback from more proximal muscles was focused on the distal musculature (Nichols and Ross 2009; Ross and Nichols 2009). Therefore, rather than a modular model in which each muscle is separately regulated, the evidence suggested that limb stiffness is regulated by a proprioceptive network in the spinal cord, and that the site of the regulation is the musculature of the distal limb, muscles which are directly responsible for the mechanical interaction of the body with the environment.

Data has also accumulated supporting the hypothesis that an excitatory pathway from Golgi tendon organs is active during locomotion (Guertin et al. 1995; Angel et al.

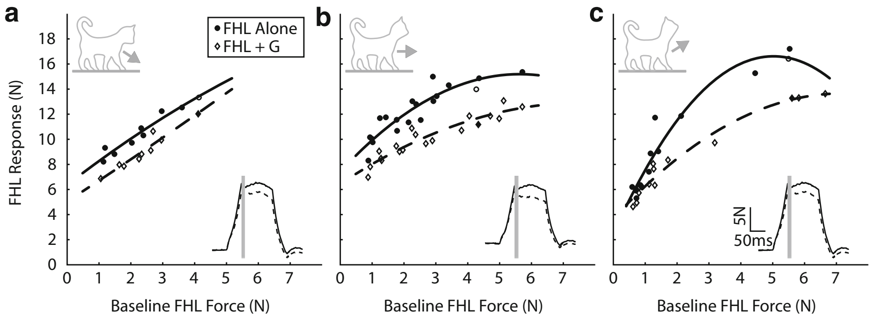

Fig. 4.4 Evidence that the change in limb stiffness after head tilt in a labyrinthectomized, decerebrate animal is due at least in part to modulation of inhibitory force feedback. The central panel represents the control condition with the head level. Closed circles represent force responses (obtained at the end of a ramp stretch (see inset, *solid lines; vertical gray bar* denotes time of measurement)) of the flexor hallucis longus muscle (*FHL*) obtained at different background forces (group 1). Force was modulated using a crossed-extension reflex, a response that naturally habituates with time, providing a range of background forces, and was obtained by electrical stimulation of the tibial nerve in the contralateral limb. *Open diamonds* represent the responses of FHL when the gastrocnemius (*G*) muscles were stretched simultaneously (group 2, *dashed* responses in insets). The data points corresponding to the force trajectories shown in the insets are denoted by *open circles* and *closed diamonds*, respectively, for groups 1 and 2. The *lines* signify *quadratic least squares* fits to the data points. The extent of inhibition corresponds to the difference between the two fitted lines. The *left panel* depicts the condition in which the head was tilted down, corresponding to walking up a slope. Note that the magnitude of inhibition was reduced across the range of forces. The right panel depicts the condition for downslope walking. Note that inhibition was greater than in the other two conditions. In this experiment, the animal was not stepping, indicating that the modulation of force feedback can occur under steady postural conditions as well

1996; Duysens et al. 2000; Donelan and Pearson 2004). We observed what appeared to be excitatory force feedback during locomotion in premammillary preparations (Ross et al. 2005), but this feedback was limited to autogenic feedback around the gastrocnemius (G) muscles and coexisted with intermuscular inhibitory feedback. Since the G muscles are biarticular, linking the ankle and knee joints, this excitatory feedback would have the effect of coupling the two joints and influencing ankle stiffness as well. Therefore, the net stiffness of the limb, and the distribution of stiffnesses at the different joints of the limb would be strongly influenced by the three sources of feedback, excitatory length feedback from muscle spindles, and inhibitory and excitatory force feedback from Golgi tendon organs.

Since we had shown that limb stiffness varies with the motor task through the body orientation signal, we sought to identify the underlying mechanisms. We undertook a new project evaluating the magnitude of excitatory length and inhibitory force feedback when the body orientation signal was varied. In order to do this, we measured the magnitudes of the stretch reflex and of force-dependent inhibition in decerebrate (intercollicular), labyrinthectomized animals (Tuthill and Nichols 2008). The main result can be illustrated using the G muscles and the long toe flexor, the flexor hallucis longus muscle (FHL). The tendons of these muscles were dissected free from their insertions and connected to servo-controlled linear motors. The femur and tibia of the limb were rigidly fixed to a baseplate. Stretches were applied to FHL over a range of forces, and the effect of stretching G on those responses was tested at matched forces. In order to control for fatigue and other time varying factors, we alternated stretching FHL alone with stretches of both muscles simultaneously as force declined during a crossed-extension reflex. Previous research in which this protocol was used had shown strong inhibition from G to FHL (Bonasera and Nichols 1994). The central panel (b) of Fig. 4.4 illustrates the previous result, namely, that stretch of G reduces the response of FHL over a wide range of forces, and this inhibition increases with background force. In the condition shown in panel (a), the head was pitched downward corresponding to upslope walking, and the inhibition was found reduced. The most dramatic effect was observed when the head was pitched up, corresponding to downslope locomotion (panel c), where inhibition substantially increased. The magnitude of the stretch reflex was relatively little affected by the pitch angle of the head, suggesting that autogenic length feedback was not greatly affected by changes in the body orientation signal. Therefore, the evidence supports the hypothesis that pathways mediating inhibitory force feedback constitute a major site of modulation in the regulation of limb stiffness. Future work will be directed toward generalizing this result to other intermuscular pathways.

4.5 Conclusions

Taken as a whole, these studies shed light on the manner in which pattern-generating networks and proprioceptive pathways are modulated during slope walking in quadrupeds to meet the mechanical demands of these tasks, including propulsion and braking (Ahn and Full 2002). Upslope walking is characterized by the need for propulsion and concentric muscular work. Hamstrings and antigravity muscles are engaged for weight support and propulsion. During downslope walking, hip flexors are recruited to oppose the propulsion of the animal due to gravitational force, and the hamstrings are not recruited in order to prevent excessive propulsion. Distal muscles such as the triceps surae group are recruited to provide braking as well as weight support. Limb stiffness is reduced during downslope walking since a more compliant interface is required to prevent damaging forces due to the interaction of the limb with the support surface. Actions due to length and force feedback are automatically tailored to the task (Maas et al. 2007). During downslope walking, muscle spindles in the ankle extensors are likely to be particularly responsive and would regulate muscular stiffness during active lengthening of these muscles. Golgi tendon organs in the braking muscles are likely to provide regulation of distal limb stiffness through intermuscular pathways to the distal musculature. The patterns of activity of the hind limb muscles and their regulation through proprioceptive feedback are appropriately regulated according to their specific functions in these motor tasks. These principles of regulation were investigated most directly in quadrupedal animals, but, as discussed above, similar changes in the activation patterns of lower limb muscles as well as trunk orientation occur in humans during or in anticipation of ramp walking. Therapeutic approaches aimed at preserving these mechanisms in elderly individuals would seem to be important in the prevention of instability and falls in real-world locomotion.

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Chapter 5
Subcortical Visuomotor Control of Human Limb Movement

Brian L. Day

Research into the visual control of movement over the past 30–40 years has focused predominantly on cortical networks. These cortical networks are fed by information travelling along pathways from retina to occipital cortex and then to motor cortical areas via parietal cortex (dorsal “where” stream) or temporal cortex (ventral “what” stream) (Ungerleider and Mishkin 1982). Although these cortical networks are very powerful, they are not the only routes by which visual information can influence action. This chapter reviews some behavioral, neurophysiological, and neuroimaging data which converge on the idea that subcortical structures have a significant role to play in the visual control of reaching, even in primates.

5.1 Fast Arm Reactions with Limited Modifiability by Intention

It was thought for a long time that visual information influences movement through a process that is relatively sluggish compared to other sensory channels. For example, proprioceptive signals can drive muscle responses in the human hand at latencies of ∼25 ms through spinal circuitry, but even when the motor cortex is involved proprioceptive input can evoke hand-muscle responses at a remarkably short latency of 50 ms (Marsden et al. 1976). In contrast, the latency of visually driven reactions was traditionally put at 200–300 ms (Keele and Posner 1968; Beggs and Howarth 1970). From the 1980s onwards, however, experiments investigating the speed at which new visual information can modify ongoing limb movements revised this value down dramatically to 100–150 ms (Carlton 1981; Soechting and Lacquaniti 1983; Zelaznik et al. 1983; Paulignan et al. 1990, 1991; Prablanc and Martin 1992).

The explanation for this halving of visuomotor latency was not immediately apparent. It could have been due to methodological differences or possibly due to

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technological advances offering more sensitive means of recording limb trajectories. Another and more physiological possibility is that these discrepant latencies actually reflect the operations of distinct visuomotor processes. This was indeed the conclusion that was reached based on the results of an experiment that investigated the ability of human subjects to modify voluntarily their visually driven reach adjustments (Day and Lyon 2000).

In this experiment, subjects were seated in a darkened room and were required to reach out and touch an illuminated disk with the index finger. In random and sparse trials (one in three), at the instant the finger was lifted, the illuminated disk slid 10 cm either to the right or the left with equal probability. In one block of trials, subjects were instructed to keep trying and touch the disk even if it moved. In a separate block, they were instructed to touch the disk if it remained stationary, but if they saw it move, then to move their finger in the opposite direction. In effect, this was an anti-reach task not dissimilar to that of an oculomotor anti-saccade task (Hallett 1978; Hallett and Adams 1980). The idea here was to see whether the fast visual-evoked reach adjustments are truly voluntary. If so, subjects should have no difficulty in replacing the fast response in the direction of target movement with an equally fast response in the opposite direction during the anti-reach task. The results of the experiment showed clearly that subjects were unable to do this.

When the target moved during the pro-reach task, subjects adjusted the trajectory of the reaching finger at latencies of between 120–160 ms, ending up accurately on the shifted target. In the anti-reach task, more often than not the finger's trajectory was also adjusted at short latency, but as in the pro-reach task this acted to take the finger in the direction of the target rather than in the opposite, instructed direction (Fig. 5.1). Despite this inappropriate early adjustment, the finger underwent a subsequent reversal at around 220 ms, this time to drive the finger in the opposite direction to comply with the instructions.

The two sequential responses observed in the anti-reach task are highly suggestive of two processes being active. One appears to be a fast-acting process that spatially links the arm movement with the target movement in a compatible and relatively inflexible way. The other process takes longer to act but is flexible allowing an arbitrary spatial association between the visual stimulus and the action. It is tempting to speculate that this slower, flexible process involves cortical processing (Wise et al. 1996) whereas the fast inflexible one is subcortically organized.

5.2 Does the Leg Behave like the Arm?

Most people spend a good proportion of their waking hours reaching for objects with their hand. Perhaps with the exception of professional soccer players, the foot is not routinely used in this way. However, ordinary walking often requires accurate foot placement that relies upon on-line visual control (Reynolds and Day 2005b). It is reasonable to enquire, therefore, whether the lower limb has access to the same fast-acting visuomotor process that controls the upper limb. One might expect this to be the

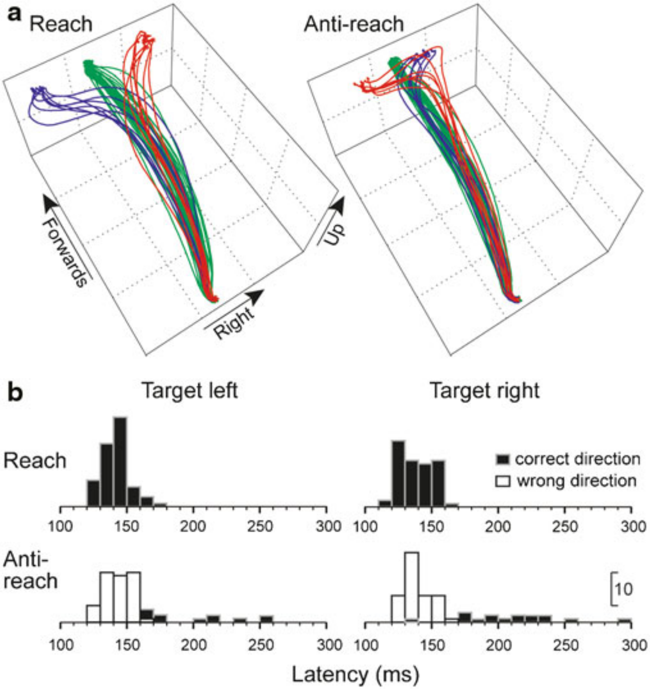

Fig. 5.1 Spatial and temporal properties of arm reach adjustments evoked by a moving target. **a** 3-D superimposed trajectories of the finger from multiple trials of one representative subject when the target remained stationary (*green*), moved right (*red*), or moved left (*blue*). The subject executed either a normal reach (*left panel*) or an anti-reach (*right panel*) task (see text). Note the initial deviation of the finger towards the target in both tasks. **b** Latency histograms of the *initial* deviation of the finger in all trials in which the target moved. Responses grouped in 10 ms bins and shaded according to whether in the correct (*black bars*) or incorrect direction (*white bars*). Note for the anti-reach task most responses were initially in the incorrect direction, with the same latency as correct response in the normal reach task. The small number of initially correct responses in the anti-reach task tended to occur with longer and more variable latency. (Modified from Day and Lyon 2000)

case if upper-limb reaching movements have evolved from stepping movements, as has been suggested (Georgopoulos and Grillner 1989). On the other hand, mid-flight adjustments of a stepping foot carry potentially serious consequences that upper limb adjustments do not. This arises from the need to maintain balance when stepping. It has been shown that the trajectory of the body during a step and the position of the stepping foot at the end of the step are closely coordinated and determined before the foot leaves the ground (Lyon and Day 1997, 2005). Any mid-flight alteration of stepping-foot trajectory will violate this relationship and potentially leave the body in an unstable state should the foot return to the ground at an unplanned location.

To examine this issue, experiments analogous to the arm-reaching experiments were performed using a jumping floor-mounted target which subjects stepped onto

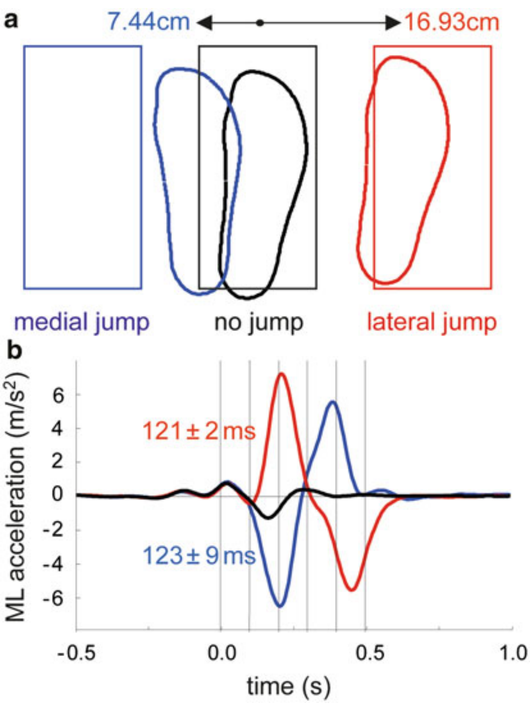

Fig. 5.2 Spatial and temporal properties of foot adjustments when stepping onto a floor-mounted jumping target. **a** Group mean final foot position at the end of the step when the target remained stationary (*black*), jumped laterally (*red*), or jumped medially (*blue*). Note the smaller deviation of the foot for medial target jumps. **b** Group mean mediolateral acceleration of the foot with time (lateral positive), colour coding as in **a**. Note the short latency of foot adjustment irrespective of target-jump direction. (Modified from Reynolds and Day 2005)

(Reynolds and Day 2005a). In one condition, subjects stepped in a natural fashion onto the rectangular illuminated target, which in some trials could jump laterally or medially at the instant the foot left the ground. In a second condition, the same stimuli were employed with the subject upright, but now fully supported by an external framework. In this latter condition, therefore, the usual balance constraint was not present and the leg movement task more closely resembled an arm-reaching task. The key result of this study was that the jumping target evoked short-latency (< 150 ms) mid-flight adjustments of the leg indistinguishable in latency from those of the arm (Fig. 5.2b). The amplitude of the leg adjustment, particularly for medial target jumps (Fig. 5.2a), was less during free steps compared to frame-supported steps, reflecting the limitations imposed by the need to maintain balance. However, the latency was identical irrespective of whether or not the body was supported by the frame. Thus, it seems that the leg, like the arm, has access to a fast-acting visuomotor process, but with additional integration with balance processes. Given the correspondence in latency, a parsimonious explanation is that the upper and lower limbs share a common fast-acting visuomotor mechanism.

5.3 Testing the Subcortical Hypothesis

The opportunity arose to test the hypothesis that the fast (< 150 ms) visual-evoked reach adjustment stems from a subcortical visuomotor process (Day and Brown 2001). This was provided by a patient who was discovered to have agenesis of the corpus callosum and an absent or vestigial anterior commissure, and therefore no direct connection between the left and right cerebral cortices. She was unaware of her condition and was otherwise healthy (apart from a headache that initiated the brain magnetic resonance imaging (MRI) scan to reveal the abnormality) with normal functioning corticospinal tracts. The idea was to measure the crossed–uncrossed latency difference in this patient, a method that was conceptualized 100 years ago (Poffenberger 1912) and which had been used previously in the study of split-brain patients (Jeeves 1969; Kinsbourne and Fisher 1971; Milner 1982; Milner et al. 1985; Clark and Zaidel 1989). The method relies upon cortical lateralization whereby visual information in each hemifield is transmitted to contralateral occipital cortex while each upper limb is controlled by contralateral motor cortex. If the visual hemifield and responding limb are on the same side (e.g., right arm reaching for right-sided target while looking straight ahead), then all cortical processing can be done within one cerebral hemisphere resulting in an "uncrossed" response. However, if the arm and visual hemifield are on opposite sides (e.g., right arm reaching for left-sided target), then information has to pass from one hemisphere to the other resulting in a "crossed" response. In the absence of a corpus callosum, which is the most direct route for communication between the left and right cortices, a more circuitous route is required resulting in a crossed response with a longer latency than normal.

To establish the soundness of this theory in the acallosal subject, a task was employed that required an arbitrary movement in response to a visual stimulus. It was thought that the arbitrary association between visual stimulus and action would engage a cortical network (Wise et al. 1996) and reveal a significant crossed–uncrossed latency difference. The tasks were to lift vertically either the index finger (distal movement) or the forearm (proximal movement) in response to illumination of a disk randomly presented laterally in one or the other hemifields while fixating a central light-emitting diode (LED). As predicted, the crossed reaction time in the acallosal subject was 36 ms slower on average than the uncrossed reaction time (Fig. 5.3a), a difference that was not present in healthy subjects.

Having established a clear crossed–uncrossed latency difference in the acallosal subject for arbitrary visuomotor associations, the next step was to see whether the same difference was present for the nonarbitrary task of reaching for a jumping target. Importantly, the target and its locations for this task were identical to that used in the arbitrary association task. The critical observations were that for this reaching task, the reaction times were considerably faster than for arbitrary visuomotor associations (120 vs. 320 ms) and were the same irrespective of which hand was used and which hemifield the target jumped into (Fig. 5.3b). In other words, for the acallosal subject, there was no apparent crossed–uncrossed latency difference when executing a mid-flight reach adjustment to acquire a displaced target. This result could not be explained by very early eye movements bringing the displaced target back into central vision since for this subject, lateral saccades always occurred after the arm adjustment was initiated (Fig. 5.3b). The compelling conclusion was therefore that the visual-evoked reach adjustment did not use the cortical networks employed for arbitrary visuomotor associations. This suggested strongly that subcortical centers were being employed to drive the hand towards visually presented targets.

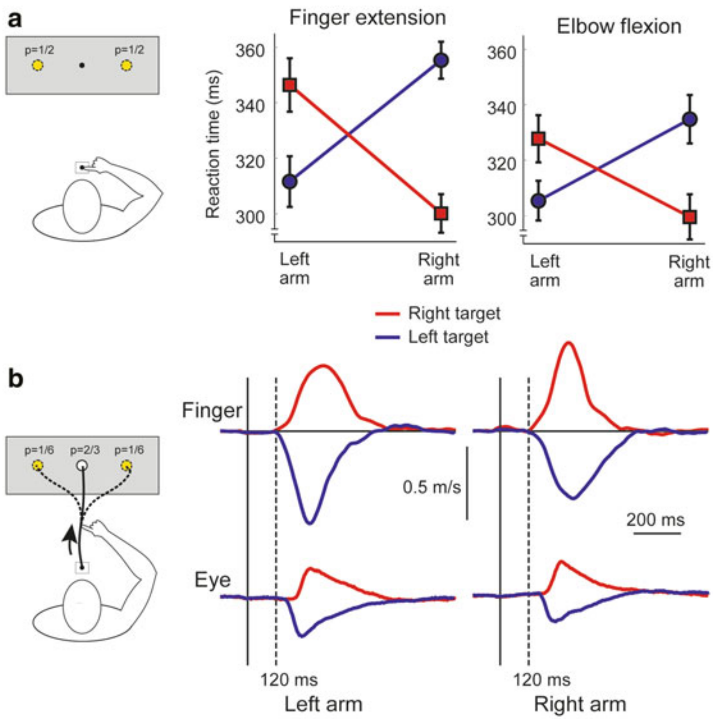

Fig. 5.3 Manual responses to visual stimuli appearing in the right or left hemifield in a subject with agenesis of the corpus callosum. **a** Reaction time to initiate arbitrary motor tasks (finger extension, elbow flexion) in response to target appearance in right (*red*) or left (*blue*) hemifield during central fixation. Note the significant interaction between arm side and target side for both arbitrary tasks. **b** Mediolateral motion of the finger and eyes when reaching to a central target which unpredictably jumped into right (*red*) or left (*blue*) hemifield during the reach. Top traces show mean mediolateral velocity of finger in jump trials after subtraction of mean no-jump trials. Bottom traces show mediolateral motion of the eyes in jump trials recorded electro-oculographically (high-pass filtered). Note the same short latency of finger deviation irrespective of limb side or target side, and that eyes deviated towards target after limb movement was initiated. *P*-values above targets (*left panels*) denote probability of target appearance at respective locations. (Modified from Day and Brown 2001)

5.4 Evidence for Involvement of the Superior Colliculus in Visually Guided Reaching

The superior colliculus and underlying mesencephalic reticular formation are good candidates for a subcortical visuomotor processing centre controlling the limbs. The superior colliculus receives visual input directly from the retina (Kaas and Huerta 1988), and, although classically involved in gaze control through control of eye (Sparks 1978) and head (Cowie and Robinson 1994), was discovered also to contain arm-movement-related neurons (Werner et al. 1997a). These neurons occur throughout the depth of the monkey's superior colliculus, apart from the most superficial layers, as well as in the underlying mesencephalic reticular formation. The "reach" neurons have a different spatial distribution to visually responsive cells or saccadic units in that they occur most frequently in the deeper layers (Werner et al. 1997b). For retinal information to drive arm movements, visual signals need to undergo transformation from an oculocentric coordinate frame to an arm-centered frame. There is some evidence of this sort of transformation in the superior colliculus as shown by two kinds of reach neurons (Stuphorn et al. 2000). One type, located in intermediate layers of superior colliculus, has links to an oculocentric frame in that its firing is gaze-related. The other type, located in the deep layers of superior colliculus and underlying mesencephalic reticular formation, is gaze-independent and therefore associated with an arm-centered frame. Their firing patterns correlate well with electromyography (EMG) patterns of arm muscles during reaching movements, particularly for the proximal muscles of the shoulder girdle (Stuphorn et al. 1999).

Evidence in man for the involvement of these structures in reaching control comes from a functional MRI (fMRI) study (Linzenbold and Himmelbach 2012). In this study, human subjects simply reached with either arm to visual targets presented in the left or right hemifields, whereupon increases in the BOLD signal were observed in the region of the superior colliculus. Unsurprisingly, some of this signal change could be attributed to saccadic activity, but there was another dissociable activity present. This activity, in contrast to saccade-related activity, tended to be lateralized to the reaching arm and occurred in deeper layer locations. Thus, the spatial distribution of these human signals corresponds to the distribution of reach neurons in the monkey superior colliculus and plausibly reflects the operation of an analogous process.

If activity within the superior colliculus is rapidly able to influence reaching movements, there must be a fast-acting route that transmits the motor signal from colliculus to spinal motoneurons. Courjon and colleagues showed that such a motor pathway is functional in the cat during a visually guided reach (Courjon et al. 2004). They stimulated in the deep layers of the superior colliculus using a 300 Hz train of stimuli for 70–200 ms during a reach for a piece of food. This stimulus consistently caused the cat's reaching limb to deviate from its unstimulated trajectory with an average latency of just 56 ms. In about half the stimulated trials, this deviation occurred without a concomitant gaze or head perturbation thereby ruling out the possibility of the limb deviation being indirectly evoked by a gaze shift. The output pathway could be via direct tectospinal fibers, which project to C3–C4 propriospinal neurons (Illert et al. 1978) thereby engaging spinal reach machinery. They are dense in the cat (Nudo and Masterton 1989; Olivier et al. 1991), but much less so in other mammals including primates (Nudo and Masterton 1989). An alternative and not mutually exclusive possibility is that motor signals travel via the tectoreticulospinal tract (Werner et al. 1997b). Alstermark and colleagues provided some support for the involvement of this pathway by demonstrating a prolongation of the cat's reach adjustment latency to a jumping target after a presumed lesion of the tectoreticulospinal tract (Alstermark et al. 1987).

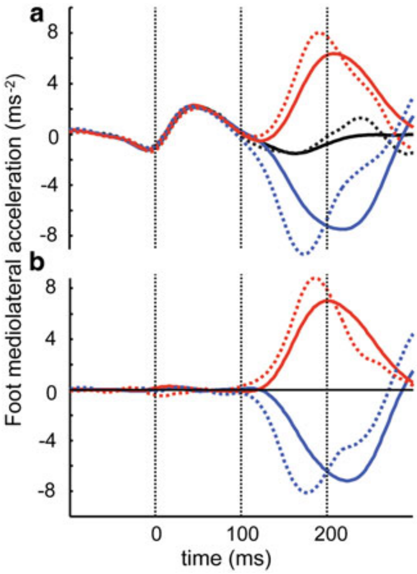

Fig. 5.4 Effect of loud sound on latency of foot adjustments to a jumping target during a step. **a** Group mean mediolateral acceleration of foot during trials with no target jump (*black*), lateral target jump (*red*) or medial target jump (*blue*), and with (*dashed lines*) or without (*continuous lines*) a loud sound at moment of foot lift from floor. **b** Same as **a** but with foot acceleration during no-jump conditions subtracted from all traces. Note the hastening of response to target jump when combined with a loud sound. (Modified from Reynolds and Day 2007)

5.5 Indirect Evidence for Reticulospinal Involvement in Man

Reticulospinal tracts are thought to transmit the auditory startle response from the caudal reticular formation of the human brainstem to spinal cord both in healthy subjects (Brown et al. 1991a) and in patients with pathological exaggerated startle or hyperekplexia (Brown et al. 1991b). This raises the possibility that the putative subcortical mechanism controlling visually guided reaching may share some circuitry with the auditory startle mechanism. This was investigated during stepping to visual targets by interacting target jumps and loud sounds (Reynolds and Day 2007).

In this experiment, subjects stepped naturally onto an illuminated rectangle, which in a third of trials jumped to the left or right with equal probability at the moment the foot lifted from the ground. In just 18 of the total 240 trials, a startling loud sound (120 dB SPL) was given through headphones at the point of foot lift, but with the startle trials occurring with equal probability during no-jump, jump-right, and jump-left trials. Therefore the loud sound conveyed no information about the presence of a target jump or its direction. As in a previous study (Reynolds and Day 2005), the jumping target evoked a fast adjustment of the foot trajectory, at 134 ms on average when measured from acceleration traces, with medial displacement magnitudes being less than lateral displacements. The loud sound had no effect on control steps or on the magnitude of foot displacement following a target jump. However, the loud sound did affect the latency of the foot correction, shortening it by some 20–30 ms (Fig. 5.4).

This hastening of the visual-evoked foot trajectory adjustment was not a nonspecific effect of a startle because the foot always moved in the direction of the target jump when present and did not deviate during no-jump trials. Nor was it due to release of a subcortically stored motor program (Valls-Sole et al. 1999; Carlsen et al.

2004) since the required adjustment was not known in advance of the sound stimulus. Instead, it seemed that the sound stimulus interacted with the visual stimulus provided by the target jump to cause a reduction in visuomotor processing time. By taking account of likely afferent and efferent conduction delays, Reynolds and Day (2007) estimated that even a modest hastening of 18 ms would represent a substantial reduction of 30 % in central processing time. It is plausible that this interaction occurs in the brainstem, possibly in the superior colliculus, but perhaps more likely in the reticular formation.

5.6 Indirect Evidence for Superior Colliculus Involvement in Man

When there is choice in selecting one action over another, and if the selected action is determined by an external signal such as a visual stimulus, it is often found that the time taken to react increases with the number of choices available. This relationship between number of response choices and reaction time was formalized by Hick using information processing theory (Hick 1952) and is often referred to as Hick's law. Although Hick's law holds for many manual tasks, it does not hold for visually guided saccades. Kveraga et al. (2002) showed that the latency of a saccade to a visual target is the same irrespective of whether there are eight possible targets or just one. They explained this violation of Hick's law by referring to the anatomical arrangement of the superior colliculus, where visual afferents form a retinotopic map that lies in spatial register with an oculomotor map determining saccade direction and amplitude. With this arrangement, a visual stimulus on the retina automatically evokes a saccade that brings the visual target onto the fovea, making the central processing time immune to the number of possible target locations. When this highly compatible spatial relationship between stimulus and response was destroyed by asking subjects to make eye movements in the opposite direction to a peripheral visual stimulus (anti-saccade), Hick's law was reinstated (Kveraga et al. 2002).

It could be argued that fast visually guided limb movements also should violate Hick's law if they utilize the neural machinery of the superior colliculus. This was tested using a centre-out pointing task (Reynolds and Day 2012). For this, subjects held a finger stationary in front of a central target on a vertical board and were required to make a rapid discrete movement in response to the appearance of a peripheral target (Fig. 5.5a). Four visual targets were located 15 cm above, below, left and right of the central target. To eliminate temporal uncertainty about when an event might happen, the subject initiated a trial by raising the opposite index finger from a touch switch. In 67 % of trials this did nothing (null trials), but in the remaining 33 % it caused the central target light to be extinguished and one of the four peripheral targets to be illuminated. Subjects were given advance information which of the peripheral targets might be illuminated in a trial (between one and four targets) thereby manipulating the number of action choices. In one condition, the stimulus–response compatibility was high in that subjects were required to move

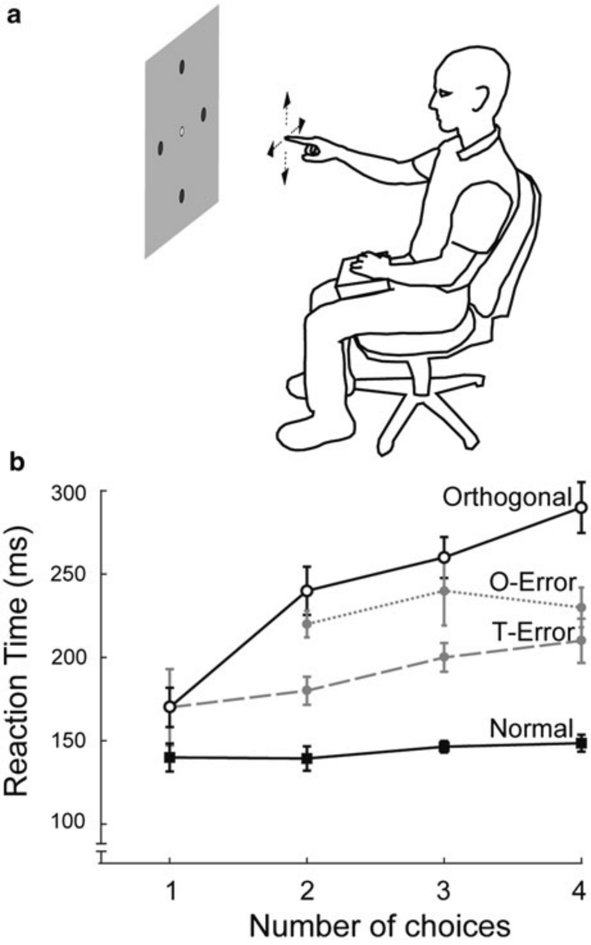

Fig. 5.5 Effect of stimulus–response compatibility and number of choices on reaction time to visual stimulus. **a** Experimental set-up (see text for details). **b** Reaction time against number of choices for high S–R compatibility (*normal pointing*) and low S–R compatibility (*orthogonal pointing*) conditions. Reaction times for erroneous responses during orthogonal pointing are shown when the finger moved in the direction of the target (T-error) or in some other incorrect direction (O-error). Note the constancy and brevity of normal pointing reaction time regardless of number of choices. (Modified from Reynolds and Day 2012)

their finger in the direction of the illuminated target (normal). In a second condition, the stimulus–response(S–R) compatibility was low as they were required to move their finger in a direction 90° clockwise to the illuminated target (orthogonal).

As predicted, for normal pointing with high S–R compatibility, the reaction time was fast at around 140 ms and remained the same regardless of the number of choices. In contrast, for the orthogonal pointing task the reaction time was slower, being 173 ms for the 1-choice condition (i.e., simple reaction time), and it increased with number of choices, thus obeying Hick's law (Fig. 5.5b). Therefore, in many ways the pointing behavior was very similar to the saccade behavior described above (Kveraga et al. 2002). As with the eyes, the violation of Hick's law when there was a direct spatial correspondence between the visual stimulus and the limb movement suggests a mechanism with relatively hard-wired direct mapping between the two. A parsimonious interpretation is that the superior colliculus lies at the heart of the mechanism for visually guided pointing as it does for visually guided saccades. The radically different behavior during orthogonal pointing suggests the possibility of a slower mechanism being brought into play. Of course, for a slower mechanism to dominate the faster mechanism, the latter would have to be suppressed in some way. Interestingly, subjects tended to make errors by sometimes pointing incorrectly at the illuminated target in the orthogonal condition (T-error in Fig. 5.5b), with these erroneous movements usually being initiated faster than the correct movements. This is compatible with two competing mechanisms where there is an incomplete suppression of the faster process. As suggested in an earlier section to explain anti-reach behavior (Day and Lyon 2000), orthogonal pointing could engage a cortical mechanism, which would give the advantage of flexibly associating any action with a visual signal thereby avoiding the necessity of a direct spatial correspondence between stimulus and response. The cost is a longer response latency that grows with choice (Hick's law) because of the additional information processing required for stimulus identification and action selection.

5.7 Communication Between Cortical and Subcortical Visuomotor Processes

The picture painted so far in this chapter is of two processes for visual guidance of limbs, one subcortical and the other cortical. The subcortical process is fast, but rigid, and is well suited for direct interactions between the limb and an object when both occupy a common space. In contrast, the slower cortical process conceivably is infinitely flexible and may be better suited for visuomotor interactions during tool use. This flexibility effectively detaches the limb from the object and allows any arbitrary spatial relationship between the two, for instance, tracking vertical movements of a target on a computer screen with a cursor controlled by forward–backward movements of a mouse. However, it is unlikely that the two processes operate independently of each other. As a minimum, the subcortical process would need to be suppressible under certain circumstances. As we have seen, when a person is engaged in interacting with an object directly with the limb, suppression is difficult to achieve and often incomplete. Thus, during an anti-reach task, invariably the limb is initially drawn towards the target's new position, although with less vigor compared to a standard reach (Day and Lyon 2000). Similarly, orthogonal pointing is possible but at the expense of occasional errors towards the visual stimulus, indicating an intrusion of the fast process (Reynolds and Day 2012). Presumably, there are stronger suppression signals available when the limb operates remotely from the near space of an object or via an interposed tool. Communication between the two processes would also be necessary if, as is likely, they act in concert during direct interactions between a limb and an object. There is a wealth of connections between action-related areas of cortex and relevant subcortical structures such as the superior colliculus (e.g., Kuypers and Lawrence 1967; Goldman and Nauta 1976; Catsman-Berrevoets et al. 1979; Fries 1984, 1985) and the reticular formation (e.g. Catsman-Berrevoets and Kuypers 1976; Keizer and Kuypers 1984). These fibres could provide the communication required for cooperation between cortical and subcortical visuomotor processes.

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Chapter 6
Rethinking the Role of Motor Simulation in Perceptual Decisions

Scott T. Grafton and Shivakumar Viswanathan

6.1 Introduction

Goal-oriented action demands a constant ebb and flow of information processing between perception and movement. Decisions about whether or not a task can be executed, such as jumping over a gap or reaching to switch a light, demand reliable perceptual evidence. Likewise, perceptual decisions that are particularly subject to optical distortion might benefit from physical knowledge gained through motor experience. For example, the inaccurate estimation of angles and azimuths during navigation could benefit from a motor-based simulation of the body moving in the world. One of the ways these kinds of decisions can be achieved is by conscious access to the motor system to form virtual movements. We can imagine jumping over the gap, and use this to influence our decision to act. Or we can imagine turning ourselves in the environment to get a better estimate of the relative bearing between locations. Increasing evidence suggests that motor simulation of this sort can aid subsequent overt motor performance, increase the rate of skill acquisition, and potentially be used to solve cognitive or perceptual problems involving the physical environment (Holmes and Collins 2001; Mulder et al. 2004). Understanding what behavioral or neural signatures constitute a motor simulation is an essential step for understanding how simulation might actually influence overt motor behavior or enhance perception. In this chapter, we consider a widely used experimental protocol that is broadly assumed in the literature to represent motor simulation, the hand judgment or laterality task (Cooper and Shepard 1975; Parsons 1987a). We provide overwhelming evidence that the behavioral phenomena associated with this task are not a result of motor simulation, and provide an alternative interpretation of these studies. The point of this review is not to undermine motor simulation as an important process or concept. Rather, we argue that progress in motor simulation

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research requires a higher standard of confirmatory evidence for what constitutes motor simulation and that the behavioral effects that are commonly reported are not necessarily sufficient to conclude that a motor simulation is occurring.

The general concept of simulation emerged in the 1970s during an explosion of cognitive science directed at understanding how mental representations were manipulated to solve problems (Shepard 1978). Simulation is now widely acknowledged to be an integral component of cognition (Barsalou 2008) and as a mechanism for manipulating or transforming internal representations to new states (Kosslyn et al. 2001). A classic example of how simulation is used in perceptual problem solving is the mental rotation of complex visual objects in matching tasks. In this case, reaction times (RTs) typically correlate with the rotation angle needed to match the orientation of one object to another, revealing a mental operator with analog properties acting on the internal representation of the object (Moulton and Kosslyn 2009). The concept of motor simulation followed suit. In this form of simulation, knowledge derived from the motor system might be used to organize virtual behavior. Motor simulation has links to explicit motor imagery or emulation, where we can imagine moving our body without actually displaying any overt action (Jeannerod and Decety 1995; Decety 1996; Jeannerod and Frak 1999; Jeannerod 2001). Similar to object rotation, the time to complete imagined movements also displays analog properties corresponding with real movement (Decety et al. 1989). However, in all of these early studies of motor simulation (or equivalently, imagery and emulation), there was no cognitive or motor problem in the experiments that actually needed to be solved by the participant. Thus, it was unclear whether motor simulation is actually a meaningful operation for solving cognitive problems. While one can imagine moving one's hand, it is challenging to find real examples where this sort of action imagery is utilized for planning or execution of everyday behavior let alone for virtual motor simulation.

One of the earliest and most widely cited examples of a motor simulation process that might actually be used to solve a perceptual problem is the laterality task (Cooper and Shepard 1975). In this wonderfully simple paradigm, the subject must decide if a visual image of a hand constitutes an image of a right or left hand, and then report their choice with a button press using their own right or left hand (Luria 1966). The three-dimensional (3-D) mirror symmetry of the two hands makes them chiral objects, which could be potentially difficult for the visual system to distinguish from each other. In the laterality task, also referred to as the hand judgment task, RTs depend on the angle of rotation between the hand stimulus and an unseen vertically oriented "virtual" hand (palms directed away from the subject with the fingers pointing upward). The analog property of RTs in the laterality task created a strong conceptual link with other forms of simulation such as object rotation, suggesting there is an internal representation of the hand stimulus that is transformed to a new orientation. Cooper and Shepard interpreted the analog delay in the laterality task as part of a decision-making process involving both perceptual discrimination and response selection. They proposed that the visual system was making a holistic analysis of the object, reorienting it, and comparing it to a canonical virtual left or right hand. They wanted to know if right versus left discrimination could be solved

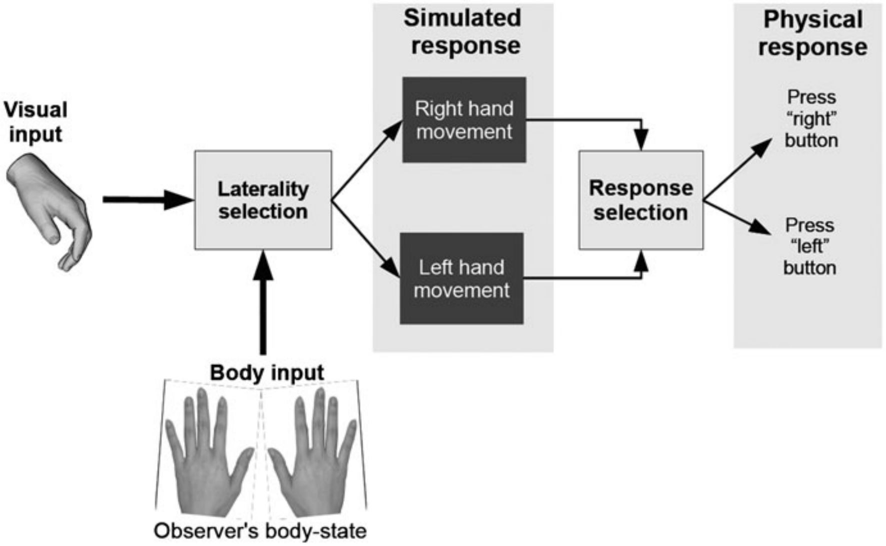

Fig. 6.1 Traditional model of motor simulation in the hand judgment task: Laterality of the visual hand stimulus is determined by comparing it to either of the "felt" hands, which are rotated by covert motor activity to a matching spatial orientation. This provides a mapping between each stimulus and the corresponding hand used to make the physical response

"without having either to preserve or to search through a store of fixed 2-D templates corresponding to all possible retinal projections." Mental rotation of the object (in this case a hand) provided an algorithm for reducing the storage and search requirements, as shown in Fig. 6.1. The simulation (and virtual hand rotation) provided new information that could be used to improve the decision-making process. While compelling as a possible cognitive mechanism, the authors fully acknowledged the fragilities of this interpretation. First, it was possible that the analog property in the laterality task was not sufficient evidence on its own to demonstrate that an object rotation was invoked to make the perceptual decision. Second, they acknowledged that if it could be demonstrated that a parts-based analysis was sufficient to solve hand identification then the use of simulated hand rotation to aid in the perceptual decision was less likely. In parts-based analysis, the observer can use local features of the object, such as the wrinkles on the palm or the pattern of the fingernails to make the identification. The alternative, a whole-based analysis, relies on understanding the complete 3-D structure of the object.

6.2 Motor Simulation and the Birth of a Conundrum

Uncertainties about what was actually being simulated or judged in the laterality task appeared early in the literature. In an experiment testing the influence of head position on laterality judgments, Sekiyama noticed that when the RTs, as a function of angle

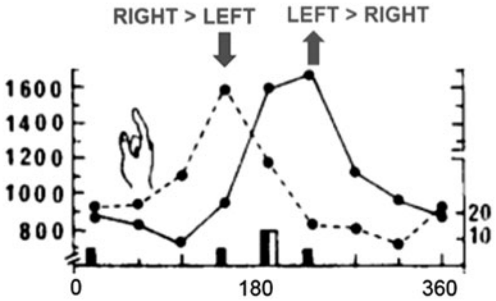

Fig. 6.2 An example of the correct-hand effect: The distribution of reaction time is different for right- and left-hand stimuli. This can only occur if the subject could distinguish the stimuli perceptually. (The plot is from Fig. 2 in Sekiyama 1982)

of rotation, were plotted separately for each hand, the profiles were not symmetric (Sekiyama 1982). They were skewed such that the RT profiles were mirror patterns for right- and left-hand responses, as shown in Fig. 6.2. This pattern was not apparent in the data from Cooper and Shepard, because they averaged the RTs for the two hands together (Cooper and Shepard 1975). The pattern of separate RT data for each hand in Sekiyama's data raised a critical issue. It could only occur if the subject was using a different mental process for each hand. This in turn implied that there was already sufficient perceptual information in the stimuli for subjects to be able to discriminate left and right hands. This possibility in turn raised the question of how if at all mental rotation of the hand actually contributed to the perceptual decision-making process. Sekiyama did not provide a clear answer. She interpreted the results from a kinesthetic framework, such that the "felt" position of the hands might be used to aid in the judgment.

The kinesthetic properties of the laterality task provided by Sekiyama were subsequently overshadowed by Larry Parsons' elegant experiments showing a range of new effects that were interpreted as overwhelmingly motoric in nature (Parsons 1987a). First, he demonstrated a remarkable sensitivity of the RTs to biomechanical constraints (Parsons 1994). RTs were highly sensitive to extreme positions such that hand stimuli in postures that normally are not comfortable led to slower RTs. Second, the analog properties of the laterality task were generalized to other body parts. They were also observed in a foot version of the task (Parsons 1987b). Third, many subjects (including the authors of this chapter) reported a sense of body motion when performing the task. Fourth, the RTs for judging hands at different rotations were proportional to the time to make actual movements from that position to a neutral point with the joint angles at mid-position. These effects led Parsons to note, "These imagined paths seemed to simulate the paths used for physically moving the hand or foot between their task orientation and the orientation of the stimulus" (Parsons 1987a). All of these findings have stood the test of time and continue to be replicated 25 years later. In addition, follow-up studies demonstrated that the RTs were sensitive to the posture of the participant as they performed the task (Sirigu and Duhamel 2001; Ionta et al. 2007). For example, placing the left hand behind the back would slow the RTs for left-hand judgments. They entrench the notion that the perceptual decision making in the laterality task is based on motor simulation (Ionta et al. 2007; ter Horst et al. 2010; Ferri et al. 2011; Ní Choisdealbha et al. 2011), motor imagery (Grush 2004) or motor emulation (Moulton and Kosslyn 2009). The motor simulation mechanism continues to be used to interpret findings in a variety of patient populations as well (Deconinck et al. 2009; Helmich et al. 2009; Williams et al. 2011).

However, as with Sekiyama's data, Parsons' work also reveals the remarkable skewing of RT profiles when the two hands are plotted separately. This skewing can only occur if the participants knew which hand to covertly rotate on each trial. This correct-hand effect shows that perceptual identification of hand chirality is orientation-invariant, even in the face of the added challenges imposed by the visual mirror symmetry of the hand stimuli. Despite the seemingly impregnable interpretation that a motor simulation is used in the laterality task, the correct-hand effect observed in data from Sekiyama, Parsons, and countless follow-up studies introduces a fundamental conundrum. A consistent limb-specific mirror skewing of the RT profiles could only occur if subjects identified the correct hand, invariant to orientation, prior to any putative motor simulation. *If simulation is used in perceptual decision making, then how does the motor simulator always choose the correct hand in the first place and, more importantly, why bothr with motor simulation at all?* The conundrum clearly speaks to Cooper and Shepard's original concern that if local perceptual features could be used to discriminate the stimulus, then the argument that simulation is used for perceptual decision making is flawed. In the face of this uncertainty, Parsons proposed an alternative explanation that could sustain motor simulation as a putative mechanism, as shown schematically in Fig. 6.3. He noted that "Performance in the left-right judgment task appears to involve these operations, some of which may occur concurrently: (a) analysis of the orientation and handedness of the stimulus; (b) analysis of the orientation of the internally represented corresponding hand; (c) planning a path for the internally represented hand to move (within its joint constraints) to the orientation of the stimulus; (d) mental simulation of planned action; and (e) exact-match confirmation of shape of imagined and perceived hands" (Parsons 1994). His final point addresses the conundrum by invoking a post hoc confirmation mechanism. This mechanism could take two forms. One would be a direct confirmation of the percept. However, the entire notion of a post hoc motor simulation to confirm what is already perceived is deeply problematic. It is difficult to find any other examples in the cognitive science literature where motor simulation or imagery is used to directly confirm an already correct percept. The other explanation for the post-hoc confirmation step proposes that mental rotation is needed to map the correctly perceived hand into the appropriate motor response, that is, there is uncertainty in the mappings between "right" and "left," and the sides of the body used to make the response. In a recent set of experiments where local features of the hand stimuli were manipulated, we discovered that neither of these post-hoc confirmation mechanisms is tenable (Viswanathan et al. 2012).

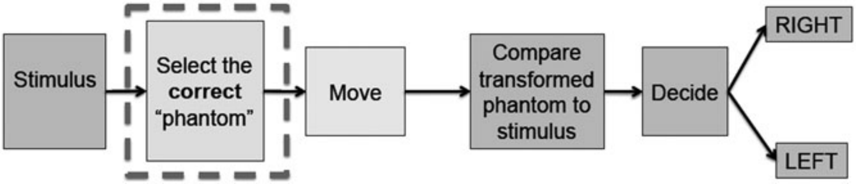

Fig. 6.3 The conundrum introduced by the correct-hand effect. A correct percept of the visual stimulus is always used as the referent for comparison in the motor simulation. Thus, it is unclear what the subject is actually deciding since they already recognize the chirality of the stimulus

6.3 Multisensory Hand Binding

We propose that the behavioral properties of the laterality task are not due to motor simulation. Instead, the analog and biomechanical features of the laterality task are a consequence of what we refer to as "multisensory hand binding." At the onset of the stimulus, the observer has simultaneous access to sensory information about the same entity (i.e., a hand) from different modalities—the visual representation of the seen hand depicted by the stimulus, and the proprioceptive representations of the observer's own felt hands (Shenton et al. 2004). There are more than enough local features in the visual stimulus used in a typical laterality experiment to uniquely identify it as the front or back of the hand. According to the multisensory hand-binding hypothesis, there is a simultaneous, (orientation-invariant) cross-modal comparison of the seen hand to the proprioceptive representation of the corresponding hand, as shown schematically in Fig. 6.4. The outcome of cross-modal comparison is not a match/mismatch signal that is used for perceptual decision making. Instead, it results in a binding of the visual representation of the seen hand to the proprioceptive representation of the "matching" felt hand or vice versa. Successful binding produces an intermodal discrepancy due to the differing orientations of the bound seen- and felt-hand representations (in a body-centered reference frame). This discrepancy automatically initiates a sensorimotor recalibration process to align the spatial representation of the felt hand to that of the seen hand—an aftereffect that can cause a feeling of moving. Critically, the motor response that is required in the laterality task is delayed until this intermodal conflict is resolved. This delay leads to the laterality specificity of the RTs. We speculate that the need to perform this recalibration between the seen and felt hand is evidence that the motor system requires an internally consistent and unique representation of body position (or state) as part of generating a motor command, although this consistency argument remains to be tested directly. Critically, the recalibration in multisensory hand binding is achieved by relating representations in different sensory reference frames with respect to each other. A critical prediction is that this occurs without requiring a motor signal from either premotor or motor cortex and does not require any sort of motor simulation, emulation, or explicit strategy. With multisensory hand binding, the response delay is related to recalibration of body position as a part of planning a normal movement and not related in any way to perceptual decision making. Thus, there is no conundrum as arises with the standard motor simulation account of laterality judgments.

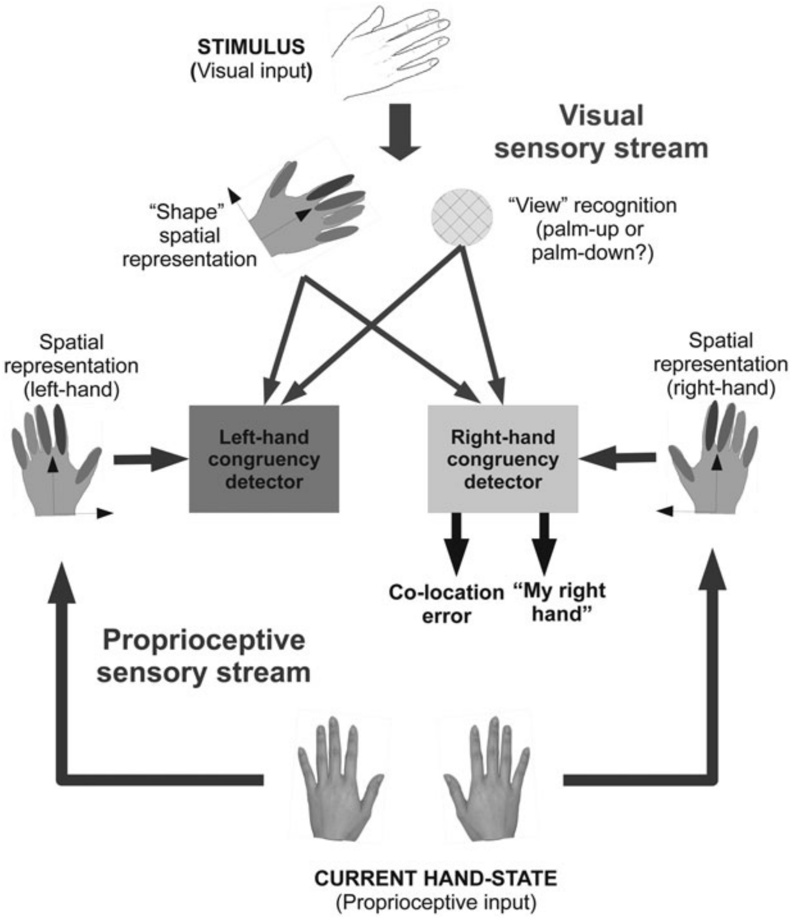

Fig. 6.4 The multisensory binding process: In the laterality task, a visual stimulus of the hand is evaluated in terms of hand shape and orientation (palm up/down) and this information is used to establish chirality of the visual stimulus. This is matched to the spatial representation of the corresponding felt hand. The planning of a motor response requires that this spatial discrepancy between two estimates of body position be reconciled

6.4 Experimental Evidence for Multisensory Hand Binding

Unlike the traditional motor simulation and confirmation model, the multisensory hand-binding hypothesis imposes strong constraints on when and whether the correct-hand effect will occur. Here, we summarize a study that used an attention manipulation to selectively induce a "wrong-hand effect" (Viswanathan et al. 2012). The experiment selectively extinguished the correct-hand effect by eliminating the contextual relevance of the proprioceptive inputs. Neither effect is plausible with

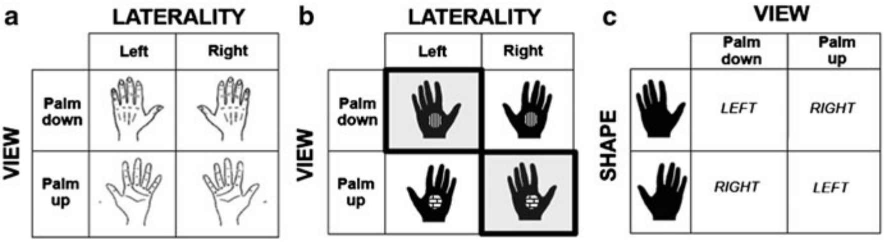

Fig. 6.5 Stimuli in the standard form of the laterality task have sufficient local features to determine chirality (**a**). In an ambiguous silhouette, each shape can correspond to either hand (**c**). With simple symbolic cues, chirality can be restored (**b**)

motor simulation. Finally, we describe a recent study that requires a simple perceptual decision of determining if two ambiguous hand silhouettes have the same or different outlines. The results show that there is an obligatory multisensory binding of the stimuli to the observer, even in a task when no right/left judgments are required.

Inducing the Wrong Hand According to the hand-binding hypothesis, only sensory information about the spatial configuration ("shape") of the visual hand representation can be correlated with the proprioceptive hand representations. The afferent proprioceptive representation of a hand codes the relative spatial position of the digits and hand, but does not itself contain information about visual attributes such as the color, lines, and textural patterns of the skin covering that hand. Therefore, the "shape" of the seen hand and the "patterns" on the seen hand should have dissociable effects on laterality identification. To test this prediction, we exploited the fact that visual hand "patterns" are indispensable in identifying the laterality of certain hand shapes. In Fig. 6.5a, the visual patterns on each hand are diagnostic of whether the palm or the back of that hand is being viewed. Without these patterns, the 2-D hand shapes exhibit multiple symmetries. The shapes of the palm-up and palm-down views of the same hand are mirror-symmetric, as are the shapes of the right and left hands having the same view as shown in Fig. 6.5c. Furthermore, the palm-up view of one hand has the same shape as the palm-down view of the other hand. Due to these symmetries, the laterality of a hand cannot be uniquely determined based on shape alone, without the view information from the visual patterns. The Cooper–Shepard paradigm was altered to include a task-set manipulation, using the hands in Fig. 6.5b as stimuli. Black silhouettes depicted hand shapes and colored dots were used to denote hand orientation. A red dot indicated a palm-down view of the hand, and a green dot indicated the palm-up view. Participants readily learned to recognize this color-to-view mapping before the experiment. The paradigm involved two independent conditions—the View-first condition and the Shape-first condition.

Each condition consisted of cued and uncued trials that occurred with (approximately) equal frequency. On the cued trials of the View-first condition, participants first saw a colored dot (red or green) indicating the view of the forthcoming test stimulus. After a brief offset, a test stimulus depicting a hand shape (without view information) was presented at a variable picture-plane orientation. On the uncued trials, the advance cue (a gray dot) did not provide any task-relevant information, and the subsequent test stimulus contained both view and shape information together. Participants had to combine view and shape information, whether presented serially (cued trials) or simultaneously (uncued trials), to identify the laterality of the hand. The stimulus ordering on the cued trials was reversed in the Shape-first condition—the advance cue was a hand shape, followed by a test stimulus depicting that hand's view. Critically, the uncued trials were identical in the Shape-first and View-first conditions. We assumed that participants would selectively attend to one and then the other visual attribute of the stimulus in the same sequence used in the cued trials of that condition. With this assumption, the hand-binding hypothesis predicts that response times on the *uncued* trials should differ in a very specific manner between the View-first and Shape-first conditions. On the View-first condition, "view" should be processed before "shape." According to the hand-binding hypothesis, view representations should therefore be available to mediate the subsequent perceptual correlation of hand shape to the proprioceptive hand representations, thus leading to a unique and "correct" laterality binding solution. Consistent with this, the RT profiles for these stimuli were mirror-reversed in the View-first condition, consistent with the correct-hand effect reported by previous studies. On the Shape-first condition, "shape" would be processed before "view." A hand shape without view information has an ambiguous laterality. Due to the *participant's* palm-down hand position, each shape should be correlated with the spatial configuration of a unique proprioceptive hand representation. Consequently, the ambiguous hand shapes are automatically bound to the correlated felt-hand representation, according to the hand-binding hypothesis. This "premature" binding, without incorporating stimulus-defined view information, leads to a critical result. Stimuli having identical shapes but different views were bound to the very same felt hand. RT profiles for these stimuli were *not* mirror-reversed in the Shape-first condition, unlike the predictions for the View-first condition. Due to this premature binding, palm-up stimuli were consistently bound to the "wrong" felt hand, in violation of the correct-hand effect. Note that this "wrong-hand effect," while eliminating the asymmetry of RT profiles, does not necessarily result in "wrong" laterality judgments. When the binding enters awareness, participants can evaluate whether the stimulus-defined view corresponds to a palm-down or a palm-up view, and respond accordingly with either the bound hand or the opposite hand.

Binding Without Laterality Judgments We performed a variant of the Cooper–Shepard paradigm to demonstrate that hand binding could be tightly controlled by the experimenter. Participants had to interpret an ambiguous hand silhouette palm up or palm down, rather than left or right hand. We tested if this perceptual decision, which had no laterality judgment, would again interact with the responding "felt" hand. On each trial, participants first received an advance cue specifying the laterality of the forthcoming test stimulus. That is, subjects knew in advance if a right- or left-hand stimulus would be presented, eliminating hand judgment altogether. The left/right instruction also indicated which hand to use to indicate their palm-up/palm-down decision. In doing so, the decision making has no uncertainty in the mapping between "right" and "left" stimuli and the side of the body to be used to respond. After a short delay, a test stimulus depicting only a hand shape was presented. Participants judged whether the test stimulus depicted the palm-up or the palm-down view of the hand of known laterality with an index or ring finger button press. Despite explicit prior knowledge of the expected hand laterality, pre-attentive mechanisms involved in laterality identification were predicted to still be involved. We found that the advance preparation of the response hand induced a "selective attention" to the felt representation of the responding hand, while inhibiting inputs from the other (nonresponding) hand. Consistent with the hand-binding hypothesis, only shapes correlated with the palm-down position of the response hand led to successful binding, but not shapes corresponding to the palm-up view, even though these latter shapes are correlated with the palm-down position of the nonresponding/unattended hand. The palm-down stimuli of each hand were associated with the characteristic RT mirror asymmetry of the correct-hand effect, but not the palm-up stimuli. This systematic difference in RTs between the palm-down and palm-up stimuli supports the assumption of the hand-binding hypothesis that successful binding is the basis for recalibration and the associated illusory movement reported by many subjects. These results further argue that the mechanism causing the illusory movements is not under direct strategic control, despite the extensive voluntary control over the sensory inputs and the interpretation of the outputs. If it were a "strategy," then it would require participants to pre-identify the palm-up and for palm-down stimuli in order to apply a different strategy to each. Furthermore, since the palm-down stimuli for one hand are identical to the palm-up stimuli for the other hand, these results are inconsistent with the exclusive use of a strategy exploiting the visual position of the thumb. Additionally, if participants used "simulated" movements to either confirm or disconfirm their decisions, the RT asymmetries based on the correct-hand effect should be present on both palm-down and palm-up stimuli, contrary to the observed results (Fig. 6.6).

Automatic Multisensory Hand Binding When It Is Irrelevant We further tested if multisensory hand binding is an automatic process, unrelated to hand judgment, in a two-handed version of the laterality task. Subject's observed two ambiguous hand silhouettes positioned one above the other (Fig. 6.7a). The task was to decide as quickly as possible if the two silhouettes were rotated versions of the same shape, or different, mirror-symmetric versions of the two shapes. The main axes of the two shapes were always oriented 120° apart (Fig. 6.7b). Extensive research in perceptual matching studies of rotated objects has established that the solution to this problem is to mentally rotate one object to match the orientation of the other and the time to do this depends on the arc length or angle of the rotated object (Cooper and Shepard 1984). Because the two orientations are always 120° apart, the time should be the same irrespective of the absolute orientation of the images (as shown on the circle in Fig. 6.7c). The orientations were chosen such that subjects could not use visual symmetry as a perceptual "shortcut" for detecting two mirror shapes. Critically, if there is multisensory hand binding, then the automatic binding of either of the seen

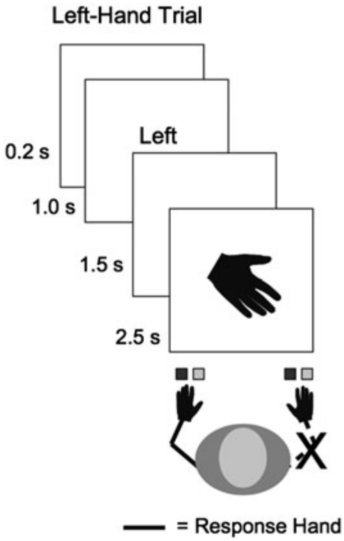

Fig. 6.6 Binding without laterality judgment: In this task, subjects are told if the stimulus is a left or right hand and told to respond with the corresponding left or right hand and report if the stimulus corresponds to a palm-up or palm-down orientation. Thus, there is no laterality judgment and no uncertainty over the laterality of the motor response. Subjects demonstrate a correct-hand effect for palm-down hand stimuli that match the responding hand, but not for matching palm-up stimuli

hands and the observer's responding hand will lead to biomechanically constrained delays in response time and a dependency of RT as a function of where the axes are positioned (Fig. 6.7d). This RT dependency on position was found to be particularly dramatic for orientations associated with the most uncomfortable position to rotate the hands into (Fig. 6.7e). When results of this two-handed version of the laterality task are combined with the traditional single-hand judgment studies, the generality of the results as well as the automaticity of the behavior constitute strong evidence that multisensory binding is an ecologically valid process (De Gelder and Bertelson 2003).

6.5 Reinterpreting the Laterality Task

Multisensory hand binding and recalibration of body position are sufficient to explain much of the behavioral phenomenology typically found in experiments that use the laterality task or its variations. First, it is well known that conflicts between seen and felt body positions can induce a sense of motion without any overt motor command or covert motor simulation. Anyone who has experienced aftereffects of motion from a carnival ride or experienced "sea-legs" after returning to the shore can attest to this (Cohen 1996). In other words, a sense of motion by itself is insufficient evidence to conclude that a motor simulation is occurring. Second, the sensitivity of the laterality task to extreme body postures could be based on biomechanically constrained boundary conditions placed on an internal model of the body schema rather than on limitations to the range of possible simulated motor commands. That is, our ability to mentally represent the position of our body in space (irrespective

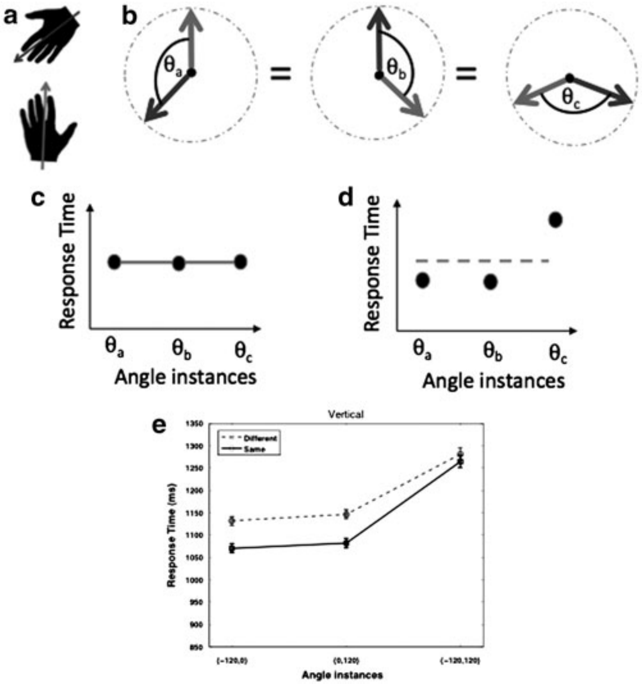

Fig. 6.7 In the two-handed matching task, two hand silhouettes with ambiguous chirality are presented, and the subject must decide if they are the same hand or a mirror (different) pair (**a**). The stimuli are presented one above the other to avoid perceptual mirror symmetries. The two hands are always presented with the primary axis rotated 120° with respect to each other (**b**). Mental rotation of one object to another would lead to response times that are invariant to the absolute angle instances (**c**). In contrast, if hand binding occurs, there will be delays in response times as a function of angle instance (**d**). Data from subjects performing this task confirm there is a strong hand-binding effect (**e**)

of our generation of motor commands) is strongly constrained by real biomechanics. Furthermore, as amplified below, any clinical disorder that disturbs the body schema (amputation, locked-in syndrome, chronic pain) could distort the internal representation of body position and influence the time needed to relate this internal schema with visual hand stimuli. Third, the sensitivity of response times to the static posture of the observer could be due to peripheral, proprioceptive influences on the internal model of the body position, irrespective of any motor involvement (Riemer et al. 2010). Fourth, experimentally distorting hand position (using methods such as vibrotactile stimulation of the biceps tendon) should influence RTs in the laterality task (McCormick et al. 2007). Fifth, the multisensory hand-binding process appears to be pre-attentive or automatic. Laterality judgment delays are resistant to explicit control such as instructions that tell the subject a stimulus is their own or another person's (Ferri et al. 2011).

6.6 Neural Mechanisms of Multisensory Binding

The multisensory hand-binding model proposes that the registration of different estimates of body position plays a dominant role in the preparation for action. Proprioceptive representations of one's hands are continuously accessible as they provide a running estimate of the position of the hands relative to the body, both when the hand is at rest and in motion, and even when the hands cannot be seen. It is known that the cross-modal comparison of the representations of a seen hand with that of the felt hand is critical for maintaining the coherence of one's body schema (Graziano and Botvinick 2001; Ehrsson et al. 2004), and essential for enhancing motor performance (Desmurget et al. 1995). Intersensory conflicts can result in a variety of body schema distortions such as the rubber hand illusion (Botvinick and Cohen 1998; Pavani et al. 2000), extracorporeal perception, and errors of agency attribution (Petkova and Ehrsson 2008; Slater et al. 2009).

The need for coherence across sensory modalities implies that there is a high level of specificity to the perceived visual stimulus, as a visually seen right hand should not be confused with a felt left hand, and vice versa. Neurons identified in Brodmann's area 5 of the superior parietal lobule (SPL) of the nonhuman primate exhibit such specificity (Graziano et al. 2000). They have a graded response depending on the angular disparity between the felt arm and a seen artificial arm. Furthermore, these neurons respond in the same manner to an inverted hand (the back of the same hand) but not when the visual cues imply that the inverted hand belongs to the opposite arm. In this latter case, the neurons responded as if there was no stimulus present at all. Similar properties are observed in dorsal premotor cortex (PMd) (Graziano 1999). These two areas form a network that transforms vision and body-centered reference frames (Caminiti et al. 1996; Crawford et al. 2011). The properties of neurons within these two areas in nonhuman primates form a compelling substrate for multisensory hand binding. That said, further studies are needed to understand the relationship between the time it takes to resolve multisensory conflict and the computational processes within SPL neurons that could be mediating this process.

While direct neuronal evidence of the hand-binding process is not available in humans, a wealth of indirect evidence using functional imaging with both positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), spanning 15 years of study in 10 experiments and over 120 subjects, demonstrate localization to the SPL and to a lesser degree PMd (Hetu et al. 2013). The SPL loci are remarkably similar in location to nonhuman primate recordings in Brodmann's area 5. The specific involvement of SPL in imaging is particularly apparent when hand judgment is contrasted with object rotation, which effectively controls for motor cortex activity related to making the motor response (Bonda et al. 1995; Kosslyn et al. 1998; de Lange et al. 2005). Using parametric event-related fMRI, SPL activity scales with biomechanical complexity during the laterality task. We propose this graded response is related to the multisensory binding, analogous to what is observed in nonhuman primate neurons rather than to a simulation (de Lange et al. 2006).

Hand binding in the laterality task appears to be a highly specialized property of the superior parietal cortex, based on a comparison with other functional determinants of body representation. In a factor analysis of patients with parietal lobe stroke, a laterality task deficit was distinct from other tests of body representation including (1) chronometric scaling while imagining moving the fingers contralateral to the lesion, (2) localization and identification of body parts, and (3) understanding the relative position of different segments of the arm (e.g., that the wrist is distal to the elbow). Furthermore, lesion overlap maps demonstrated increased involvement of the SPL for patients with laterality deficits that were different from probable lesion locations for the other body representation disorders (Schwoebel et al. 2001). The behavioral and lesion location differences of laterality judgment and imagined finger movements are quite important, as the latter is generally considered to be a prototypical example of motor simulation (Sirigu et al. 1995).

Each parietal-premotor cortex represents to a greater degree the proprioceptive state of the contralateral hand (Bernier and Grafton 2010). Thus, binding should only occur between a seen hand and the felt hand of only one hemisphere. This might be reflected in PET and fMRI experiments by greater brain activity for one hand than the other. However, most imaging studies show bilateral recruitment of SPL and PMd cortices in the laterality task, even when activity for each hand is modeled separately (de Lange et al. 2006). This might be expected, given that the hemispheres are reciprocally connected, and activation of one will co-recruit the other. Patient studies could possibly provide evidence that only one hemisphere is “bound” per trial. In stroke patients, lesions of the left hemisphere lead to slowing of judgments to either hand stimulus whereas right brain damage slows neither (Tomasino et al. 2003; Daprati et al. 2010). Irrespective of the side of the lesion, there might be mechanisms unrelated to multisensory binding influencing patient performance. The lesion location is diverse across subjects, there is an influence of hemispheric specialization for hand dominance, and patients may under go reorganization post stroke. The best evidence that the SPL is specialized to bind vision and proprioception of the opposite hand can be found in patients with a sectioning of the corpus callosum (Parsons et al. 1998). Using hemifield stimuli and the hand laterality task, it is clear from error rates that each hemisphere only matches the contralateral hand.

6.7 Is the Motor Cortex Involved in the Laterality Task?

One possible acid test of motor simulation in the laterality task would be a demonstration that the motor cortex of healthy subjects is involved during performance of the task. Motor cortex can clearly be activated in tasks explicitly cueing imagined movement (Lotze et al. 1999; Sharma et al. 2008). However, the evidence for motor cortex engagement in the laterality task is by no means apparent. Early PET imaging experiments of the laterality task using block designs reported activity of the motor cortex (Kosslyn et al. 1998). With well-balanced experimental designs and higher-resolution imaging, it became evident that motor cortex activity is not greater for hand judgment than object rotation (Bonda et al. 1995). Furthermore, motor cortex activity only appeared at the time of a response, presumably after any perceptual decision had occurred (de Lange et al. 2005). A recent meta-analysis of 75 imaging studies of motor simulation compared localization in the laterality task with other forms of motor simulation, such as kinesthetic or visual motor imagery (Hetu et al. 2013). With the laterality task, motor cortex activation is rare whereas the other forms of motor imagery task demonstrated motor cortex involvement about 25 % of the time. When single-pulse transcranial stimulation (Ganis et al. 2000) or slow, 1 Hz, repetitive transcranial magnetic stimulation (TMS; Pelgrims et al. 2011) was used to create a "virtual" lesion of motor cortex, there was a general slowing of RTs in the laterality task. However, these results did not influence the correct-hand effect and only described a generalized slowing of responses. Furthermore, in a detailed single-pulse TMS experiment in which virtual lesions of motor cortex were chronometrically manipulated and the correct-hand effect was carefully measured, there was a complete failure to disrupt hand judgment performance at any stimulation time post stimulus, establishing that there is no time window during which the motor cortex makes a contribution to mental rotation of the hand (Sauner et al. 2006). Although motor cortex may be involved in other motor simulation paradigms such as kinesthetic motor imagery, there is no compelling evidence that it is used in hand laterality judgments, undermining the argument for a motor simulation process in this task.

6.8 The Malleable Body Schema

State estimation is a computational process that has been proposed as a way to integrate sensory and motor information of position in real time (Tin and Poon 2005; Mulliken et al. 2008). Retinotopic-based reference frames appear to play a dominant role in representing space and planning action under typical experimental conditions. Vision provides a powerful and accurate map of limb position and the environment and may serve as a default reference frame for organizing body state and action (Cohen and Andersen 2002). There is growing consensus that the reference used to determine position is not absolute, but contingent on available evidence from different sensory channels (Denève and Pouget 2004; Faisal et al. 2008; McGuire and Sabes 2009). While vision-based information typically dominates, body-based reference frames can also be used under degraded vision. However, maps of the body position based on proprioception as well as tactile input are far less veridical than visual inputs (Kammers et al. 2009). They are easily distorted by illusions induced by visual–tactile (Botvinick and Cohen) or visual–proprioceptive (Burrack and Brugger 2005) mismatches and do not clearly map onto the body topology precisely (Longo and Haggard 2010). Nevertheless, the correct-hand effect of the laterality task suggests that recalibration relies on a body-centered reference frame with a "default" proprioceptive configuration: palms down and fingers pointed upwards.

Notably, the default configuration that is “bound” in the laterality task can be reshaped by additional information such as repositioning of the subject (Riemer et al. 2010). It is also influenced by the illusion of wrist flexion induced by vibrotactile stimulation to the wrist extensor tendons. In this case, RT delays were only observed when judging hand stimuli corresponding to the side of the stimulation (McCormick et al. 2007). It also appears to be overridden by biases induced by experimental context, such as constraining motor responses to one side or the other, as well as handedness (Ní Choisdealbha et al. 2011). Other contextual influences, such as ongoing observed or executed action, also influences the estimated body configuration (Conson et al. 2009). Interestingly, in young children, motor behavior is strongly shaped by a body representation that is close to the default position described in the laterality task and they are less influenced by their own body position (Saimpont et al. 2009). As they develop and acquire knowledge of the dynamics of their bodies, their body representation becomes more closely aligned with the actual physical position and this is reflected in a sensitivity of laterality judgment times to the participant’s position. It is possible then that in the face of uncertainty about limb position, adults might resort to this developmentally more primitive map of body position.

6.9 Multisensory Binding in Patients

Many patient populations have been tested with the laterality task and abnormal findings have invariably interpreted as evidence for deficits of motor simulation, even when there is no lesion of the motor system. In many cases, a more direct explanation can be drawn from multisensory binding. An illustrative case is patients who have undergone a limb amputation. It is well established that they can have a significantly distorted body schema (Ramachandran and Hirstein 1998). In the framework of multisensory binding, it is the poor alignment of a visual hand to a distorted body map that leads to the delays of laterality judgment, particularly for the hand stimulus corresponding to the distorted body schema (Reinersmann et al. 2010).

Another illustrative population who has abnormalities of laterality judgment is patients with pain disorders. For those with unilateral, chronic limb pain, there is a delay in laterality judgments to the hand stimuli corresponding to the affected side. The delay is also related to the duration of symptoms and to the pain that would be evoked by executing the movement (Moseley 2004b; Coslett et al. 2010b; Reinersmann et al. 2010). When a picture of a foot is used as the stimulus, delays in judgment are also observed for the stimuli corresponding to the painful foot, even when the subject responds with their intact hands (Coslett et al. 2010a). The fidelity of the laterality task for tracking pain severity has led to the proposal that it be used as an objective independent measure of subjective pain (Coslett et al. 2010b).

Schwoebel interpreted the response delays for stimuli corresponding to the painful limb (whether hand or foot) as evidence that there was a sensitivity of the internal representation of body position, particularly the nonvisual representation, to pain

(Schwoebel et al. 2001). The multisensory binding model draws on the same general explanation that the delay is related to a distortion of the body schema. However, with multisensory binding, there is an important new distinction worth amplifying. In most of the studies of chronic pain, including the original paper by Schwoebel, the "movement" of the body representation is assumed to be a motor simulation or emulation, where the subject volitionally manipulates a body schema to solve the laterality task. This of course reintroduces the conundrum of the correct-hand effect and is inconstant with new experimental evidence (van Elk et al. 2012). In contrast, with multisensory binding the rotation of the body schema is automatic and driven by the incongruence with the observed hand position. This actually simplifies the explanation.

It has been found that patients with chronic neuropathic pain can actually gain some relief as measured by subjective pain scales when "treated" with the laterality task. Explanations for this improvement have been uncertain, and based on recruitment of motor and premotor networks (which we now know is not an accurate account of the networks used in this task) or perhaps due to focused attention on the affected hand (which could just as readily make the pain worse) (Moseley 2004a). The multisensory binding model provides an alternative explanation: One of the consequences of chronic pain could be a distortion of the body schema, particularly for the affected limb. Normalizing this distortion either by overt motor activity or through coregistration of seen and felt limb positions in the laterality task might reduce the distortion by image and associated pain.

6.10 When Does Binding Occur?

The laterality task reveals an illusion where a seen and felt hand are perceptually bound and spatially matched. When does this illusion generalize? Evidence to date would suggest the phenomenon also occurs with foot stimuli (Parsons 1987b). However, it is not at all clear that a correct-hand effect is observed when the hand stimulus is replaced with a glove (Daprati et al. 2010) or is attached to a body (Zacks et al. 2002). In this case, RT effects are more consistent with typical object rotation tasks or spatial compatibility effects. This would suggest that there is something special about disarticulated hands and feet as sources of perceptual confusion. Binding for these stimuli appears irrespective of the 3-D orientation of the stimulus (Parsons 1987b, 1987a). This undermines an assumption in some experiments that uncomfortable positions of visual stimuli would be treated by the observer as allocentric, whereas comfortable positions would be egocentric (Brady et al. 2011).

Another important and unanswered question is whether an analogous binding mechanism might be involved in the matching of the proprioceptive felt hand to an object in the environment. Consider a primate swinging through the trees. Limb grasping would require rapid accurate matching of limb orientation with a palm-centric reference frame. This could be performed through a rotation of visual and proprioceptive reference frames, with planning time influenced by biomechanical effects including end-state comfort. As with the hand-binding model, there is no need for motor cortex "simulation" to solve this realignment problem. Of note, when subjects make perceptual decision about how their hand should be oriented to make a power grasp on a dowel, the decision times have all these properties (Johnson 2000b). Furthermore, imaging studies demonstrate that both the SPL and PMd are associated with the simulated hand rotation, in regions that are remarkably similar to those found in the laterality task (Johnson et al. 2002). Finally, patients with hemiparesis and motor cortex damage can continue to perform this grasp selection task, further undermining a motor simulation account (Johnson 2000a). We speculate that the object itself provides a visual reference frame that the felt hand can be bound to without any need for motor simulation. For more complex behavior, including the manipulation of tools, additional control mechanisms and estimates of position would certainly need to be invoked.

6.11 What Should We Call Motor Simulation?

A consequence of the hand-binding model is that the perceptual judgment of a hand does not rely on a motor simulation process. At a certain level, this is not surprising. The perceptual demands of making a hand laterality judgment are not particularly difficult when considered in the context of many other difficult perceptual problems we face every day, and where no motor simulation is required. The hand-binding model also suggests that much of the evidence that is used to make a case for motor simulation, whether it is an objective behavioral measure or subjective report of movement, is inadequate. The observation that RTs are sensitive to hand orientation, to biomechanical constraints, to body posture, to physical injury, or to a distorted body scheme are insufficient evidence on their own to conclude that a motor simulation is occurring in a task. Similarly, a sense of motion could be based purely on sensory mismatch. This does not mean we are proposing that motor simulation cannot occur. Instead, we simply argue that the range of tasks involving motor simulation may be smaller than is commonly stated. The outcome of our work with the laterality task is that a higher burden of proof is needed to conclude that a motor simulation is involved in cognitive problem solving. The most convincing experiments suggesting that a motor simulation is occurring require subjects to explicitly imagine they are achieving specific action goals, such as walking to a target, tapping fingers in a specific sequence, drawing, reaching, tracking, and making bimanual actions (Decety et al. 1989; Sirigu et al. 1995; Decety 1996; Vargas et al. 2004). In all these cases, there are chronometric links between real and imagined actions. The tasks clearly involve willful, explicit motor emulation centered on a goal, rather than on a perceptual decision.

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Chapter 7

Use of the Uncontrolled Manifold (UCM) Approach to Understand Motor Variability, Motor Equivalence, and Self-motion

John P. Scholz and Gregor Schöner

7.1 Characterizing Variability in Motor Performance

Variability of motor output often has been considered a form of noise that interferes with reliable performance. This assumption, however, depends on the level of the motor system under consideration. For targeting tasks, variability of the end-effector position will affect the consistency of targeting, depending on the task requirements and the size of the target. Variability of coordination patterns used in artistic performance may impact the aesthetics of performance. However, variability at the level of the motor elements, including small variations in coordination patterns, often reflect task flexibility that is only possible when the motor system exhibits sufficient motor abundance (Latash 2012). Consider, for example, performing cardiopulmonary resuscitation (CPR) on an infant, with the index and middle fingers exerting the necessary force to produce adequate chest compression. If fluctuation in the compression force of one finger leads to a tendency for higher total force output, then reduction in the forces exerted by the other fingers is necessary to compensate and maintain a consistent total compression force. This is only possible because there are two fingers contributing to a single total force output. Note that an alternative approach would be to attempt to control precisely, to the extent possible, the variability of individual finger forces such that each finger generates approximately the same force on each repetition. The presence of compensatory finger forces, however, has been well documented (Latash et al. 2001, 2002a, 2002b), and is consistent with the notion of a functional synergy among the motor elements (Latash et al. 2007).

Determining whether variability of motor output reflects motor noise or flexible motor patterns is not trivial, however. Bernstein observed that when blacksmiths hit

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the chisel with the hammer there appeared to be more variability of the trajectories of individual joints than there was for the trajectory of the hammer (Bernstein 1967). This led him to conclude that a movement is never repeated in exactly the same manner. Although his intuition was correct, there was no way to clearly establish this fact. For one thing, the trajectory of the joints and the end effector (hammer) are measured in different units and the number of degrees of freedom of each is quite different. How does one compare variability of up to 10 joint motions (including scapular motion) measured in radians to the variability of three dimensions of end-effector motion measured in meters? Schöner and Scholz (Schöner 1995; Scholz and Schoner 1999) developed the uncontrolled manifold (UCM) approach to overcome this problem and to quantify statistically the extent to which variability of motor elements tends to lead to noise or error in performance versus reflecting the use of flexible patterns of coordination. In this approach, all analysis to answer this question is performed at the level of the motor components, e.g., joint motions, finger forces, and muscle modes.

To accomplish this, the UCM approach requires a model that relates how changes in elemental variables affect the task level (e.g., hand position in space, total force output). This model can be obtained formally, as when relating joint motions to movement of the hand in space (e.g., $\Delta x = l_1 \cos\theta_1 + \cos(\theta_1 + \theta_2) + \cdots$) or via regression analysis when a formal model is not readily available or excessively complicated (Freitas and Scholz 2010). The null space of the equation relating the task space to the space of motor elements provides a linear estimate of all combinations of the motor elements that do not affect the value of the task variable at that point in a movement trajectory or in time (e.g., $J(\theta_{\text{mean}})\,\Delta\theta_i = 0$ where J is the Jacobian matrix of partial derivatives relating small changes in the elemental variables to changes in the task variable). The null space is computed around the mean value of the motor elements (θ_{mean}) at each point in the movement trajectory. Experimentally measured mean-free values of the motor elements ($\Delta\theta_i = \theta_i - \theta_{\text{mean}}$) for each movement repetition at a given point in the normalized movement are projected into the null space and its compliment, or range space (the subspace of motor elements in which different combinations of the motor elements lead to different values of the task variable of interest). This is done for each repetition and the variance of the projection lengths is then computed and normalized to the dimensions of the subspace to make the analysis more conservative. Greater variance in the null space or UCM subspace than in the range space suggests a control strategy in which the central nervous system provides stabilizing control signals that restrict variations of the motor elements when they affect the desired value of the task variable but allows for some degree of variability in combinations of those variables if they have no effect on the task variable (i.e., variations within the UCM).

Studies of many different motor tasks have shown that variability at the level of motor elements is more consistent with the use of flexible combinations of those elements that preserve a stable state (e.g., posture) or produce a consistent trajectory (e.g., reaching) of a task-level variable (e.g., center of mass position, trajectory of the hand). In contrast, range space variability typically is shown to be significantly smaller (Scholz and Schoner 1999; Scholz et al. 2000; Latash et al. 2001; Scholz et al. 2001, 2002; Krishnamoorthy et al. 2003, 2007; Latash et al. 2002a). UCM analysis also has been able to differentiate between movement synergies in persons with neurological dysfunction and healthy control subjects (Reisman and Scholz 2006; Park et al. 2012, 2013). In addition, different hypothesized task variables can be evaluated with this approach to help determine what variables are of greatest importance to task performance (Scholz et al. 2000). The results are in agreement with the minimum intervention principle, which suggests that allowing variability in redundant (abundant) dimensions is the optimal control strategy in the face of uncertainty (Todorov and Jordan 2003), although a control structure more in line with the UCM hypothesis than optimal control has been shown to better account for detailed characteristics of movement trajectories (Martin et al. 2009).

The dependence of the outcome of a UCM analysis of motor variability on the variables used to describe the effector system has recently been criticized (Sternad et al. 2010). For example, the authors suggest that movements may equally well be planned in joint or segment angle coordinates. They provide an example of a minimally redundant effector system in which the UCM method leads to quite different results when either of these sets of variables is used. This criticism is relevant and emphasizes that researchers must make considered choices of the variables used for analysis. Three clarifications are in order, however:

1. A choice of variables fixes the space in which configurations of the effector are described. If we choose joint angles as variables, then we describe the effector in joint space. A point in that space represents one particular configuration of the effector. A metric must be fixed as well, which assesses the distance between any two points in that space, that is, between two configurations of the effector. Typically, the Euclidian metric is used, in which the squared distances along each of a set of orthogonal coordinate axes are summed and the square root is taken. The UCM approach is then actually invariant under any change of coordinate frame that leaves the metric invariant (Schöner and Scholz 2007). This includes, in particular, rotations of the coordinate frame. This invariance reflects the fact that the UCM analysis is based on a geometrical view of variance, in which the shape of the cloud of points in joint space is observed across trials at a particular point during a movement. If that shape is elongated along the direction of the null space, then the UCM hypothesis is confirmed. The shape of the cloud of points is invariant under any coordinate transform that preserves the metric of the space spanned by the chosen variables. This is useful in some cases, such as for the shoulder joint, for which there is no principled way to select a particular coordinate frame to represent the three degrees of freedom that reside in that joint. Any orthogonal set of coordinate axis is equally meaningful, so that invariance under rotation of a coordinate frame is desirable. The randomization method (Müller and Sternad 2004), in contrast, is essentially a form of nonlinear, multivariate correlation. In that approach, the coordinate frames matter as they do for correlation. If the cloud of points is elongated along a coordinate axis, for instance, then that shape is not picked up as correlation but as inherent variability of that particular degree of freedom.

2. Transformations that do not leave the metric invariant matter in the analysis of variance and this is how the choices of variables that set up the configuration space come into play. For instance, representing joint configurations through segment angles or through joint angles does not lead to the same shape of the cloud of points. Mathematically, going from segment angles to joint angles is a transformation that does not leave distances invariant: It is not a metric preserving transformation, unlike the rigid rotations that may be used to link different orthogonal axes for joint angles anchored in the shoulder. This dependence on the embedding space is shared, of course, by all approaches to the analysis of multidimensional variance (e.g., Müller and Sternad 2004; Cusumano and Cesari 2006).
3. Fortunately, the choice of embedding space can be guided by what we know about physiology. Specifically, the choice of joint over segment angles is not arbitrary. Known sensory receptors provide information to the nervous system about changes in joint angles (Grigg 1994). There are no known sensory receptors signaling orientation of a limb segment in external space, although transformation of sensory receptor information can be used to estimate limb orientation (Poppele et al. 2001). Segment angles are inherently dependent on each other. For example, a flexion of the ankle brought about by a signal sent to muscles that act on the ankle joint leads to changes of all segment angles along the kinematic chain of the upright body, including joints not linked to the ankle by any muscle. Similarly, changing the segment angle that the humerus forms with an external reference frame also changes the segment angles of the forearm and hand, without any activity by muscles acting on these more distal joints. Thus, distal segment motion in an open kinematic chain is not independent of proximal segment motion. This is not the case with joint angles. Changing one joint angle does not necessarily affect another joint angle, unless there are particular mechanisms that bring about such dependence like multi-articular muscles or coordinated neural signals.

Thus, it seems to us that the best of two worlds is achieved by combining the geometrical view of the UCM approach, which is conceptually attractive, with the analytical power of the correlational approach. This is now routinely done by researchers who select a set of variables and a particular coordinate frame based on substantive hypotheses. They can then use the surrogate data procedure of the correlational approach to verify if the shape of the variance in the UCM analysis truly comes from covariation among the variables identified as meaningful rather than from inherent differences in variance among the different degrees of freedom (see, for example, Yen and Chang 2009; Verrel et al. 2010).

7.2 Quantifying Motor Equivalence

More recently, the geometrical perspective of the UCM approach has been used to address additional issues in motor control, namely, motor equivalence and self-motion. The term motor equivalence has been used in a variety of ways, but is defined here as a change in the configuration of motor elements after a perturbation that tends to preserve the outcome of a task or the stability of a task-relevant variable. Kelso and colleagues (Kelso et al. 1984) performed a seminal study of motor equivalence in the context of the control of speech utterances. They found that adjustments in the articulators were task-specific, dependent on the nonsense syllable that subjects spoke when a perturbation was delivered to depress the jaw. Further evidence was provided when naïve subjects were unable to distinguish utterances performed during perturbed and nonperturbed trials. However, in many cases, distinguishing between adjustments of motor coordination that lead to disturbance of the task versus being a reflection of motor equivalent adjustments to preserve the task is not trivial. For example, when reaching to a target, a transient perturbation of a joint will lead to at least some effect on the motion of the end effector. If the end effector still reaches the target, this suggests that motor equivalence must be present. What if the hand, however, hits the target but deviates from its position on nonperturbed trials or what effect does the perturbation have on the path of the hand itself? Presuming that there are readjustments in the joint configuration or muscle firing patterns due to the perturbation, how can one determine the extent to which the adjustments account for observed deviations in the hand path or whether more of the adjustments tend to act to preserve the hand path? A modification of the UCM approach allows this question to be addressed quantitatively. If one takes a set of nonperturbed trials, the null space of the Jacobian matrix relating small changes in the motor elements to changes in a hypothesized task variable (e.g., the hand position) can be computed using the mean value of the motor elements across trials. This null space corresponds, as in UCM variance analysis, to a linear estimation of all combinations of joint configurations that lead to the same value of the task variable. Again, this analysis is performed at each point in the normalized (to 100 %) movement.

One can then obtain the vector of the configuration of motor elements from a perturbed (pert) trial, subtract it from the mean of the nonperturbed (nonpert) trials $\left(\theta_{\text{pert}} - \bar{\theta}_{\text{non-pert}}\right)$, and project this difference vector into the null space (UCM) and range space of the nonperturbed trials. If the null space projection is significantly larger than the range space projection, then this suggests that more of the adjustment in the joint configuration due to the perturbation is motor equivalent, tending to preserve the nonperturbed value of the relevant task variable. This approach, therefore, provides a statistical method for determining the extent to which motor equivalence is present.

In a collaborative study with Fay Horak and John Jeka, motor equivalence relative to the position of the center of mass of the body was measured in persons standing on a moveable force platform that was perturbed by different amplitudes, keeping the velocity of perturbation constant (Scholz et al. 2007). An example of the results obtained immediately after the transient perturbation are presented in Fig. 7.1. Note that the projection into the UCM subspace or null space was larger, and significantly so, than the projection into the range space, both computed based on the nonperturbed trials. This difference increased with greater amplitudes of perturbation. Thus, most of the change in the joint configuration as a result of the perturbation was motor equivalent, tending to preserve the pre-perturbation position of the center of mass of the body.

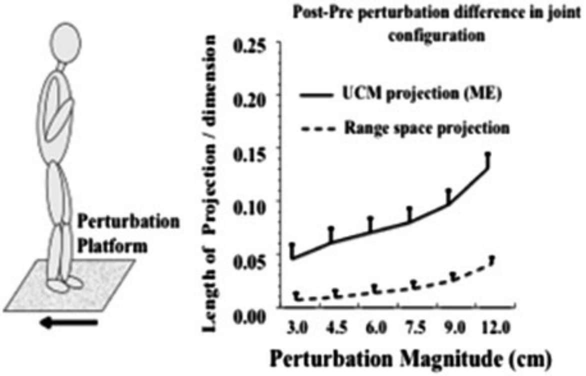

Fig. 7.1 *Left:* Participants stood upright when the support platform was abruptly moved by a varied amount (perturbation amplitude). *Right:* Six degrees of freedom were included in a motor equivalence analysis. The difference vector between joint configurations in perturbed trials from the mean configuration in unperturbed trials was projected into the UCM subspace (*solid line*) and the range spaced (*dashed line*). The plot shows the average length of these differences vectors across perturbation trials per degree of freedom together with the SME (*error bars*) as functions of the perturbation amplitude. The data are from Scholz et al. 2007 (Fig. 4 there)

7.2.1 Quantifying Self-Motion

UCM variance analysis indicates how fluctuations of the motor elements across repetitions or, in the case of relatively steady state behavior, across time are structured. For example, in upright posture, to what extent do joint fluctuations over time lead to postural sway of the center of mass versus being coordinated to flexibly stabilize the center of mass location? Nonetheless, fluctuations of the motor elements could be relatively small or large, depending on the task. The amount of self-motion provides an estimate of the magnitude of changes in the motor elements that lie in the UCM subspace and, therefore, do not affect the value of a task variable and those that change the value of the task variable. The concept of self-motion comes from the robotics of redundant effectors and, in that context, refers to the magnitude of the vector of time-dependent changes (e.g., velocity) in the motor elements that lies in the null space or UCM subspace. In contrast, range space motion refers to that component of this vector that lies in the range space, or actually moves the task variable with reference to which the analysis is applied.

Consider reaching to a target with the hand. One might suspect that the most efficient movement of the hand would occur if the joints were coordinated such that their velocities were directed primarily toward that goal. If so, then the range space velocity component of the joints, which actually moves the hand in space, would be expected to be substantially larger than the self-motion or UCM component. Self-motion might be advantageous in some circumstances, however. For example, when carrying a relatively full glass of Guinness stout, if a fly lands on your elbow, you

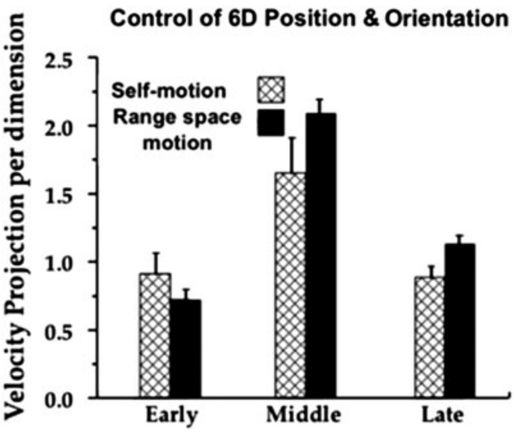

Fig. 7.2 Reaching with ten degrees of freedom to a target was analyzed with respect to self-motion, using a Jacobian that took into account both the 3D end-effector position and the 3D orientation of the hand for a total of six degrees of freedom in task space. Mean self-motion and range space motion per degree of freedom averaged across participants is shown for the early, middle, and late phase of reaching when reaching at a fast speed to a target. Data are from Scholz et al. (2011; compare to Fig. 3 there, which includes other conditions as well)

might want to flick the elbow to get it to go away without spilling the precious stout! Internal motion of the arm joints that does not affect the hand position is, by definition, self-motion. But how much self-motion is present for a given task when motion to achieve a secondary task is not required?

To answer this question, we developed a method of analysis that can be carried out on individual trials or on means across trials. The method was adapted from the UCM approach to the analysis of variance. The Jacobian, J, that relates the joint velocity vector, $\dot{\theta}$, to the velocity of the hand, $\dot{x} = J(\theta)\dot{\theta},$ is computed from a geometrical model of the effector. It is evaluated at the instantaneous joint configuration, $\theta,$ at each point in time. Based on this Jacobian, the null (UCM) and range spaces can be determined. The joint velocity vector, $\dot{\theta},$ is computed from the time series by numerical differentiation and is projected into either subspace. Finally, the length of these projections is computed and divided by the number of dimensions of each subspace.

Figure 7.2 presents an example of this analysis from a recent article investigating self-motion at different speeds of reaching (Scholz et al. 2011). The results for reaching at a self-selected fast speed are depicted. Note that although range space motion (component of the joint velocity vector projection that moves the hand in space) generally was larger than self-motion, self-motion was nonetheless quite substantial. The results were similar at slow and moderate speeds of reaching, although self-motion was not quite as large as compared to range space motion. Of interest was that at all speeds of reaching, self-motion actually was larger than range space motion at the early stage of reaching, probably because the arm had to be adjusted to exit the trough in which it rested as the reach was initiated.

The results suggest that even during the performance of goal-oriented targeting tasks there is a substantial amount of self-motion, i.e., joint configuration motion within the UCM subspace of joint space, even when an obvious secondary task is not involved. It is hypothesized that this amount of self-motion is a reflection of the nature of the control system that minimally restricts combinations of motor elements for a task that do not interfere with successful performance even when the configurations deviate from the initially planned configuration.

7.3 Conclusion

The UCM approach was developed originally to investigate the role of motor variance and has been successfully applied to a variety of motor tasks from finger force production to reaching to postural control. In most cases, variance consistent with flexible combinations of the motor elements that maintain a consistent value of an important task variable has been shown to be significantly greater than variance leading to variability of the task variable. The approach allows one to test hypotheses about the importance of different task-relevant variables based on the structure of variance of the underlying motor elements and to evaluate how different motor elements contribute to that structure.

Recently, the approach has been extended to address additional important issues in motor control such as motor equivalence in the presence of a perturbation and the extent to which motor abundance is used in the control of motor tasks through self-motion analysis. A model of a control strategy based on the UCM hypothesis and consistent with the recent results was developed by Martin, Scholz, and Schöner (Martin et al. 2009) and applied to postural control by Reimann et al. (2011). We believe that the geometrical perspective offered by UCM thinking will be useful both to interpret experimental signatures of control hypotheses and to investigate possible neural processes that bring about the coordination of the many degrees of freedom of the motor system. Ultimately, we will need to understand how spatial information and timing constraints for the motion of effectors in space can be translated to control signals at the level of each muscle (Bullock et al. 1993; Butz et al. 2007). That transformation sets up the geometry uncovered by the UCM method.

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Chapter 8
Acquisition of Novel and Complex Motor Skills: Stable Solutions Where Intrinsic Noise Matters Less

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8.1 Introduction: Acquisition of Skill and Experimental Control

While professional quarterbacks like Peyton Manning make passing a football look effortless, it takes a lifetime of disciplined practice for these elite athletes to reach such a high level of skill. The principal responsibility of the quarterback in American football is to throw a forward pass to his teammate. This skill, however, is not as trivial as it may appear. To achieve a successful pass, he must accurately throw to a target that is moving, while he himself is in motion. But even before the pass is thrown, he must quickly decide which receiver will have the best chance of catching the ball, judging from the continuous movements of the defensive team. He must also choose what style of throw and what initial conditions (i.e., position, velocity) are appropriate for where he aims the ball. This decision-making process cannot last more than a fraction of a second or he risks being tackled by opponents twice his size. This ability to choose from a vast—in fact infinite—set of actions is an integral part of many sport skills. Such complexity is what makes events like the Olympic Games fascinating, not only to spectators around the globe, but also to movement scientists, who want to unravel how humans achieve coordinated actions. How does the brain acquire and control such complex spatiotemporal skills?

It is somewhat sobering to then look into the laboratories and see how motor skill is typically studied. The vast majority of experiments have focused on highly simplified tasks, such as finger-to-thumb opposition (Karni et al. 1998), finger tapping (Wing and Kristofferson 1973), sequenced isometric contractions (Shim et al. 2005;

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Waters-Metenier et al. 2014; Wu et al. 2012), or reaching and pointing (Landi et al. 2011; Shabbott and Sainburg 2010; Shadmehr and Mussa-Ivaldi 1994). Unfortunately, the requirements of experimental control, measurement, and quantification have stripped motor skills of most aspects that have made them interesting in the first place. Simplified tasks permit precise assessment of performance variables, show relatively consistent patterns across subjects, and thereby permit scientifically stringent testing of hypotheses. Such focal movements are also well suited for neuroimaging studies, such as fMRI, where the subject's head must be still and more extensive movements distort the magnetic field. Yet, all these benefits come with the risk of oversimplification of task demands, to the point that findings from these tasks may no longer generalize to more complex and realistic scenarios. These simple movements shed light on fundamental neural underpinnings, but they show little or no improvements with practice, as the movements are already part of the behavioral repertoire of the participants. How can learning and neuroplasticity be studied to look closer at the spectacular agility and complexity of movements in real life?

Motor Adaptation One line of research that has been extremely successful and gone beyond the simple movement to study learning and neuroplasticity is the experimental paradigm on reaching with adaptation to external perturbations. Following a seminal study on adaptation to a force field by Shadmehr and Mussa-Ivaldi (1994), a prolific line of research ensued that addressed questions on adaptation and generalization (Criscimagna-Hemminger et al. 2003; Shadmehr and Moussavi 2000), consolidation (Baraduc et al. 2004), and trial-by-trial learning (Donchin et al. 2003; Thoroughman and Shadmehr 2000), to name only a few research directions. The paradigm employed simple horizontal reaching movements that were perturbed via an external complex force field or a prismatic distortion of its path. It is important to point out that subjects initially perform straight-line reaches, as is intrinsic to their behavioral repertoire (Morasso 1981).When the perturbations were applied, subjects committed large deviations from the direct path, but soon learned to adapt and compensate, and their performance returned to the initial straight path. When the force field or visual distortion was subsequently removed, performance temporarily worsened, as the compensation to the perturbation persisted. These so-called aftereffects indicated that the nervous system has learned something. In the absence of further perturbations, however, the return to the level prior to the experiment was relatively fast and persistent.

Can we consider these results to reveal mechanisms underlying the acquisition of *skill*? In our thinking, the answer is no, because at the end of the experiment, there is no net change in *skill* (Fig. 8.1a). Even though there are aftereffects and even though in a second encounter with the force field, adaptation may proceed faster (reflecting "savings"), these compensatory processes only *reestablish,* or maintain, previous behavior. The subject has not acquired any truly novel skill that she did not know before.

Skill Acquisition Compare this motor adaptation to the scenario of learning how to throw a Frisbee. Here, the learner attempts a *novel* combination of arm, hand, and body movements, with a *novel* object that has *novel* flight properties that he or she

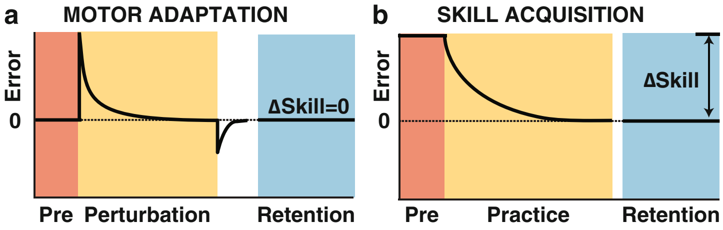

Fig. 8.1 **a** Motor adaptation paradigm. The participant starts with a highly learned movement, such as reaching, which is performed with zero error in the pre-stage (*red*). A perturbation is applied during a block of trials (*yellow*), until the participant adapts and reestablishes the initial performance. When the perturbation is removed, there is a short aftereffect, indicating that something has been learned. However, the original movements are resurrected quickly (*blue*); thus, there is no net change in skill. **b** Skill acquisition. In the pre-stage, the participant performs a novel motor skill with high error (*red*). The participant decreases error over practice (*yellow*). Error in the retention stage (*blue*) is less than the error in the pre-stage (*red*), reflecting the acquisition of the novel skill

has never encountered before. With practice, he or she learns to release the Frisbee to lead to an accurate return, reflecting increased proficiency or skill (Fig. 8.1b). Note that there is no imposed perturbation. The skill is new and persists after training, indicating retention. There is much anecdotal and some experimental evidence that once a motor skill is learned, it persists for a long time over years of no practice (Draganski et al. 2004; Nourrit-Lucas et al. 2013; Park et al. 2013; Swift 1910). While in motor adaptation there are also savings, it remains to be tested whether such savings persist for a similarly long time. If not, this would suggest that the temporary adaptation processes involve different forms of neuroplasticity than the acquisition of a novel skill. Hence, we conclude that the first desideratum for studying skill acquisition is that the movement task poses a *novel* challenge to the neuromotor system.

Intrinsic and Extrinsic Redundancy However, novel skills such as throwing a Frisbee are complex and difficult to study in the laboratory without at least some experimental reduction. Therefore the question is: What are the minimal requirements for an experimental task to still allow for the study of skill, but in a controlled and hypothesis-driven fashion? We propose that the essence of skill is redundancy. As exemplified by the quarterback's forward pass, a skill should allow for multiple solutions to achieve the task. Unlike in adapting a reaching movement in an external force field to restore the initial straight path, subjects should be able to explore different solutions to find the best one with practice. Such solutions may also differ between individuals.

Two types of redundancy can be distinguished: *intrinsic* to the organism and *extrinsic* in the task. The role of intrinsic redundancy has been widely recognized in motor control. Our complex neuromuscular system is hierarchical with an infinite number of degrees of freedom at any one level. The most frequently used example for redundancy is at the level of joints: Pointing to an object with a multi-joint arm can be achieved with an infinite number of joint angle configurations (Bernstein 1967).

Equivalently, at the level of muscles, multiple muscle contraction patterns may lead to the same kinematic pattern (d'Avella et al. 2003; Ting 2007). This excess of degrees of freedom for any movement goal repeats itself at the level of motor units and further. However, the task remains unique: The finger needs to point to one location in space.

Extrinsic redundancy, in contrast, would allow pointing to a whole region in space. For example, grasping and bringing a cup of coffee can be achieved using multiple approach paths, multiple finger contact points, and multiple contact points with the mouth. Yet, the task is only successful if the person brings the cup to the mouth, drinks, and does not spill the coffee. There are infinitely many combinations of execution that lead to success with zero error. This kind of task redundancy has received less attention in motor learning than the intrinsic redundancy. Returning to the quarterback example, not only can different throwing styles achieve the same target but also different throwing releases may lead to the same target. Extrinsic, or task redundancy allows the actor to "decide" what combination of execution-relevant variables to use in pursuing the task goal. Note that "decision" does not always imply a conscious weighing of alternatives with high-level cortical involvement (Araujo et al. 2006). Rather, the situation forces the quarterback to make extremely fast decisions, which may happen at much lower levels of the neural hierarchy. Hence, the second desideratum for studying *skill* and *skill acquisition* is that the task should include redundancy to allow for choices between many solutions that achieve a given task goal.

How can we capture this redundancy and study the acquisition of novel skills in the laboratory without losing experimental control and precise measurement? Unlike several decades ago, measurement of complex movements is no longer the problem, as both technology and analysis methods have significantly advanced. New camera systems and wearable sensors have outdated tedious digitizing of video recordings. In addition, virtual technology and programmable robotic devices have created a whole new arena for experimental manipulations and measurement. However, simply measuring trajectories of Peyton Manning's throwing arm, even in truly ecological settings, does not tell us much about his skilled performance. Without experimental control and hypotheses, the multitude of data simply redescribe the performance. A hypothesis-driven approach to skill requires some simplification—but without "throwing the baby out with the bathwater."

8.2 A Methodological Approach to Understanding Skill Acquisition

We developed an approach using mathematical modeling and virtual technology to study the acquisition of novel skills with extrinsic redundancy. In the following, we first describe our methodological steps and then present three examples following this approach: throwing a ball to a target, rhythmically bouncing a ball, and carrying a cup of coffee:

1. *Select a skill*: The first step is to choose a skill that represents some core aspects germane to many other tasks. In throwing, for example, the timing of release is one such core aspect. Carrying a cup filled with coffee exemplifies manual interaction with a complex object. Next, it is essential that the experimental task has a well-defined goal and yet allows for a variety of solutions to achieve this goal: Task redundancy should be center stage. For example, the quarterback throwing a ball to a receiver can use a variety of strategies to throw to the intended wide receiver. Further, the task should be novel and sufficiently challenging to require practice to achieve success. Improvement should be visible within one or few experimental session(s), but also require fine-tuning at a longer time scale.
2. *Mathematically model the task*: The next step is to model the relevant physics that govern the task. A model is a useful simplification of the real phenomenon because it formalizes the assumptions about the task and prunes away the irrelevant aspects of the real-life task. What is the simplest system that captures the challenge to manipulate a dynamically complex object? What exactly determines timing of release? One core element in the modeling stage is to distinguish between the *execution variables* and the *result variables:* The result variable(s) are defined by the task goal and capture the quality of performance; this is typically an error measure. Execution variables are under control of the performer and fully determine the task result. The functional relationship between execution and result is the essence of the model.
3. *Formulate hypotheses*: Based on the mathematical model, the space of all possible solutions to the task can be derived. As the model system is typically nonlinear, the space of solutions, or result space, is complex and reveals additional properties of solutions, such as risk or dynamic stability, as we explain below. Depending on the model, different mathematical tools can be used to derive predictions about stability or robustness to perturbations. Importantly, exact quantitative hypotheses can be formulated about which solutions have the greatest probability of success.
4. *Render the model task in a virtual environment*: Based on the explicit mathematical understanding, the task can be rendered in a virtual environment. The execution variables are the ones that the subject controls via an interface with the virtual system. The result variables can be precisely measured in the virtual world. For example, while the subject performs a throwing task, the arm trajectory is real and controls the ball release, but the ball and target are virtual. The virtual rendering has the advantage that it confines the task to exactly the variables and parameters that were analyzed. There are no uncontrolled aspects as would occur in the real world. Further, the execution and the result variables can be manipulated at will to test hypotheses about the performance strategies.
5. *Measure subjects' performance and test hypotheses*: Subjects interact with the virtual physics of the task via a manipulandum. The variables measured from the subjects' movements should correspond to the execution variables in the model. The measured execution variables and the task result are then evaluated against the space of all solutions. Hypotheses about solutions derived from the model can be evaluated.

8.3 Hypothesis: Exploit Redundancy and Seek Stable Solutions that Make Intrinsic Noise Matter Less

Before detailing this approach, it is necessary to be more specific about the overall research aim. Given the intrinsic and extrinsic redundancy of the task and performer, we pursued the hypothesis that individuals improve their performance by *seeking solutions that are robust with respect to perturbations to make their intrinsic noise matter less*. Due to the intrinsic redundancy of the hierarchical and complex neuromuscular system, subjects always show variability or intrinsic noise, even when they want to repeat the same movement under fixed external conditions (Faisal et al. 2008). In the presence of extrinsic redundancy with infinite equivalent task solutions, we hypothesize that the neuromotor system chooses those solutions that are most tolerant to this ever-present noise. As highlighted above, tasks with redundancy provide options that subjects can explore and exploit. This overall hypothesis will be operationalized for each task on the basis of the model. The following review exemplifies how we pursued this approach in three different paradigms.

8.3.1 Paradigm 1: Skittles, a Discrete Throwing Skill

The Skill This experimental paradigm was motivated by the British pub game "skittles," which is a table version of the American game "tetherball." The actor throws a ball that is tethered to a post by a string like a pendulum; the goal is to hit a target skittle on the opposite side of the pole (Fig. 8.2a). Accurate throwing requires a controlled hand trajectory that prepares the ball release at exactly the right position and velocity that sends the ball onto a trajectory that hits the target skittle. The task has redundancy as elaborated below and timing is one essential element of this skill.

The Model To simplify the task, the movement of the ball was confined to two horizontal dimensions, eliminating the elevation due to the pendular excursion (Fig. 8.2b). In the model, the ball is attached to two orthogonal, massless springs with its rest position at the center post. To execute a throw, the ball is deflected from its rest position by the hand—a virtual lever arm that moves in correspondence to the real arm movements of the participant (Fig. 8.2b). Upon release, the ball traverses an elliptic path generated by the restoring forces of the two springs (Müller and Sternad 2004b). The equation for ball position in the x- and y-directions at time t is:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} x_p \\ y_p \end{pmatrix} \cos \omega t + \begin{pmatrix} \cos \phi_r & -\sin \phi_r \\ -\sin \phi_r & \cos \phi_r \end{pmatrix} \begin{pmatrix} l \cos \omega t \\ v_r / \omega t \end{pmatrix}.$$

The frequency ω denotes the natural frequency of the springs, and (x_p, y_p) denotes the pivot point and l the length of the arm. For a given throw, two execution variables, angle ϕ_r and velocity v_r, of the virtual hand at the moment of release fully determine the ball trajectory.

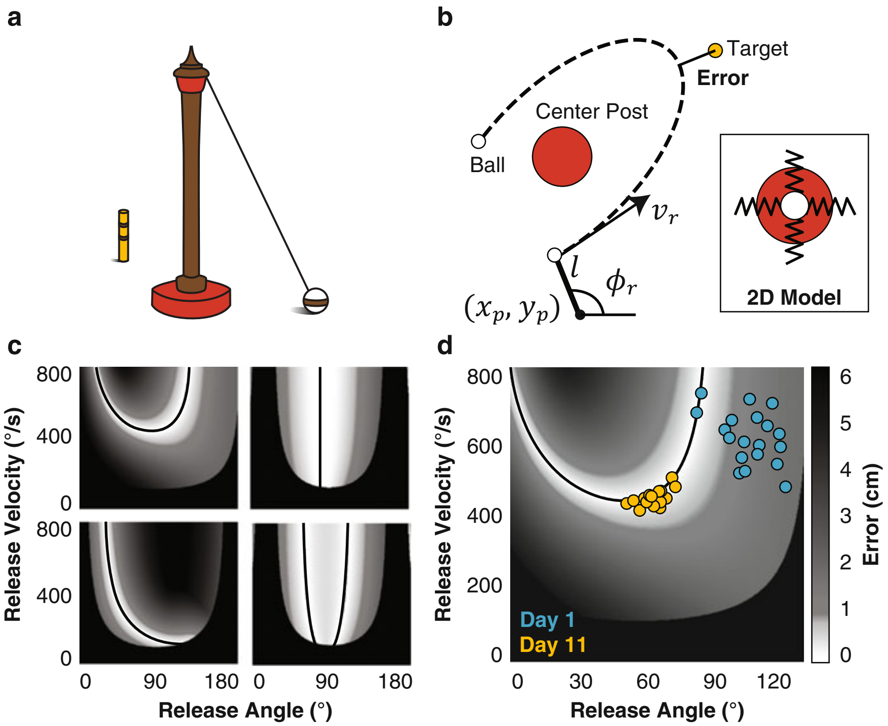

Fig. 8.2 **a** Real-life skittles game. **b** Two-dimensional mechanical model of skittles. The ball (*white circle*) is attached to two orthogonal springs centered at the origin of the center post (*red circle*). The ball trajectory (*dotted line*) upon release is determined by the springs and depends on two execution variables: release angle ϕ_r and velocity v_r of the ball. Error is defined as the minimum distance between the ball trajectory and the target center (*yellow circle*). **c** Execution space for four different target locations. Error is calculated for each point in execution space and indicated in shades of gray; the *lighter shades* denote lower errors. The *black line* represents the one-dimensional solution manifold. **d** Execution space with nonlinear solution manifold with two data sets representing 20 throws collected on the first day (*blue*) and after 11 days of practice (*yellow*)

Similar to the real skill, the actor's goal is to throw the ball to hit the target skittle, without hitting the center post. The location of the target is defined in (x, y)-coordinates; the error is defined as the minimum distance between the ball trajectory and the center of the target (Fig. 8.2b). Thus, the result variable is the error and is fully determined by the two execution variables. Importantly, there is more than one combination of angle ϕ_r and velocity v_r that leads to zero error. Figure 8.2c illustrates this functional relationship: For each point in execution space, spanned by release angle and velocity, error is depicted by shades of gray. Lighter shades indicate smaller errors; black signifies that releases hit the center post, which is a penalty area in the experiment. The thin black lines denote the one-dimensional set of zero-error solutions or solution manifold. The solution manifold can be analytically derived and is defined by the following equation:

$$\frac{v_r}{\omega} = \frac{\left|(-l\sin\phi_r - y_p)x_t + (l\cos\phi_r + x_p)y_t\right|}{\sqrt{(l + \cos\phi_r x_p + \sin\phi_r y_p)^2 - (\cos\phi_r x_t + \sin\phi_r y_t)^2}}.$$

An interesting feature of this task is that the result space and the solution manifold depend on the target location in ways that would be hard to predict without the model (Fig. 8.2c). For example, for target position at $x = 0.6$ m and $y = 1.5$ m, the result space is nonlinear and U-shaped, as shown in the top left example (Cohen and Sternad 2009). For the target position $x = 0.05$ m, $y = 1.055$ m, the solution manifold is a vertical line, such that only the angle of release determines the error, as shown in the top right example (Sternad et al. 2011). In the two examples in the lower panels, the solution manifolds terminate on the penalty area, which makes those solutions risky. Importantly, the difficulty of the task is determined by the shape of the solution manifold and can vary significantly for different target locations.

Hypotheses In principle, subjects can release the ball with any of the position–velocity combinations on the solution manifold. However, Fig. 8.2d illustrates that this is not what subjects do: The two data sets represent 20 throws collected on the 1st day (blue) and after 11 days of practice (yellow). Each data point on this figure corresponds to a throw and, as to be expected, the data show significant scatter, especially in the beginning. The two distributions also show that the subject improved, as the throws early in practice have visibly higher errors on average (in dark colored area). The throws late in practice are aligned with the solution manifold, with smaller errors. What drives this change? What solutions do humans prefer and why? The hypothesis is that individuals improve their performance by *seeking solutions that are robust with respect to perturbations to make their intrinsic noise matter less*.

The sample data illustrate how three conceptually different routes to performance improvement can be distinguished: (1) Subjects shift their solutions in execution space to those regions on the solution manifold where small changes in the angle and velocity of release do not lead to large decreases in the magnitude of error. Wider bands of light gray on the right branch indicate that deviations from the solution manifold do not incur large errors. We refer to this as error *tolerance*. (2) Subjects reduce the amplitude of their dispersion. We refer to this as *noise reduction*. (3) Subjects rotate or reshape their distribution to align with the solution manifold. We refer to this as *covariation*. All three routes channel variability to make their intrinsic noise matter less for the quality of the performance. The specific hypothesis is that learners first improve their performance by shifting their throws to error-tolerant solutions in result space. This first stage includes exploration of options. The second stage involves rotating, or covarying, the data with respect to the solution manifold. Having exploited these two routes, the final stage is to reduce the dispersion. This latter route corresponds to reducing intrinsic noise.

Quantitative measures of *tolerance, noise,* and *covariation* (TNC) were first introduced by Müller and Sternad (2003, 2004a, 2004b, 2009) and subsequently reformulated as cost measures by Cohen and Sternad (2009). The *TNC-cost* measures

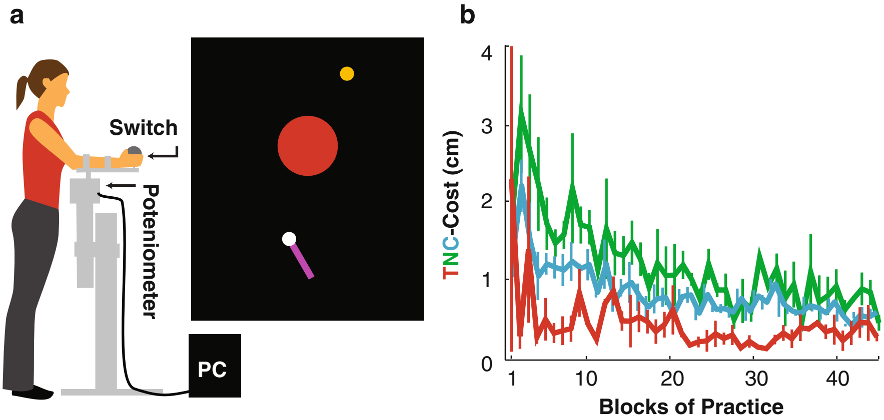

Fig. 8.3 **a** Participant interacting with the virtual environment in the skittles setup. The center post (*red*) and target (*yellow*) and the movements of the lever arm (*magenta*) and the ball (*white*) are presented to subjects on the rear projection screen in front of them. **b** Mean T-cost (red), N-cost (*green*), and C-cost (*blue*) for three expert participants over 45 blocks (15 days) of practice. Error bars show standard errors across participants

assess to what degree the result of a set of data could be improved, if one of these components were optimized. The numerical analysis method was detailed in Cohen and Sternad (2009). Note the similarity with the uncontrolled manifold (UCM) method (Scholz and Schöner 1999), but Müller and Sternad (2009) also outlined some key conceptual differences between the methods. One critical methodological issue is that the UCM method, as one of the many covariance-based methods, is more prone to coordinate transformations, although the TNC method, in particular the covariation cost, is not immune to this problem either (Sternad et al. 2010).

Virtual Environment To test the hypothesis, the mechanical model was rendered in a virtual setup, where subjects interacted with the model via a manipulandum. In the experiment, the actor grasped a ball attached to the distal end of a manipulandum and performed a forearm rotation to throw a virtual ball to a target in the virtual environment (Fig. 8.3a). Initially, the subject closed a contact switch with her index finger; lifting the finger opened the switch and triggered the release of the virtual ball. A potentiometer continuously sampled the angular position of the manipulandum, and the movements of the arm were mapped onto the displayed virtual arm; angular velocity of the arm was estimated online. The ball traversed around the center post as determined by the angular position and angular velocity at the moment of release (Fig. 8.3a).

Experimental Findings Cohen and Sternad (2009) tested the hypothesis that learners improve their performance by first locating error-tolerant solutions in result space and then by channeling and reducing their intrinsic noise. In their study, nine participants with average and three participants with extensive throwing experience practiced three blocks of 60 throws each day for 6 and 15 days, respectively. Each block of

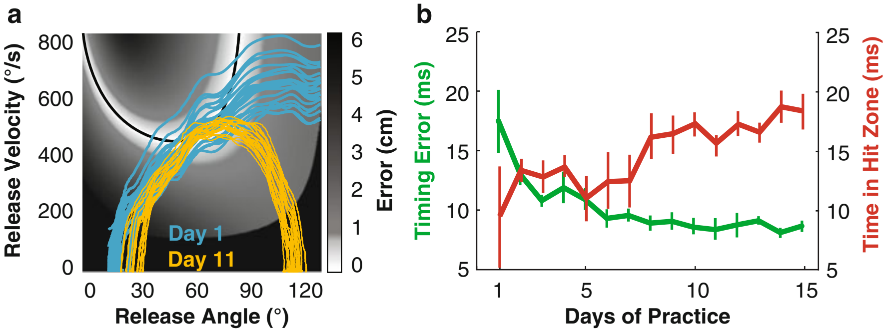

Fig. 8.4 **a** Execution space with two sets of arm trajectories representing 20 trials collected on the first day (*blue*) and after 11 days of practice (*yellow*). **b** Mean *timing error* (*green*) and *time in hit zone* for three expert participants over 15 days of practice. Error bars show standard errors across participants

60 throws was analyzed as a distribution and the three components *tolerance, noise,* and *covariation* were quantified: Each data set was translated to obtain *T-cost,* scaled for *N-cost,* or oriented via recombination for *C-cost* to find the optimal mean result for this component. Note that each transformation left all other aspects of the data invariant. The cost was then defined as the difference between the mean result, error, of the original data set and the optimally transformed data set.

The *TNC-cost* analysis showed that both novices and expert throwers revealed similar patterns of change in *T*-, *N*-, and *C-costs* over practice (Cohen and Sternad 2009). Figure 8.3b shows all three costs for the expert throwers. *T-cost* (red) decreased very early in practice followed by a considerably slower decrease in *C-cost* (blue). *N-cost* (green) decreased at the slowest rate and remained the highest cost to performance. The overall rank ordering of these costs was similar across participants and expertise levels. This pattern of results suggests that early in practice participants tried out different performance strategies and searched for the most error-tolerant region of the solution manifold. They then improved covariation to better align with the solution manifold. The stochastic *Noise* component was reduced only modestly, suggesting that intrinsic noise is relatively inaccessible to practice.

How does the actor achieve these changes? Particularly, how can covariation between position and velocity be achieved? Extending initial work by Müller and Loosch (1999), Cohen and Sternad (2012) tested the hypothesis that subjects learn to align their trajectory of the arm with the solution manifold. For this analysis, it is interesting to recognize that the execution space, spanned by position and velocity, is equivalent to state space. Hence, not only the release points but also the continuous trajectory can be analyzed in this space (Fig. 8.4a). The solution manifold corresponds to an ideal trajectory, which would achieve the desired result at every point. Evidently, the arm trajectory cannot exactly follow the solution manifold, but a trajectory that at least temporarily follows the solution manifold gives the subject a time window to release the ball that achieves a successful hit. Cohen and Sternad (2012) hypothesized that with practice subjects shape their trajectories to travel along the solution manifold so that the ball can be released within this time window and achieve a successful hit. This strategy exploits the redundancy of the task and ameliorates the effects of intrinsic noise in timing.

The same participants' data from the first study were analyzed. Each continuous arm trajectory was converted to a trajectory of error over time, assuming that every angle–velocity point on the trajectory was a release (its associated error was computed using the model equations). To measure the shaping of the arm trajectory with respect to the solution manifold, *time in hit zone* was defined as the time that the trajectory spent below a given error threshold. Timing accuracy or *timing error* was defined as the time difference between actual and ideal release time. The ideal release time was the time when the arm trajectory crossed the solution manifold. Cohen and Sternad (2012) found that with extended practice, performance improved due to continued shaping of the trajectory (Fig. 8.4a). Interestingly, timing error decreased first but then asymptoted at 9 ms at approximately Day 6, while *time in hit zone* continued to improve (Fig. 8.4b). This suggests two interpretations: When timing error reached a plateau, performance improvement could only be achieved by aligning the trajectory with the solution manifold. Alternatively, subjects did not need to further improve their timing accuracy, as their trajectory was in the hit zone and made any further improvement in timing superfluous.

Interim Conclusions Analysis of the throwing skill exemplified our approach to skill acquisition using a discrete task with redundancy. The results showed that redundancy allows the performers to choose their performance strategy to minimize the potentially detrimental effects of intrinsic noise on performance. These findings support the overall hypothesis that when performing a new skill, humans exploit the redundancy of the task and find the error-tolerant regions to enhance their performance.

8.3.2 Paradigm 2: Rhythmically Bouncing a Ball: Humans Exploit Dynamically Stable Solutions

The Skill Rhythmically bouncing a ball on a racket is a seemingly simple and playful task. Yet a closer look reveals that it requires a high level of perceptually guided coordination to repeatedly intercept the ball to hit a target amplitude, i.e., perform in a rhythmic fashion (Fig. 8.5a). As in skittles, success is determined at one critical moment when the racket hits the ball, as this impact fully determines the trajectory of the ball. Hence, a core feature of this task is the control of collisions, which is germane to numerous other behaviors, ranging from running to clapping, and numerous sport skills, such as volleyball. One key difference to skittles, however, is that these impacts are performed in continuous rhythmic fashion, and errors from one bounce propagate to the next. Via the repeated interactions with the ball, the actor becomes part of a continuous dynamical system.

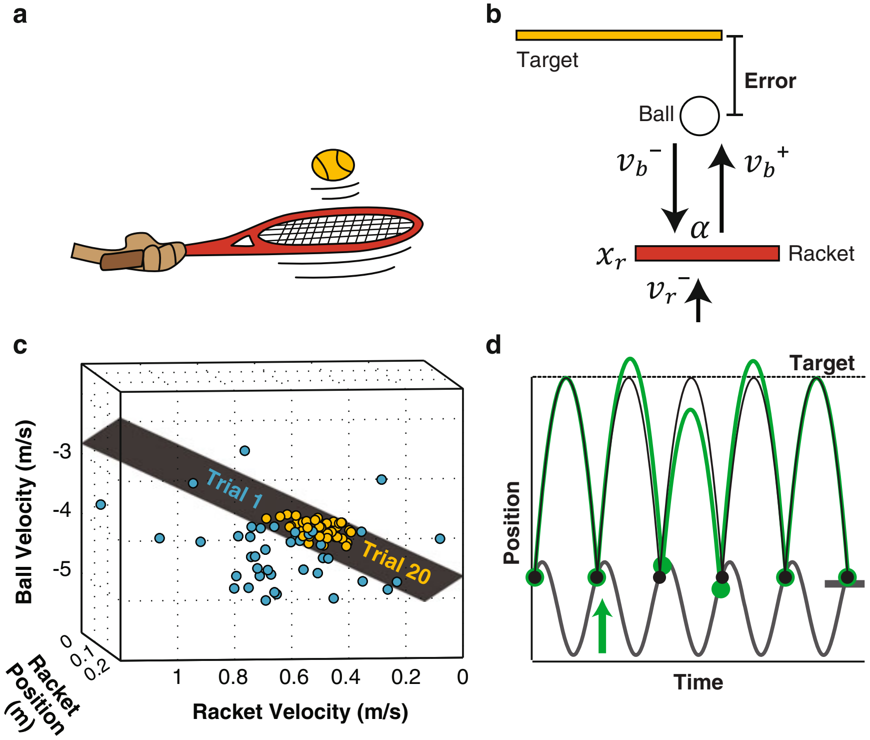

Fig. 8.5 **a** Real-life rhythmic ball bouncing skill. **b** Model of the racket–ball system. The vertical ball position between each instantaneous impact follows ballistic flight, which depends on three execution variables: *ball velocity* v_b^- and *racket velocity* v_r^- velocities just before impact, and *racket position* x_r at impact. Error is defined as the absolute difference between the target height and maximum ball height. **c** Execution space of the racket–ball system. The *gray plane* represents the two-dimensional solution manifold. Two data sets represent bounces in first trial (*blue*) and after 20 trials of practice (*yellow*). **d** Illustration of dynamic stability associated with negative acceleration. The *black trajectory* of the ball exemplifies stable performance. A positive perturbation to racket velocity just before impact was added to the green ball trajectory at the arrow. The error from the perturbation is corrected after three bounces without any changes in the sinusoidal racket trajectory

The Model The model for this task is a well-studied nonlinear dynamical system, originally developed for a particle bouncing on a vibrating surface (Guckenheimer and Holmes 1983; Tufillaro et al. 1992). The simple model consists of a planar surface moving sinusoidally up and down, and a ball or point mass that impacts the surface with instantaneous contact (Fig. 8.5b). The vertical position of the ball x_b between the kth and the $k+1$th racket–ball impact follows ballistic flight:

$$x_b(t) = x_r(t_k) + v_b^+(t - t_k) - g/2(t - t_k)^2,$$

where t_k is the time of the kth ball–racket impact, x_r is racket position, v_{b}^{+} is the ball velocity just after impact, and g is the acceleration due to gravity (9.81 m/s^2). With the assumption of instantaneous impact, the ball velocity just after impact v_{b}^{+} is determined by

$$v_b^+ = (1+\alpha)v_r^- - \alpha v_b^-,$$

where v_b^- and v_r^- are the ball and racket velocities just before impact, and the energy loss at the collision is governed by the coefficient of restitution α. The maximum height of the ball between time t_k and $t_{\mathrm{k}+1}$ depends on the ball and racket velocities just before impact and the position at impact x_r, as shown by the following equation:

$$\max_{t_k \le t \le t_{k+1}} x_b(t) = x_r(t_k) + (((1+\alpha)v_r^- - \alpha v_b^-)(t - t_k))^2/2g.$$

The task goal is to bounce the ball to a target height, and the error is defined as the difference between the maximum height of the ball and the target height (Fig. 8.5b). Even in this simplified form, the task has redundancy, as the result variable error is determined by three execution variables: v_{b}^-, v_{r}^-, and x_{r}. Figure 8.5c shows execution space with the solution manifold, i.e., the planar surface that represents all solutions leading to zero height error. The blue and yellow data points are two data sets from early and late in practice, respectively; each data point corresponds to one ball–racket contact. As to be expected, the early data show a lot of scatter, while the late practice data cluster around the solution manifold.

Hypotheses The representation of bounces in execution space affords analysis of the data using the TNC method. As in the two-dimensional version in skittles, the data can be transformed to estimate the contributions of *tolerance, noise,* and *covariation*. The same hypothesis as in skittles can be pursued in ball bouncing. However, an important difference to skittles is that only racket position and velocity at impact are under the actor's direct control; the third execution variable, ball velocity, is determined by the previous contact (which in turn is determined by the previous contact, etc.). Therefore, continuous rhythmic control of the ball depends on the preceding contacts, which adds an additional challenge to the controller. As mentioned above, the task is a dynamical system that lends itself to different analyses and predictions.

To model the racket and ball system as a continuous dynamical system, the racket movements need to be specified. To this end, the model assumes simple sinusoidal motion of the racket. With this assumption, racket position and velocity at impact collapse into a single state variable, racket phase, or acceleration at impact. Further, the continuous system can be discretized at the ball–racket contact, where ball and racket positions are identical. A discrete map can be derived based on two state variables, the ball velocity just after impact v_k^+ and the racket phase at impact θ_k:

$$v_{k+1}^+ = (1+\alpha)A\omega\cos\theta_{k+1} - \alpha v_k^+ + g\alpha(\theta_{k+1} - \theta_k)/\omega$$

$$0 = A\omega^2(\sin\theta_k - \sin\theta_{k+1}) + v_k^+\omega(\theta_{k+1} - \theta_k) - g/2(\theta_{k+1} - \theta_k)^2,$$

where A and ω are the amplitude and frequency of the sinusoidal racket movements (Dijkstra et al. 2004; Schaal et al. 1996).

This ball–racket system is a nonlinear system that displays dynamic stability and, despite its simplicity, shows the complex dynamics of a period-doubling route to chaos (Guckenheimer and Holmes 1983; May 1976; Tufillaro et al. 1992). As the task requires simple periodic bouncing, only periodic behavior was considered. Local linear stability analysis of this discrete map identifies a fixed-point attractor, when racket acceleration at impact a_r satisfies the inequality (Schaal et al. 1996; Sternad et al. 2001):

$$-2g\frac{(1+\alpha^2)}{(1+\alpha)^2} < a_r < 0.$$

In this dynamically stable state, small perturbations of the racket or ball die out without requiring any corrections. To make this property of the task more intuitive, consider the illustration in Fig. 8.5d: While hitting the ball with negative racket acceleration (the upwardly decelerating phase), a ball that contacts the racket earlier is hit with relatively higher velocity, which leads to a higher ball amplitude following the contact. Conversely, a ball that contacts the racket later, such as after an amplitude overshoot, is hit with relatively lower velocity, which leads to a lower maximum ball height on the next bounce. Note that this purely physical relation automatically compensates for an over- or undershoot in the previous ball amplitude. This automatic compensation via covariation among the execution variables is the underpinning to the error compensation in dynamically stable performance.

This property leads to an interesting hypothesis for human control: If subjects establish such a dynamically stable regime, they need not correct for small perturbations that may arise from the persistent motor noise. Thus, we hypothesized that subjects learn this “smart” solution of hitting the ball with negative racket acceleration to exploit dynamic stability. *This dynamically stable solution makes intrinsic noise matter less.*

Virtual Environment In the experiment, the participant stood in front of a rear projection screen and was instructed to rhythmically bounce the virtual ball (white) to a target line (yellow) using a real table tennis racket (Fig. 8.6a). The projected racket movements (red) were shown on the screen impacting the ball. One trial usually lasted 40 s. A light rigid rod with two hinge joints was attached to the racket and run through a wheel, whose rotations were registered by an optical encoder. While the joints allowed the racket to move and tilt with minimal friction in all three dimensions, the encoder only measured the vertical displacement of the racket, in analogy with the model. Racket velocity was continuously estimated. The displacements of the virtual racket were controlled by the measured position of the real racket, and the vertical position of the virtual ball between impacts was determined using the ballistic flight equation. To simulate the haptic sensation of a real ball hitting the racket, a mechanical brake, attached to the rod, was activated at the ball–racket impact of each bounce. Racket acceleration at impact was analyzed after the experiment and served as the primary measure of dynamic stability to test the hypothesis (Wei et al. 2007).

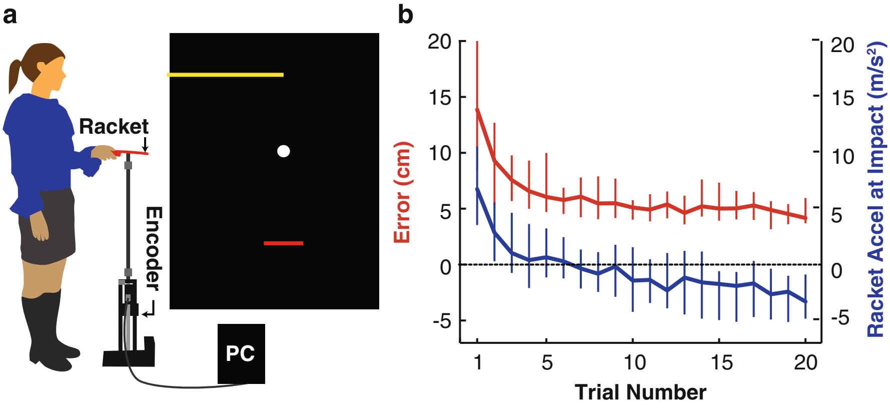

Fig. 8.6 **a** Participant interacting with the virtual environment. The movements of the racket (*red*) and ball (*white*) and the target height (*yellow*) are presented to subjects on the large screen in front of them. **b** Median *error* (*red*) and *racket acceleration at impact* (*blue*) for 48 novice participants over 20 trials of practice. Error bars show the 25th and 75th percentiles across participants

Experimental Findings The hypothesis was tested in an experiment that involved 48 novice subjects, who performed 20 trials of 40 s each (which corresponds to approximately 60 bounces per trial; Ehrlenspiel et al. 2010). Figure 8.6b shows the medians over subjects in each trial. The error (red) declined with practice as to be expected. More importantly, this improvement was paralleled by a decrease in racket acceleration at impact (blue), starting from positive values at the beginning to assuming negative values after about eight trials. This result highlights that the intuitive solution for novices is to accelerate to impart energy to the ball in the upward direction. Yet, this is not the most effective approach, when the ball is hit repeatedly with periodic racket movement. Further, from a biomechanical perspective, hitting the ball with maximum velocity, i.e., at the moment of zero acceleration, would be the most energy-efficient solution. Maximum velocity would result in the highest ball amplitude for a given rhythmic racket trajectory. Nevertheless, subjects reliably converge to solution where the racket is in its decelerating phase at ball contact. Additional support for this strategy was revealed by estimating covariation among the three execution variables at impact (Ehrlenspiel et al. 2010). These results highlight that adopting solutions that afford dynamic stability is not trivial, but is a smart solution that requires practice.

A series of studies tested the generality of this result in different experimental renderings to rule out the possibility that this could be the fortuitous effect of the tight constraints in the virtual setup. The experimental setups ranged from having the participant manipulate a pantograph linkage that allowed precise control of the haptic contact (Schaal et al. 1996; Sternad et al. 2001), a real tennis racket to bounce a real ball attached to a weighted boom that confines the ball to a vertical path (Katsumata et al. 2003; Sternad et al. 2000, 2001), to having the participant freely bounce a real ball with a real tennis racket in 3D (Sternad et al. 2000, 2001). The findings were robust: Experienced performers hit the ball with negative racket acceleration. Further support that humans seek dynamically stable solutions came from a study by Morice et al. (2007), where the visuomotor phase between the real racket and ball movements was shifted, performers still learned to exploit dynamic stability, *where intrinsic noise matters less.*

Interim Conclusions Just as in the skittles task, participants were shown to find stable or error-tolerant solutions in the redundant space of solutions to achieve the task. Further analysis of *covariation* and *noise* is still to come. The commonality of the two paradigms is that the subject's control of the ball was confined to a very short moment. A first extension from this momentary interaction was made in an experiment that extended the duration of contact: A beanbag replaced the elastic ball, such that the contact duration became long enough to afford corrections and essentially became a catch followed by a resetting of initial conditions to throw (Katsumata et al. 2003). However, real-life skills include numerous examples that involve continuous interaction with objects. Hence, the next step is to design an experimental paradigm that features continuous interaction with a complex object: a cup of coffee.

8.3.3 Paradigm 3: Complex Object Manipulation: Carrying a Cup of Coffee

The Skill Grasping a cup of coffee and leading it to one's mouth is a seemingly mundane task. Yet, it exemplifies a class of movements that require continuous interaction with an object that has internal dynamics (Mayer and Krechetnikov 2012). While one moves the cup, the coffee is only indirectly controlled via moving its container (Fig. 8.7a). How the CNS controls interactions with such objects is intriguing, as the moving liquid creates time-varying reaction forces that have to be accounted for to keep the cup under control and not spill the coffee. The essential challenge of this task is to perceive these time-varying dynamics and establish a safety margin for transporting the cup of coffee.

The Model Leading a cup of coffee to one's mouth is a tall order to model mathematically. Hence, we again simplified the situation by modeling of the cup as a bowl with a ball moving inside it—representing the internal degree of freedom that affect the system's dynamics (Hasson et al. 2012a, b, Hasson and Sternad 2014) as shown in Fig. 8.7a. Assuming that the cup's movements are confined to the horizontal direction and the ball can swerve within the cup, this reduced system is approximated by the well-studied cart-and-pendulum system (Fig. 8.7b). The cart corresponds to the cup and the bob's pendular movements represent the sloshing liquid. The governing equations of the system dynamics are

$$(m + M)\ddot{x} = F$$

$$\ddot{\theta} = (\ddot{x}/l)\cos\theta - (g/l)\sin\theta,$$

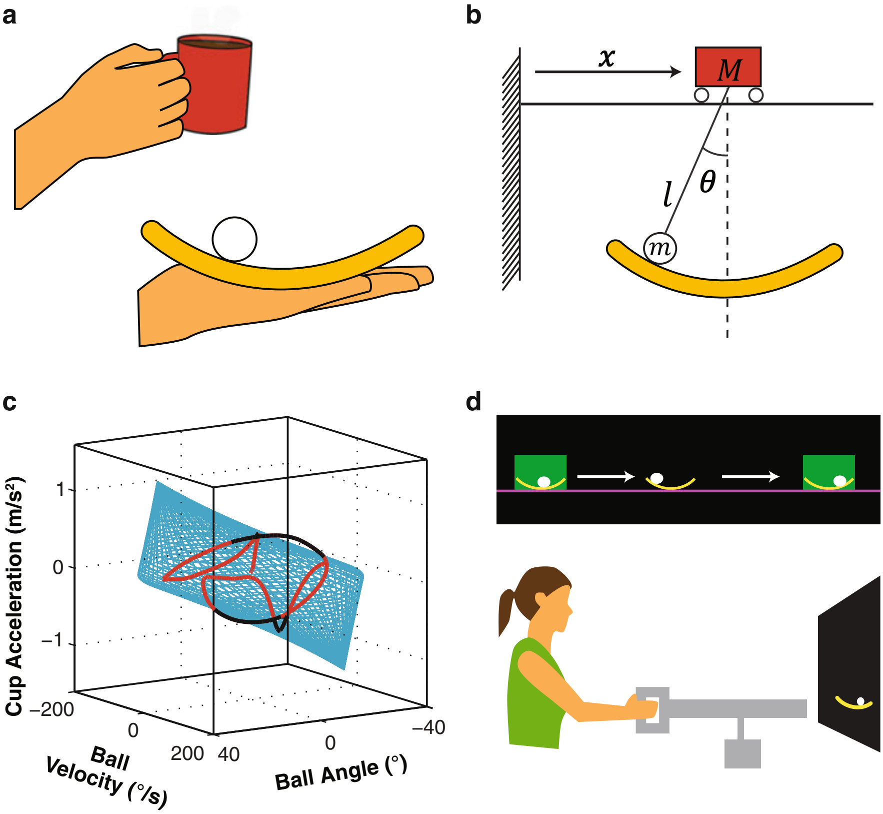

Fig. 8.7 **a** Holding a cup of coffee simplified as holding a cup with a ball inside. **b** Model of the cart-and-pendulum system. In the mathematical model, x is the cart/cup position, θ is the ball angular position, M is the cup mass, m is the ball mass, and l is the pendulum length. **c** An exemplary successful trajectory (trial) in three-dimensional execution space, spanned by ball angle and velocity and the acceleration of the cup, which together specify the *energy margin* of the ball. The *energy margin* describes a two-dimensional manifold (*meshed blue surface*). Assuming the cup acceleration is unchanged, the trajectory inside the manifold has a positive safety margin and the ball will remain in the cup (*red trajectory*); if the trajectory is outside (*black trajectory*), the energy margin is negative and the ball will escape unless a correction is made. **d** Participant interacting with the virtual environment. A haptic manipulandum provides the mechanical interaction with the object model and the movements of ball and cup appear on the rear projection screen. The task is to transport the cup from the left green start box to the right green target box as fast as possible (minimum-time condition) or in exactly 2 s (target-time condition) without letting the ball escape from the cup

where θ, $\dot{\theta}$, and $\ddot{\theta}$ are angular position, velocity, and acceleration of the ball; x, $\dot{x}$, and $\ddot{x}$ are the cart/cup position, velocity, and acceleration, respectively; F is the net force acting on the cart/cup. Parameters of the system are m and M representing the masses of ball and cup, respectively; l is the length of the rod (pendulum length); and g is the gravitational acceleration. Hence, the model has four state variables x, $\dot{x}$, θ, and $\dot{\theta}$ and the externally applied force F that determines the behavior of the ball-and-cup system. The task is determined by five variables. The new problem is that only one variable (force) is under direct control of the subject, and even this variable is continuously influenced by the reaction forces of the ball. In fact, F is the net force, as the ball or pendulum bob moves under the influence of the cart dynamics and gravity and imparts a time-dependent force to the cup in addition to the active force supplied by the actor. This makes the distinction into execution and result variables significantly more complicated than in the previous two examples.

Hypotheses Nevertheless, the core feature of redundancy is present also in this task: Transporting the cup from one position to another can be achieved by multiple trajectories. How can one conceive of a result space determined by execution variables? One important constraint of the task is to keep the ball within the cup, which reduces the range of all available trajectories by limiting the forces that the actor can successfully apply. This task constraint can be expressed via the energy of the ball and its distance from escape (see more detail in Hasson et al. 2012b). Briefly, the current energy of the ball is a sum of its potential, kinetic, and inertial energy (energy conferred to the ball due to the acceleration of the cup). Potential energy is defined by the height of the ball within the cup, kinetic energy is defined by the velocity of the ball, and the inertial energy is provided by the instantaneous acceleration of the cup (Hasson et al. 2012b). At each sampled point in the movement, one can define an energy margin as the difference between the current energy of the ball and the energy that would make the ball escape. This energy margin is the dynamic analogue to the safety margin, as defined in studies on grip force in object manipulation (Flanagan and Wing 1997; Johansson and Westling 1984). The energy margin is positive, when participants use accelerations that keep the current energy smaller than the energy level that would make the ball escape—a safe strategy. A more risky strategy would yield values of energy margin near zero, getting the ball close to the rim of the cup. Negative energy margin values indicate that the ball would escape in the near future, assuming no change in the currently applied acceleration.

When the task result is defined in these terms, execution space spans only three variables: acceleration of the cup/cart, position, and velocity of the ball/pendulum. Figure 8.7c visualizes this execution space including a result surface that specifies the energy margin of zero. The area inside this manifold captures those executions that have positive energy margins (from 0 to 1); all solutions outside the manifold would lead to ball escape (assuming no change in acceleration). The plotted trajectory demonstrates an example evolution of the execution variables during a single trial of moving the cup. Note that the trajectory may leave the volume bounded by the blue surface temporarily, but as long as participants quickly adjust their acceleration, they can prevent ball escape. However, larger deviations will lead to ball escape.

Extending previous arguments that *performers acquired solutions with stability to make intrinsic noise matter less,* we tailored this hypothesis to the current task. As subjects moved the cup from A to B, and not "spill the coffee" (lose the ball), we hypothesized that with practice subjects will seek solutions that have large energy margins. Further, we hypothesized that individuals with greater movement variability, or intrinsic noise, would seek solutions that were less risky (and vice versa).

Virtual Environment The cart-pendulum system was rendered in a virtual environment where participants only saw the bob of the pendulum and the arc of its trajectory that represented the cup (Fig. 8.7d). Participants controlled the virtual cup using a robotic manipulandum that was constrained to move the cup in the horizontal direction (Haptic Master, Moog, Netherlands). The task goal was to transport the virtual cup from an initial position to a target position at 40 cm distance (green boxes). In two conditions, subjects moved the cup either as fast as possible (minimum-time group) or at the specified time of 2 s (target-time group). The time window was signaled to subjects by a white box that began descending onto the target box at constant velocity upon leaving the start box. Two seconds passed when the white box was exactly overlaid on the target box.

Empirical Findings Two groups of nine participants each practiced this task for 300 trials in each of the two conditions (Hasson et al. 2012b). The motivation for the target-time condition was to create a condition where there was redundancy: 2 seconds gave subjects ample time to develop different strategies. We hypothesized that they would seek *stable strategies* that optimized the energy margins to *allow for noise and perturbations to matter less*. For comparison, the minimum-time condition only presented one optimal solution. To increase speed, subjects were expected to decrease their energy margins. In the two conditions, changes in both directions would signal that subjects were aware of their variability.

With practice, all participants in the target-time group became better in placing the cup in the target box in the specified 2-second interval; similarly, the minimum-time group decreased their movement time. Further, in both conditions, participants lost the ball less often and their trial-to-trial variability decreased. The most central variable was the energy margin, which was calculated for each point along the cup trajectory, yielding a time-varying pattern. Figure 8.8a, 8.8b exemplifies the pattern of results in both conditions and their change with practice. In the target-time condition, participants increased their energy margin, indicating that strategies became safer with practice. This result is consistent with the hypothesis, because higher energy margin values provide more tolerance to intrinsic noise. In contrast, the minimum-time group decreased their energy margin, indicating that their strategies became more risky as a compromise to increase speed. Yet, the number of ball losses still decreased, reflecting that subjects were sufficiently sensitive to their variability. Figure 8.8c summarizes the change in energy margin with practice in all individuals in the two conditions.

To test the second hypothesis stating that the preferred energy margin should be adjusted to each individual's variability, we examined the correlation between the variability of the total energy throughout the movement and the energy margin during that same movement in the last 30 trials of the experiment (for details, see Hasson et al. 2012b). The results showed that participants in the minimum-time group (blue circles) who had more variability also showed greater energy margins, suggesting that more variable individuals used safer movement strategies (Fig. 8.9). However, this correlation was not present in the minimum-time group (red triangles). One explanation is that the variability in the total energy did not simply reflect the

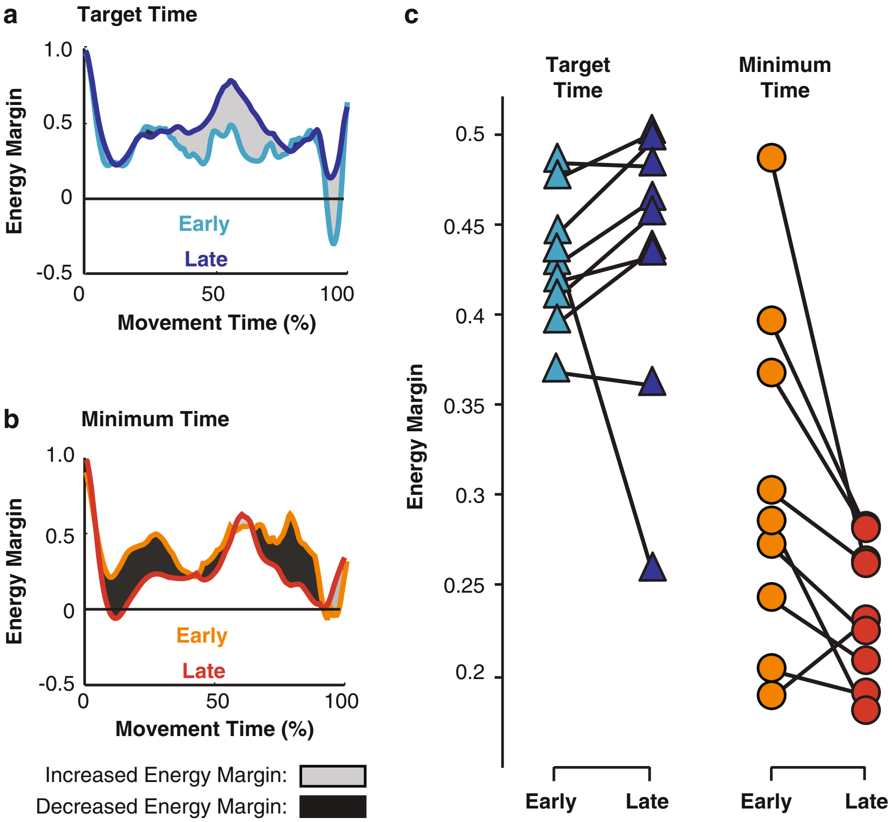

Fig. 8.8 Energy margin over the time of a trial (normalized to 100 %) for an exemplary participant from the **a** target-time group and the **b** minimum-time group. *Dark/light shading* indicates a decrease/increase in energy margin between the average for first 30 versus last 30 trials. **c** Summary of changes in energy margin with practice. Each data point represents the average for the first (*early practice*) or last (*late practice*) 30 trials for the target-time (*triangles*) and minimum-time group (*circles*)

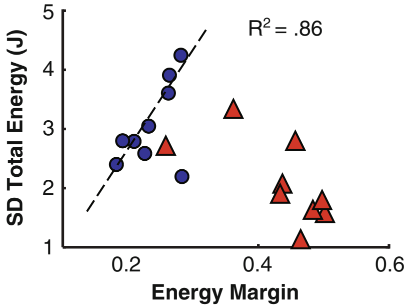

Fig. 8.9 Correlations between energy margin and trial-to-trial variability (standard deviation) of total energy during the last 30 trials for the target-time group (*triangles*) and the minimum-time group (*circles*)

variability at the "physiological limit," but also captured the greater variability in the movements when less constrained. Despite this partially inconsistent result, the findings lend support to the hypothesis that actors take stability properties of the task and their own intrinsic noise characteristics into account when learning to manipulate a "cup of coffee."

8.4 Conclusions and Outlook

This chapter aimed to present a methodological approach to study the acquisition and control of novel and more complex skills that capture coordination challenges inherent to real-life motor skills. This work differs from much of the more recent research on motor learning or adaptation, where an existent movement pattern is adapted to external manipulations. We advocated to study more complex tasks to understand the acquisition of *novel skills,* which is an essential and ubiquitous process that enables humans not only to perform extraordinary actions, such as skateboarding, but also to eat with knife and fork or drive a car. How the brain changes and stores such infinitely many new skills that essentially define our human existence remains one of the core open questions in human neuroscience.

We proposed that the minimal ingredient for *skill* is redundancy, in particular *extrinsic* or *task* redundancy that allows individuals to make choices or even decisions about how they perform the task. This contrasts with much of the previous work in motor neuroscience that has tended to focus on simple and well-defined movements with a single goal. These experimental paradigms are well suited to study simpler forms of learning, including habituation and sensitization, classical and operant conditioning, and motor adaptation. In order to extend the realm of scientific study and address more high-level skills, we developed a methodological approach that still afforded hypothesis-driven research. In three examples, we exemplified our model-based approach.

All three experimental paradigms involved interaction with an object and thereby exemplified different aspects of tool use, a fundamental human skill. They form a logical progression in the physics they involve: In skittles, the trajectory of the thrown ball is fully determined at the moment of release; there is no further interaction with the ball. Every trial is a new start, setting new initial conditions. In ball bouncing, subjects again contact the ball at a very brief moment that fully determines the subsequent ball trajectory. However, unlike in skittles, the successive ball contacts are not independent: The ball's trajectory from the previous impact influences the next ball impact. Lastly, in the cup-and-coffee task, the force applied to the cup and the force exerted by the sloshing coffee onto the cup are in continuous and complex interplay. In this continuous dynamical system, every moment in human control matters. Due to this increasing complexity, the methods for analysis in the three paradigms need to be different. Nevertheless, even though the models are different and render different variables, all three experiments pursued one core hypothesis: Humans seek stable solutions where intrinsic noise matters less.

Each experimental task was designed to allow an infinite number of solutions to a given task. Given these multiple options, it is necessary to have a model as reference to evaluate the observed variability within subjects across practice, but also across subjects. It is essential that the model described not only the physics of the task, but also how the subject interacted with the physics, i.e., how the subject executed the task to achieve a result. If the functional relationship between execution and result is known, the space of all solutions is known and the manifold of solutions can be calculated. With this knowledge, not only can the practice-induced progression in performance be characterized but individual differences can also be studied in a more principled way. For example, a person with high variability may prefer safer strategies, while a person with low intrinsic noise may prefer a more risky strategy. While this is a first start, more work is needed to better understand interindividual differences (Cesqui et al. 2012).

While our current research has focused on developing and testing the approach on healthy individuals, the experimental platforms are ideal to take the next step: diagnose coordination deficits and design interventions to accelerate learning and modify behavior of patient populations. For example, the virtual rendering of the task lends itself to perceptual modifications that may shape the characteristics of behavior. One study exemplifies the initial step in this direction: Using a modified skittles task, we showed how a decrease in perceived variability could affect movement strategies in children with dystonia (Chu et al. 2013). Following such first forays, the arena of questions and applications is wide open.

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Chapter 9
The Dynamical Analysis of Inter-Trial Fluctuations Near Goal Equivalent Manifolds

Joseph P. Cusumano, Joseph M. Mahoney and Jonathan B. Dingwell

9.1 Introduction

The human body possesses a number of degrees of freedom far in excess of that needed to accurately execute a typical goal-directed movement. It is natural to expect this redundancy to play an important role in the regulation of motor variability as well as to influence its experimentally-observed structure. An important class of data analysis methods, based on the notion of task manifolds (Scholz and Schoner 1999; Müller and Sternad 2004; Cusumano and Cesari 2006), has been developed to examine the effect of this redundancy. In this chapter, we present a data analysis paradigm that integrates a consideration of redundancy at the task level with the dynamical analysis of inter-trial fluctuations arising from repeated goal-directed movements. We ground our discussion by presenting a study of variability in a virtual shuffleboard task, and model inter-trial fluctuations as the output of a perception-action loop whose primary function is to reduce error from one trial to the next. We show that the fluctuation dynamics in the vicinity of the task's goal equivalent manifold (GEM) (Cusumano and Cesari 2006; John and Cusumano 2007; Dingwell et al. 2010; Dingwell and Cusumano 2010; Dingwell et al. 2013; Cusumano and Dingwell 2013) allow us to characterize not only the "static," geometrical distribution of the variability, but also its temporal structure. This combined space-time analysis of observed variability yields an improved understanding of how goal-level errors are regulated and generated.

Task manifolds are surfaces in an appropriate body state space (e.g., joint kinematic variables) that contain all possible task solutions. Since, by definition, every

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point in a task manifold corresponds to body states that result in perfect task execution, only deviations off of the manifold result in error at the goal level. While this same basic idea underlies multiple methods of variability analysis, a different approach has been taken to implement it in each case, largely motivated by a difference in analytical focus. Uncontrolled manifold (UCM) analysis (Scholz et al. 2000; Scholz and Schoner 1999; Latash et al. 2002; Schöner and Scholz 2007) assumes that the task manifold is defined at each instant along a given movement trajectory, and uses an average movement in a time-normalized set of trials to represent the task's goal. Given the hypothesis that control will only be applied to correct deviations off of the manifold, ratios of normalized variances perpendicular and tangent to a candidate manifold are used as a test: the expectation is that, for a true UCM, there should be greater variance along it than there is normal to it. With a primary focus on motor learning, the tolerance, noise, and covariation (TNC) method (Cohen and Sternad 2009; Müller and Sternad 2004; Ranganathan and Newell 2010; Sternad et al. 2011) statistically decomposes observed variability into the three empirical "costs" in its name, each of which are defined relative to a task manifold. The TNC approach defines the task manifold in a minimal space of variables needed to specify the outcome of a task, such as the position and velocity of a ball at release during a throwing task. TNC analysis does not just focus on the orientation of variability with respect to the task manifold (via the covariation cost) but also takes into consideration the total body-level variability (the noise cost), and relates the goal-level error to variability at the body level (via the tolerance cost).

The GEM concept (Cusumano and Cesari 2006) was initially developed to carry out experimental sensitivity analyses explicitly relating variability at the body and goal levels. The GEM approach defines the task manifold in a manner similar to that of the TNC approach, however it does so by emphasizing the role of a goal function, a mathematical hypothesis on the task strategy that encodes the relationship between the body and goal needed for perfect task execution. The zeros of the goal function are used to analytically define the GEM. In addition, the derivative of the goal function gives the body-goal matrix, the singular values of which characterize the task's sensitivity to body-level errors (Cusumano and Cesari 2006; John and Cusumano 2007), independent of any control considerations. Motivated by the fact that optimal control, particularly in the form of the minimum intervention principle (MIP), has been proposed as a theoretical basis for modeling the neuromotor system (Scott 2004; Todorov and Jordan 2002; Todorov 2004), optimal control ideas were incorporated with the GEM approach. The resulting dynamical data analysis framework allows one to create models of inter-trial fluctuations that can be tested against movement data from human subjects (Dingwell and Cusumano 2010; Dingwell et al. 2010; Dingwell et al. 2013), providing an analysis of human motor variability data that combines task manifold, optimal control, and time series analysis approaches (Cusumano and Dingwell 2013).

In what follows, we describe GEM-based fluctuation analysis, and, as an illustration, use it to study data from a virtual shuffleboard task. After defining the key concepts, we obtain the geometric stability properties of the inter-trial dynamics for skilled players operating near the shuffleboard GEM. The eigenvalues and eigenvectors of a linear update equation estimated from the data characterize the way inter-trial fluctuations are organized around the GEM. We show that subjects exhibit strong control of fluctuations in an eigendirection transverse to the GEM, but weak control of fluctuations in an eigendirection nearly tangent to it. Furthermore, we demonstrate that our dynamical analysis is robust under coordinate transformations in a way that non-temporal variance-based methods are not. We conclude by discussing how our results support a generalized interpretation of the MIP, and in doing so, suggest the possible involvement of competing costs other than pure goal-level error minimization.

9.2 The Goal Equivalent Manifold

Consider a task for which we can express the goal-level error, **e**, in terms of a *goal function* as:

$$\mathbf{f}(\mathbf{x}) = \mathbf{e} \tag{9.1}$$

where $\mathbf{x} \in \mathbb{R}^B$ (the *body space*), $\mathbf{f} \in \mathbb{R}^E$ (the *goal space*). For redundant systems, $B > E$, that is the dimension of the body state space is greater than that of the space of goal-level errors. This introduces the possibility that there are many (possibly infinite) **x** that result in the goal-level error being zero. This particular set of body states is called the *goal equivalent set* (GES), and is expressed mathematically as the set $\mathcal{G}$:

$$\mathcal{G} \triangleq \{\mathbf{x} \,|\, \mathbf{f}(\mathbf{x}) = \mathbf{0}\}.$$

If the GES forms a surface in the body space, then it is referred to as a GEM. By definition, changes in the body state variables that remain in $\mathcal{G}$ do not change the performance at the goal, because the error remains zero.

Fluctuations in the body state are mapped to their resulting fluctuations at the goal. Given an operating point on the GEM, $\mathbf{x}^* \in \mathcal{G}$, we write the state for small body-level fluctuations, $\boldsymbol{\xi}$, away from a state on the GEM, $\mathbf{x}^* \in \mathcal{G}$. The sensitivity of the goal-level error to the body-level fluctuations $\boldsymbol{\xi}$ is found using a Taylor series expansion of the error:

$$\mathbf{e} = \mathbf{f}(\mathbf{x}^* + \boldsymbol{\xi}) = \mathbf{f}(\mathbf{x}^*) + D\mathbf{f}(\mathbf{x}^*)\boldsymbol{\xi} + O\big(||\boldsymbol{\xi}||^2\big),$$

where $D\mathbf{f}(\mathbf{x}^*) \triangleq \mathsf{J}$ is the Jacobian of the goal function evaluated at $\mathbf{x}^*$. By hypothesis, $\mathbf{f}(\mathbf{x}^*) = 0$, and, for skilled task performance, we expect small errors and, hence, small fluctuations away from the GEM ($\|\boldsymbol{\xi}\| \ll 1$). Thus, the error is expected to be well approximated by the linear relationship:

$$\mathbf{e} \approx D\mathbf{f}(\mathbf{x}^*)\boldsymbol{\xi} = \mathsf{J}\boldsymbol{\xi}. \tag{9.2}$$

In this context, J is referred to as the *body-goal variability matrix* (Cusumano and Cesari 2006): it maps the fluctuations at the body level, $\boldsymbol{\xi}$, to the error at the target, **e**.

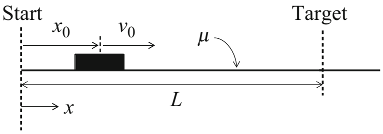

Fig. 9.1 Schematic of shuffleboard task. The subject releases the puck at position x_0 with an initial velocity v_0. The goal is for the puck to come to a stop at the target. The coefficient of kinetic friction is constant along the length of the board

Since $B > E$ (by hypothesis), the $E \times B$ matrix J has more columns than rows, and so can be decomposed into orthogonal subspaces: the null space, $\mathcal{N}$, and the column space, $\mathcal{C}$ (Poole 2010; Golub and van Loan 1996), where:

$$\mathcal{N} \triangleq \{\boldsymbol{\xi} \mid \mathsf{J}\boldsymbol{\xi} = 0\}, \tag{9.3a}$$

and

$$\mathcal{C} \triangleq \{\boldsymbol{\xi} \mid \boldsymbol{\xi}^T \mathbf{w} = 0 \;\forall \mathbf{w} \in \mathcal{N}\}. \tag{9.3b}$$

As defined in Eq. (9.3a), all perturbations away from $\mathbf{x}^*$ that belong to the null space will not cause the error to change from zero, to linear order in $\boldsymbol{\xi}$. In contrast, perturbations in the column space (Eq. 9.3b) will create nonzero error at the target. Thus, in the context of movement variability analysis, we call $\mathcal{N}$ and $\mathcal{C}$, the *goal equivalent* and *goal relevant* subspaces, respectively. Geometrically speaking, the null space is tangent to the GEM at $\mathbf{x}^*$, whereas the column space is orthogonal to the GEM.

As an illustration, consider the simple shuffleboard task shown in Fig. 9.1, for which $B = 2$ and $E = 1$. The goal of this task is to release a puck at some initial distance, x_0, with some initial velocity, v_0, and have it stop on the target line that is located at a distance L from the start position, $x = 0$. Once released, the puck is decelerated by a Coulomb friction force until it comes to rest, so that, by Newton's second law (Greenwood 1988):

$$\ddot{x}(t) = -\mu g, \tag{9.4}$$

where μ is the coefficient of kinetic friction and g is the local acceleration of gravity. Solving the above differential equation gives the final position, x_f as

$$x_f = x_0 + \frac{v_0^2}{2\mu g}. \tag{9.5}$$

For convenience, we rescale the release position and velocity into dimensionless quantities, x and v, using

$$x = \frac{x_0}{L} \quad \text{and} \quad v = \frac{v_0}{\sqrt{2\mu g L}}, \tag{9.6}$$

which makes our analysis universal for any length of board, coefficient of friction, or local acceleration of gravity. The goal function for the system is then obtained, following Eq. (9.1), by noting that $x_f - L$ is the scalar error, where x_f is as in Eq. (9.5). After substituting Eq. (9.6), we find the goal-level error, e, in dimensionless form as:

$$e = \frac{x_f - L}{L} = v^2 + x - 1. \tag{9.7}$$

Thus, for the shuffleboard task, the goal function is a scalar valued function, $e = f(\mathbf{x}) \equiv f(x, v)$, so that the 2D body state is $\mathbf{x} = (x, v)$. That is, the performance in one trial, as measured by e, is determined exclusively by the value of (x, v), the position and velocity of the puck at release.

The GEM is then obtained from Eq. (9.7) as $\mathcal{G} = \{(x, v) \mid v = \sqrt{1 - x}\,\}$ (for $0 \leq x \leq 1$; see Fig. 9.2), and the 1×2 body-goal variability matrix is computed by the gradient of Eq. (9.7) as

$$\mathsf{J} = (1,\ 2v). \tag{9.8}$$

Using the definitions of Eqs. (9.3a) and (9.3b), we find the unit normal and unit tangent, $\hat{\mathbf{n}}$ and $\hat{\mathbf{t}}$, respectively, to be

$$\hat{\mathbf{n}} = \left[\frac{1}{\sqrt{1+4v^2}}, \frac{2v}{\sqrt{1+4v^2}} \right]^{\mathsf{T}} \tag{9.9a}$$

and

$$\hat{\mathbf{t}} = \left[-\frac{2v}{\sqrt{1+4v^2}}, \frac{1}{\sqrt{1+4v^2}} \right]^{\mathsf{T}}, \tag{9.9b}$$

where the superscript T indicates the matrix transpose. The unit vectors are shown in Fig. 9.2.

9.3 Inter-Trial Control

Fluctuations in movement arise from inherent physiological noise that is present at multiple scales (Eldar and Elowitz 2010; Faisal et al. 2008; Osborne et al. 2005; Stein et al. 2005; McDonnell and Ward 2011). Thus, during repeated task execution, a subject will strive to make adjustments from one trial to the next in an attempt to maximize performance. We model this behavior as an iterative, error-correcting, perception-action process (Warren 1990, 2006) in which perceived error from trial k is used to estimate the body state at trial $k + 1$ in an attempt to drive the goal-level error to zero. Among the simplest models are update equations with the form

$$\mathbf{x}_{k+1} = \mathbf{x}_k + (\mathsf{I} + \mathsf{N}_k)\,\mathbf{u}(\mathbf{x}_k) + \boldsymbol{\nu}_k\,, \tag{9.10}$$

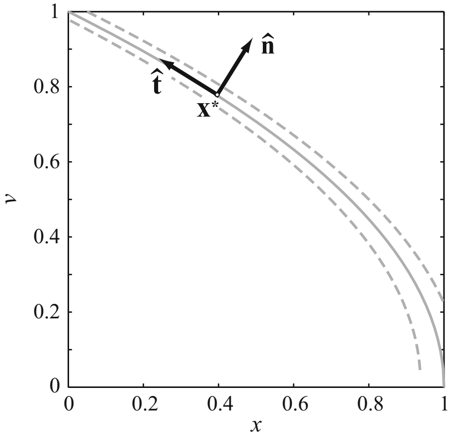

Fig. 9.2 The goal equivalent manifold (GEM) for the shuffleboard task. The *solid gray line* denotes the GEM (body states $\mathbf{x} = (x, v)$ leading to perfect task performance); *dashed gray lines* are ±5 % error contours. Also shown (*black arrows*) are the unit normal $\hat{n}$ (Eq. 9.9a) and unit tangent $\hat{t}$ (Eq. 9.9b) at an operating point $\mathbf{x}^*$. Deviations from the GEM in the $\hat{t}$ direction cause no error at the target (i.e., they are *goal equivalent*), whereas deviations in the $\hat{n}$ direction result in error at the target (i.e., they are *goal relevant*)

in which $\mathbf{u}(\mathbf{x}_k)$ is an inter-trial, error-correcting controller depending on the current state $\mathbf{x}_k$, N_k is a matrix representing signal-dependent noise in the motor outputs (Harris and Wolpert 1998), and $\boldsymbol{\nu}_k$ is an additive noise vector representing unmodeled effects from perceptual, sensory, and motor sources. For skilled movements, which are the focus of this chapter and for which the fluctuations $\boldsymbol{\xi}$ are small, similarly small multiplicative noise terms drop out of the leading order analysis (Dingwell et al. 2010; John and Cusumano 2007; Cusumano and Dingwell 2013), and so the random matrix N_k will not be included in what follows.

To motivate the above model, consider that, for a skilled subject, we expect $\mathbf{x}_k$ to lie very close to the GEM, so if there were no noise there would be no need for control (i.e., $\mathbf{u} = 0$), and Eq. (9.10) would give $\mathbf{x}_{k+1} \approx \mathbf{x}_k$. However, some noise, $\boldsymbol{\nu}_k$, is always present, and if there were no control, the fluctuations in $\mathbf{x}_k$ would display a random walk in the body space, which is not observed in experiments. These two extreme limits illustrate that the job of the controller is to keep a multi-trial performance closer to that of a perfect repetition than to a noise-induced random walk. Models of this type implicitly assume a hierarchical structure to the overall motor control system: the controller of Eq. (9.10) makes error-correcting adjustments, *between* trials, to an approximately "feed forward" controller that executes the task *within* trials. In this view, the body state $\mathbf{x}_k$ of Eq. (9.10) plays the role of a control parameter for each individual goal-directed action.

Similar models have found use for the study of motor learning (van Beers 2009; Burge et al. 2008; Diedrichsen et al. 2005), with the difference that the controllers were formulated to depend directly on the goal-level error e_k, instead of the body state $\mathbf{x}_k$. However, in our approach, the body and goal-level fluctuations are related by Eq. (9.1), so the fact that Eq. (9.10) depends only on body states yields a system that is amenable to dynamical analysis in the presence of task redundancy. However, it leaves open the question of how the controller incorporates error information, something which we now address.

As before, we let $\boldsymbol{\xi}_k$ be a fluctuation (at trial k) from an operating point on the GEM, $\mathbf{x}^* \in \mathcal{G}$, so that $\boldsymbol{\xi}_k = \mathbf{x}_k - \mathbf{x}^*$. For skilled performance, these fluctuations will be small and so we assume a proportional linear controller

$$\mathbf{u}_k = \mathsf{B}\boldsymbol{\xi}_k, \tag{9.11}$$

where B is a constant proportional gain matrix. Subtracting $\mathbf{x}^*$ from both sides of Eq. (9.10) and substituting in Eq. (9.11), we directly relate the fluctuations from one trial to the next:

$$\boldsymbol{\xi}_{k+1} = (\mathsf{I} + \mathsf{B})\boldsymbol{\xi}_k + \boldsymbol{\nu}_k, \tag{9.12}$$

where I is the identity matrix. Taking an optimal control approach, we further assume that the controller acts to specify the state at the next trial, $\mathbf{x}_{k+1}$, to minimize the expected value of a cost function Π with the following general form:

$$\Pi = \alpha_0 e(\mathbf{x}_{k+1})^2 + \sum_{j=1}^{M} \alpha_j p_j(\mathbf{x}_{k+1}) + \boldsymbol{\xi}_k^T \mathsf{B}^T \mathsf{K} \mathsf{B} \boldsymbol{\xi}_k\,, \tag{9.13}$$

with terms described as follows. The first term in $e(\mathbf{x}_{k+1}) = \|\mathbf{f}(\mathbf{x}_{k+1})\|$ (via Eq. 9.1), represents the cost of goal-level error. The summation term represents additional possible costs, as appropriate for a given problem, that may arise from biomechanical (e.g., range of motion), physiological (e.g., energy minimization), psychological (e.g., risk avoidance), or other considerations. The last term represents the cost of controller "effort." Also in Eq. (9.13), the parameters α_j $(j = 0, 1, \ldots, M)$ as well as the matrix K, are adjustable weights that can influence details of the system such as, for example, the location of the operating point $\mathbf{x}^*$.

Thus, the goal-level error is incorporated into the controller of Eq. (9.10) implicitly, via the first cost of Π. Furthermore, because the leading terms of Π are evaluated at the next step, substitution of the update equation (Eq. 9.10) into Eq. (9.13) immediately shows how the noise $\boldsymbol{\nu}_k$ enters into the optimization, explaining why we minimize the expected value, $\mathbb{E}[\,\Pi\,]$, to determine the controller.

For an ideal MIP controller, $\alpha_0 \neq 0$ and $\alpha_j = 0$ for $j \geq 1$ in Eq. (9.13), so the sole cost being minimized at the next trial is the goal-level error. Since the goal-level error deviates from zero only for goal relevant fluctuations (Fig. 9.2), such a "perfect" MIP controller would push subsequent body states onto the GEM, but would exert absolutely no control along it. The result is that in the presence of noise, the model Eq. (9.10) predicts an unbounded random walk along the GEM. However, such behavior is yet to be observed in multi-trial experiments. For this reason, in Dingwell et al. (2010), an additional cost related to minimizing the distance from a “preferred operating point” on the GEM was included as p_1 in Eq. (9.13) (with $\alpha_1 \neq 0$ and $M = 1$ in the sum). This allowed the associated models to capture the localization of multi-trial experimental data around a location on the GEM in a way that an ideal MIP model could not.

9.4 Local Geometric Stability

We can analyze the local geometric stability of the inter-trial control process using Eq. (9.12). For convenience, we let $\mathsf{A} = \mathsf{I} + \mathsf{B}$ and rewrite Eq. (9.12) slightly as

$$\boldsymbol{\xi}_{k+1} = \mathsf{A}\boldsymbol{\xi}_k + \boldsymbol{\nu}_k. \tag{9.14}$$

The eigenvalues and eigenvectors of A, which satisfy $\mathsf{A}\hat{\mathbf{e}} = \lambda\hat{\mathbf{e}}$, determine the stability properties of the inter-trial control applied to fluctuations near the GEM. The magnitude of an eigenvalue indicates the action of the system on fluctuations in the direction of its corresponding eigenvectors: after one trial, the size of the fluctuation is reduced by a factor of $(1 - |\lambda|) \times 100\,\%$. Thus having at least one eigenvalue with $|\lambda| > 1$ indicates instability, whereas if all eigenvalues satisfy $0 \leq |\lambda| \leq 1$, the system is stable (Guckenheimer and Holmes1983; Hirsch et al. 2004). Heuristically speaking, *smaller* values of $|\lambda|$ correspond to *greater* stability. To facilitate our discussion, in the remainder we focus on the case where the body states $\mathbf{x}_k$ (and hence the fluctuations $\boldsymbol{\xi}_k$) are 2D, as is true for the shuffleboard task. In this case, A is a 2×2 matrix, so there will be two eigenvalues. We also limit our discussion to the case of real, distinct eigenvalues, which has been found to be sufficient in experimental applications to date.

We label the the eigenvalues as λ_w and λ_s to classify them as “weak” and “strong,” respectively, according to their magnitude, so that $|\lambda_s| < |\lambda_w|$. The corresponding eigenvectors are labeled as $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$. Thus, after one trial, the size of fluctuations along $\hat{\mathbf{e}}_w$ is reduced much less than those along $\hat{\mathbf{e}}_s$. A typical situation is shown schematically in Fig. 9.3, which shows the orientation of the eigenvectors with respect to the GEM. Also shown are the weakly and strongly stable subspaces, $\text{span}\{\hat{\mathbf{e}}_w\}$ and $\text{span}\{\hat{\mathbf{e}}_s\}$, respectively. As illustrated in the figure, in general $\hat{\mathbf{e}}_w \cdot \hat{\mathbf{e}}_s \neq 0$.

Note that, in general, the stability subspaces are not aligned with the normal and tangential directions of the GEM. However, for an ideal MIP controller that pushes states onto the GEM but has absolutely no control along it, one finds that $\hat{\mathbf{e}}_w$ is identical to $\hat{\mathbf{t}}$, the unit tangent to the GEM (Fig. 9.2). Furthermore, the eigenvalues of an ideal single-step MIP controller are $\lambda_w = 1$ and $\lambda_s = 0$, indicating that fluctuations along the GEM are allowed to persist indefinitely, whereas those transverse to it are, in the absence of noise, eliminated after a single trial. However, as discussed at the end of the last section, such a scenario is not expected in experiments, since in the presence of noise, it would result in a random walk of body states along the GEM from trial to trial. Thus, we do not anticipate the controller to satisfy a strict interpretation of the MIP, or UCM hypothesis, but rather a generalized version for which goal-level error is still the dominant cost to be minimized (Eq. 9.13), but there is at least one

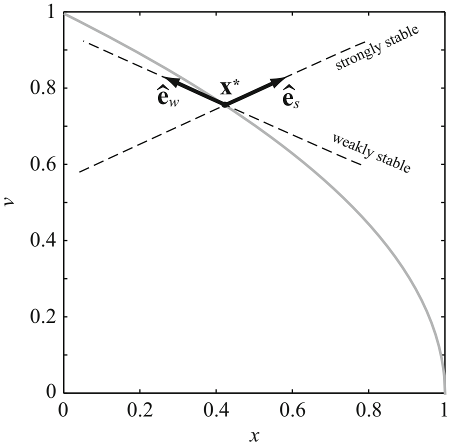

Fig. 9.3 Schematic showing the typical orientation of the weak and strong eigenvectors of matrix A (Eq. 9.12), $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$, respectively (*black arrows*) with respect to the goal equivalent manifold (*GEM*) (*gray curve*). The weakly and strongly stable subspaces (*dashed lines*) span the respective eigenvectors. The associated eigenvalues satisfy $|\lambda_s| < \lambda_w$; in general, $\lambda_s \approx 0$ and λ_w is closer to 1. The weakly stable subspace for a generalized minimum intervention principle (*MIP*) controller will be close to tangent to the GEM. The subspaces are so named because deviations off of the GEM are strongly corrected, whereas deviations along it are only weakly corrected

additional cost, $p_j(\mathbf{x}_{k+1})$, with a corresponding $\alpha_j \neq 0$. A small perturbation of this type will only slightly change the local stability, so that we still expect $|\lambda_s| \approx 0$ and $0 \ll \lambda_w < 1$. In addition, the eigenvectors will be slightly rotated from those for the ideal MIP controller, so that, in particular, $\hat{\mathbf{e}}_w$ will no longer be exactly tangent to the GEM.

As discussed in Cusumano and Dingwell (2013), consideration of the above leads to a set of generic experimental hypotheses. Here, we present only those needed for the experimental study of the 2D shuffleboard task to be discussed in the remainder of the chapter:

H1 Consistent with the hypothesis of weak (but not zero) control along the GEM, one of the eigenvectors, $\hat{\mathbf{e}}_w$, will be close to the GEM tangent, and so will make an angle $\theta_w \approx 90°$ with $\hat{\mathbf{n}}$, the GEM normal. The corresponding eigenvalue, λ_w, will be less than one but much greater than zero ($0 \ll \lambda_w < 1$).

H2 The fluctuation dynamics transverse to the GEM are strongly stable: i.e., we expect $0 \approx |\lambda_s| \ll \lambda_w$. The associated eigenvector, $\hat{\mathbf{e}}_s$, will make a much smaller angle with $\hat{\mathbf{n}}$ than does $\hat{\mathbf{e}}_w$ ($\theta_s \ll \theta_w$).

H3 Consistent with the stability properties of **H1** and **H2**, fluctuations in the weakly stable subspace will exhibit statistical persistence, whereas those in the strongly stable subspace will be non-persistent (uncorrelated). In terms of the exponent α from detrended fluctuation analysis (DFA) (Hausdorff et al. 1995; Peng et al. 1992), we expect $0.5 \approx \alpha_s \ll \alpha_w$.

Table 9.1 Experimental subject demographics (mean ± standard deviation). Assuming normal distributions, no measures, except age, had significantly different means

	Younger	Older
n	8	8
Age (years)	23.7 ± 3.8	66.2 ± 7.2
Body mass (kg)	68.6 ± 13.0	72.5 ± 8.4
Height (cm)	172.9 ± 8.4	168.0 ± 11.1
Upper arm length (cm)	30.3 ± 2.3	30.0 ± 1.9
Forearm length (cm)	26.1 ± 1.4	26.5 ± 2.8
Hand length (cm)	18.3 ± 1.3	18.4 ± 1.2

Taken together, these hypotheses can be summarized as the expectation of dynamic anisotropy in the fluctuation dynamics, consistent with the action of a generalized MIP controller that has goal-level error as its main, but not only, cost.

9.5 Experimental Implementation

In this section, we apply the ideas and methods developed in the previous sections to study the experimentally-observed variability in a virtual shuffleboard task.

9.5.1 Apparatus and Protocol

Sixteen subjects (Table 9.1) were recruited as two cohorts, eight subjects between 18 and 35 (“younger”) and eight subjects older than 60 (“older”). Subjects were screened and asked to report any neurological conditions, upper-body arthritis and joint replacement, or uncorrected vision in either eye for exclusion. Subjects were also given the Edinburgh Handedness Inventory (Oldfield 1971), and all participants were deemed right handed, having a score of at least 60 on a -100 to 100 scale. Testing was approved by The Pennsylvania State University Institutional Review Board. No statistically significant differences for the analyses carried out for this chapter were found between the younger and older cohorts, so the results presented below were computed with the cohorts merged.

A custom experimental virtual shuffleboard system was used for the task. The experimental system was composed of a manipulandum on a linear bearing attached to a linear variable differential transformer (LVDT) (Daytronic Corporation; Dayton, OH) that measured the manipulandum’s position. A linear accelerometer (ADXL320; Analog Devices, Inc.; Norwood, MA) was mounted on the manipulandum. Both the LVDT and the accelerometer were routed into a low-pass filter with a 20 Hz cutoff. Out of the filter, the data were sampled by a 12-bit PCMCIA data acquisition card (NI DAQCard-6024E; National Instruments; Austin, TX) at 1 kHz, and sent to a laptop where it was read into simulation and control software written in MATLAB (The Mathworks; Natick, MA).

The control software was used to generate a 2D, top-down view of a virtual shuffleboard court that was projected onto a screen located in front of the subjects' seat. The projected image displayed a virtual cue that moved in sync with physical motions of the manipulandum, together with a puck and a target line (recall Fig. 9.1). Each trial started with the puck at rest at its zero position. While the puck was being pushed by the cue and subsequently released, its position was displayed in real time. The puck was released when the computed virtual contact force between the puck and cue fell to zero. The velocity at release, v, was found by integrating the acceleration data, and the release position, x, was found directly from the LVDT. A numerical simulation then took over to calculate the released puck's position and velocity, based on the equation of motion (Eq. 9.4), and the puck's motion was displayed in real time. After the puck came to a stop, in addition to being able to visually see the puck's final location, subjects were shown the error e (Fig. 9.1), which was displayed at the top-right of the screen. When the cue was retracted to the start position, the next trial began.

Subjects were asked to adjust the seat to their comfort, but were required to have their forearm parallel to the ground and their right hand above their mid-thigh when the cue was at its initial position. All participants used their right hand to operate the manipulandum. Subjects were given the instruction: "On each trial, have the center of the puck stop on the black target line." Subjects were given a training session of 50 trials to familiarize themselves with the system, and then were asked to complete 5 blocks of 50 trials each that were used for analysis. Between each block, the subject was given a minimum of 90 s to rest. The release position and velocity, $\mathbf{x}_k = (x_k, v_k)$, and the error e_k (via Eq. 9.7) for each trial were recorded and stored.

9.5.2 Data Processing

All 250 trials were grouped together for each of the 16 subjects. Because we assumed that subjects performed at a skilled steady-state, the first trial of each block after the training block was removed to allow for refamiliarization after a break, and the final trial was removed in case the subject performed differently knowing it was the last trial. Any trials that involved subject errors or technical malfunctions were also removed: there were a total of only six such trials removed across all subjects, with a maximum of three for one subject. All data analyses were performed using MATLAB.

For skilled subjects, we expect the *average* performance to be nearly perfect. That is, the mean body state over all trials is very nearly on the GEM, and so we defined an empirical operating point as $\mathbf{x}^* = \bar{\mathbf{x}}$. Then the fluctuation time series was computed with respect to this mean operating point (MOP) from $\boldsymbol{\xi}_k = \mathbf{x}_k - \bar{\mathbf{x}}$.

Because of the limited length of each inter-trial time series, as well as the known sensitivity of eigenanalyses for matrices contaminated by noise (Golub and van Loan 1996), bootstrapping (Mooney and Duval 1993; Freedman 1981; Efron and Tibshirani 1994) was used to produce a confidence interval (CI) for the eigenvalue and eigenvector calculations. A set of 250 fluctuations, $\boldsymbol{\xi}_k$, and the following fluctuation, $\boldsymbol{\xi}_{k+1}$, was selected randomly with replacement from the original trial data on each iteration of the bootstrap. The matrix A was estimated via least squares, using the pseudo-inverse (Moore and Barnard 1939; Golub and van Loan 1996) for each set of $\boldsymbol{\xi}_k$ and $\boldsymbol{\xi}_{k+1}$. The eigenvalues and eigenvectors for each A were then calculated and stored. This process was repeated over 10^5 iterations of the bootstrapping procedure. Occasionally, an A matrix with imaginary eigenvalues and eigenvectors was produced: in this case, such matrices are numerical artifacts stemming from the fact that we are trying to estimate a nearly-singular matrix with one eigenvalue near zero. However, across all subjects, a mean of only 0.06 % of matrices generated during the bootstrapping iteration fell in this category, with a maximum of 0.93 % for one subject. Because of the relatively small number of instances, these matrices were simply removed from the sample and rerun with new entries.

The above bootstrapped eigenanalyses were used to test hypotheses **H1** and **H2**. To test hypothesis **H3**, we employed DFA (Hausdorff et al. 1995; Peng et al. 1992). The output of the DFA algorithm is a positive exponent, α: when $\alpha < 0.5$, a time series is said to be "antipersistent," meaning that fluctuations in one direction are likely to be followed by fluctuations in the opposite direction; when $\alpha > 0.5$, the time series is "persistent," meaning that fluctuations are likely to be followed by subsequent fluctuations in the same direction; finally, when $\alpha = 0.5$, the time series is "non-persistent" or uncorrelated. DFA has been widely used to search for long-range persistence (also called long-range correlations) in experimental time series, a topic that is beyond the scope of this chapter. However, as discussed at some length in Cusumano and Dingwell (2013), when used for this purpose, DFA is prone to false positives (Delignières and Torre 2009; Maraun et al. 2004; Gao et al. 2006). Accordingly, we emphasize that we are *not* using DFA to claim that observed fluctuations exhibit *long-range* persistence, but merely as a convenient tool to characterize persistence in general. In previous work (Dingwell and Cusumano 2010), we have shown that antipersistent time series are consistent with the overcorrecting control of fluctuations normal to a GEM, whereas persistent fluctuations suggest weak or "indifferent" control of fluctuations along it. In this chapter, instead of projecting the fluctuations onto the vectors normal and tangent to the GEM, we examine fluctuations in the weakly and strongly stable directions.

Direct application of DFA within each iteration of bootstrapping was computationally costly, so we first computed the mean value, $\overline{\mathsf{A}}$, of the 10^5 matrices A generated during the bootstrapping procedure for one subject. Using $\overline{\mathsf{A}}$, we found the "average" weak and strong eigenvectors $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$. Then we transformed the fluctuations using the linear coordinate transformation

$$\boldsymbol{\xi} = \mathsf{P}\boldsymbol{\zeta}, \tag{9.15}$$

where P is the matrix containing $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$ as its columns. This transformation projects the fluctuations $\boldsymbol{\xi}$, originally expressed in dimensionless position and velocity coordinates, onto the average eigendirections, so that we can write $\boldsymbol{\zeta} = (\zeta_w, \zeta_s)^{\mathsf{T}}$. Finally, DFA was performed on the resulting ζ_w and ζ_s fluctuation time series. These results were used to test **H3**.

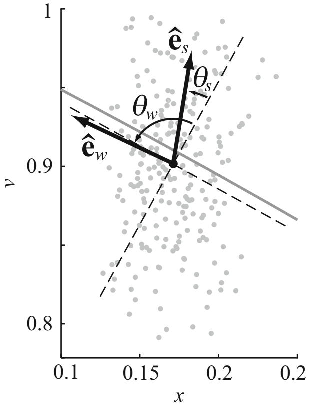

Fig. 9.4 Plot in the body space of all 250 trials (*light gray dots*) for one subject, showing the weakly and strongly stable eigenvectors, $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$, respectively, obtained from the average, $\overline{\mathsf{A}}$, of all 10^5 matrices A estimated via regression during bootstrapping. Also shown are the mean operating point (MOP, *black circle*) and goal equivalent manifold (*GEM*) (*dark gray line*). *Normal and tangential dashed reference lines* are spanned by $\hat{\mathbf{n}}$ and $\hat{\mathbf{t}}$, respectively (Fig. 9.2). The angles θ_w and θ_s to each eigenvector are measured counterclockwise from the normal, as shown

While the bootstrapped empirical probability density functions (EPDFs) obtained for this study were close to Gaussian, the aggregate distributions were typically not. Nor were they symmetric about their median. Therefore, across all subjects, a comparison of medians was done using a two-sample, two-sided sign test (Wilcoxon 1945), with significance level set to 0.05. In the box plots used throughout, the center line shows the median value, the lower and upper box edges encompass the interquartile range (IQR), and whiskers extend a maximum of 1.5 IQR. Note, however, that all data, including outliers, were included in the data analyses described above.

9.6 Results

To illustrate the geometrical features of the data analysis, a scatter plot of an ensemble of body states (release positions and velocities), collected for all 250 trials for one subject, is shown in Fig. 9.4. For reference, the GEM and the directions normal and tangential to it are also displayed. We see that the MOP is not located on the GEM, but is close to it, as expected. Also plotted are the weakly and strongly stable eigenvectors, $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$, respectively, for this figure computed from the *average* matrix, $\overline{\mathsf{A}}$, estimated during the bootstrapping process. Also displayed are the angles θ_w and θ_s that each eigenvector makes with the normal. Note also that the apparent orientation of the cloud of trials does not align with the normal and tangential axes.

Across all subjects and trials, the goal-level error was $e = -0.0204$ $[-0.1828, 0.1713]$, where the stated value is the median, and the range in square

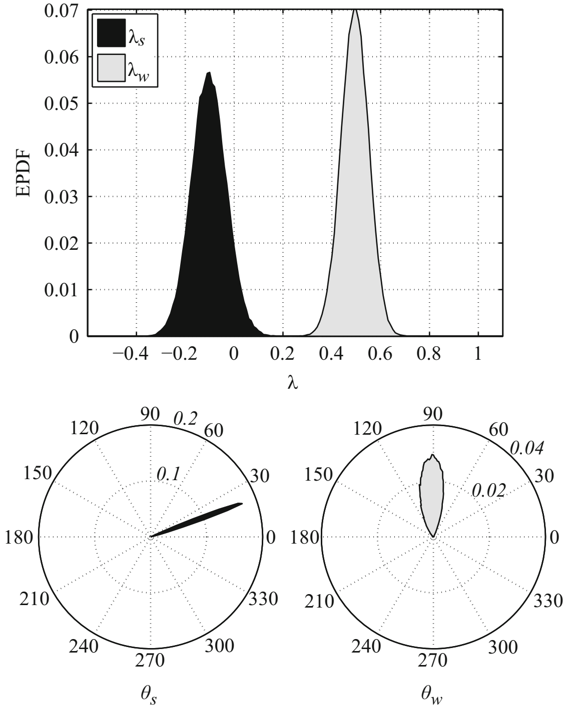

Fig. 9.5 Typical empirical probability density functions (*EPDFs*) for the local stability analysis, obtained via bootstrapping for one subject: (*top*) eigenvalues λ_w and λ_s; (*bottom*) angles θ_w and θ_s made by the eigenvectors $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$, respectively, with the normal $\hat{\mathbf{n}}$ to the gold equivalent manifold (GEM) (see Fig. 9.4 for angle definitions). In the angular EPDFs, the *radial direction* is the relative frequency, the *circumferential direction* is the angle, and the *italicized numbers* represent the relative frequency

brackets is the 90 % CI. The corresponding median distance from the GEM in the body space was $\delta = -0.0118\ [-0.0221, 0.0046]$. Thus the aggregate performance displayed, roughly speaking, about as much overshooting ($e > 0$) as undershooting ($e < 0$), though with some indication of a small bias toward undershooting. This small bias is more apparent in the stopping distance, since the CI shows a significant bias toward trials "under" the GEM curve ($\delta < 0$). Nevertheless, these overall results are consistent with the assumption that skilled performance would involve operation close to the GEM.

In Fig. 9.5 we show typical results from the bootstrapped local stability analysis using the data from all 250 trials for one subject. Figure 9.5 (*top*) displays the EPDFs obtained for the eigenvalues, λ_w and λ_s, of the matrix A (Eq. 9.14); in Fig. 9.5 (*bottom*) are the EPDFs for the angles, θ_w and θ_s that the eigenvectors $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$ make with $\hat{\mathbf{n}}$, the unit normal to the GEM (Fig. 9.4). Observe that the displayed EPDFs are unimodal and symmetric about the median, so that the mean, median, and mode are close to equal: this was found to be true for all bootstrapped distributions

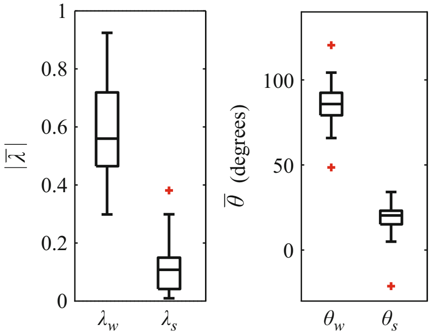

Fig. 9.6 Aggregate geometric stability results: magnitude of mean eigenvalues , $\overline{\lambda}_w$ and $\overline{\lambda}_s$, obtained from each subject's bootstrapped distributions (*left*); mean eigenvector angles $\overline{\theta}_w$ and $\overline{\theta}_s$ (*right*) . The median value of $\overline{\lambda}_w$ (0.5597) was significantly larger than that of $\overline{\lambda}_s$ (0.1076), with $p = 3.05 \times 10^{-5}$. The aggregate median value of $\overline{\theta}_w$ (85.83°) was significantly larger than that of $\overline{\theta}_s$ (20.33°), with $p = 3.05 \times 10^{-5}$. Since λ_w was positive for all subjects, these results confirm hypotheses **H1** and **H2**: $0 \approx |\lambda_s| \ll \lambda_w$ and $\theta_s \ll \theta_w \approx 90°$

generated for this study. For this subject, we find $\lambda_s = -0.1039\ [-0.2191, 0.0143]$ and $\lambda_w = 0.4947\ [0.3997, 0.5871]$, so that $0 \approx |\lambda_s| \ll \lambda_w$ as hypothesized. The fact that $\lambda_s < 0$ indicates that this subject slightly overcorrected deviations transverse to the GEM, suggesting a slightly suboptimal controller (Dingwell et al. 2010). We also find $\theta_w = 93.62°\ [73.68°, 119.74°]$, indicating that $\hat{\mathbf{e}}_w$ is nearly tangent to the GEM, whereas $\theta_s = 20.78°\ [16.82°, 24.45°]$. Thus, again as hypothesized, we find $\theta_s \ll \theta_w \approx 90°$.

Aggregate geometric stability results across all subjects are shown in Fig. 9.6. To compare eigenvalues, we look at their absolute values to directly compare the relative strength of control without regard to possible overcorrection ($\lambda < 0$) or undercorrection ($\lambda > 0$). Note, however, that for all subjects it was found that the bootstrapped distribution of λ_w was strictly positive, as in Fig. 9.5. As a comparison statistic, for each subject, we used the mean value of the eigenvalues and angles obtained from each subject's bootstrapped EPDF. In Fig. 9.6 (*left*) are box plots showing the distribution of $|\overline{\lambda}_s|$ and $|\overline{\lambda}_w| \equiv \overline{\lambda}_w$, whereas Fig. 9.6 (*right*) displays box plots for the corresponding mean eigenvector angles $\overline{\theta}_w$ and $\overline{\theta}_s$. Applying the two-sided sign test showed that the aggregate median value of $\overline{\lambda}_w$ (0.5597 [0.3026, 0.9194]) was significantly larger than that of $\overline{\lambda}_s$ (0.1076 [0.0141, 0.3564]), with $p = 3.05 \times 10^{-5}$. It was also found that the aggregate median value of $\overline{\theta}_w$ (85.83° [53.72°, 115.59°]) was significantly larger than that of $\overline{\theta}_s$ (20.33° [−13.39°, 33.35°]), again with $p = 3.05 \times 10^{-5}$. Since $\lambda_w > 0$ in all cases, we find that $0 \approx |\lambda_s| \ll \lambda_w$ and $\theta_s \ll \theta_w \approx 90°$. Taken together, these results confirm hypotheses **H1** and **H2**.

The persistence properties of the inter-trial fluctuations, computed using DFA, are presented in Fig. 9.7. For each subject, the average matrix $\overline{\mathsf{A}}$ was obtained from bootstrapping, and the fluctuations $\boldsymbol{\xi}$ were projected onto the average weakly and strongly stable directions using the transformation Eq. (9.15). The DFA algorithm was then applied to the resulting ζ_w and ζ_s fluctuation components. We found that the

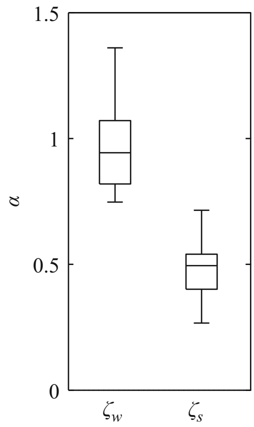

Fig. 9.7 Aggregate results for the detrended fluctuation analysis (DFA) exponent α, for fluctuations in the weakly and strongly stable directions, ζ_w and ζ_s, respectively. For ζ_w, we found $\alpha_w = 0.9433$ [0.7500, 1.2950] indicating statistical persistence consistent with weak control (Dingwell and Cusumano 2010). For ζ_s we found $\alpha_s = 0.4948$ [0.2773, 0.6863], indicating approximately uncorrelated fluctuations, consistent with strong control. The difference between the median values of α in both cases was significant ($p = 3.06 \times 10^{-5}$). These results confirm hypothesis **H3**: $0.5 \approx \alpha_s \ll \alpha_w$

ζ_w fluctuations were statistically persistent, with an $\alpha_w = 0.9433$ [0.7500, 1.2950], suggesting weak control in the weakly stable direction, which Fig. 9.6 shows is nearly tangent to the GEM. In contrast, for ζ_s, we found $\alpha_s = 0.4948$ [0.2773, 0.6863], indicating approximately uncorrelated fluctuations. This is consistent with strong control that suppresses substantial deviations from the GEM, leaving only noise. The difference between the median values of α in both cases was significant ($p = 3.06 \times 10^{-5}$). Thus, $0.5 \approx \alpha_s \ll \alpha_w$, confirming hypothesis **H3**.

Taken together, these results demonstrate that subjects exhibited strong dynamical anisotropy around the GEM, precisely as anticipated. This supports the claim that inter-trial error correction for the shuffleboard task is organized around a “GEM aware” generalized MIP controller.

9.7 Comparison with “Static” Variability Analysis

In this section, we contrast our dynamical analysis with an approach that does not consider the temporal order of the data, but instead analyzes only the “static” inter-trial variability structure. Here, we do this by applying principal component analysis (PCA) (Mardia et al. 1979; Daffertshofer et al. 2004) to the ensemble of body states. PCA calculates a new set of coordinates for the data set such that the covariance between the coordinates is zero. A principal component (PC) is an eigenvector of the data’s covariance matrix, and its associated eigenvalue, the principal value (PV)

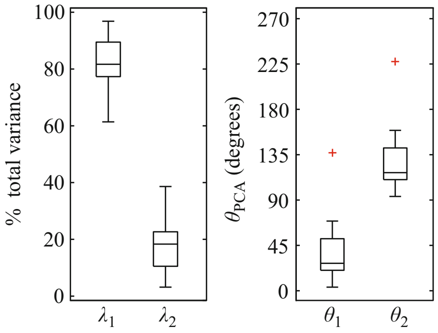

Fig. 9.8 Aggregate results of principal component analysis (*PCA*) applied to each subject's Inter-Trial data: (*left*) percent of total variance explained by each PV, λ_1 and λ_2; (*right*) the angle, θ_1 and θ_2, between each PC and $\hat{\mathbf{n}}$ (Fig. 9.2). We see that the first principal value (*PV*) explains about 80 % of the total variance (81.66 % [61.66 %, 95.58 %]), however, both PCs are approximately the same angular distance (about 27°) from the tangent, $\hat{\mathbf{t}}$, and hence do not locate the goal equivalent manifold (*GEM*) in body space

indicates how much variance lies along that direction. Thus, each PV represents a fraction of the total variance that lies in the direction of its associated PC. With 2D data, as was collected for this study, a possible interpretation of PCA results is that the first PC, which has the larger PV and, therefore, the greater variability, indicates a weakly-controlled direction because fluctuations are larger along it. The second, smallest variance PC then indicates a strongly-controlled direction. If true, that would imply that variance analysis alone could identify the organization of inter-trial variability about a candidate GEM. We here show that this interpretation does not hold, in general.

Applying PCA to our fluctuation data, we obtain the aggregate results shown in Fig. 9.8. We labeled the two PVs as λ_1 and λ_2, where $\lambda_1 > \lambda_2$, so that the associated PCs are the unit vectors $\hat{\mathbf{p}}_1$ and $\hat{\mathbf{p}}_2$. We then computed the angles that each PC made with the unit normal to the GEM, as was done for Fig. 9.6. We see that λ_1 accounted for 81.66 % [61.66 %, 95.58 %] of the total variance, whereas λ_2 accounted for 18.34 % [4.416 %, 38.23 %]. We also see that $\theta_1 = 27.23°$ [7.714°, 116.6°] and $\theta_2 = 117.2°$ [97.71°, 206.6°]. Thus, neither PC was close to either $\hat{\mathbf{n}}$ or $\hat{\mathbf{t}}$, and so they did not help locate the GEM. In particular, the angular distance of the first and second PCs from the GEM tangent was roughly 63° and 27°, respectively, thus neither could be said to identify a weakly controlled direction.

To further explore this issue, we transformed the data from one subject using a coordinate transformation that rendered the variability isotropic, for which, that is, the variance ellipse would be a circle. This is easily accomplished using a linear transformation similar to Eq. (9.15), however instead of constructing the matrix P by using the eigenvectors $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$ as its columns, we use the eigenvectors of the covariance matrix, that is, the PCs, $\hat{\mathbf{p}}_1$ and $\hat{\mathbf{p}}_2$. This projects the original fluctuations $\boldsymbol{\xi}$ onto the principal directions. After this step, each coordinate was normalized to unit variance, giving fluctuations in rescaled principal coordinates, $\mathbf{q} = (q_1, q_2)^{\mathsf{T}}$.

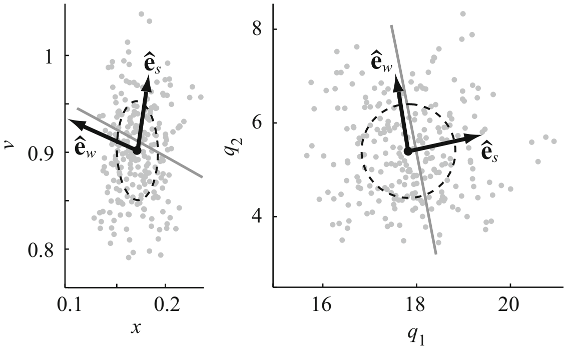

Fig. 9.9 Illustration showing the effect of a coordinate transformation that renders the variability ellipse circular: (*left*) data from one subject (*light gray dots*) together with the weakly and strongly stable eigenvectors, $\hat{e}_w$ and $\hat{e}_s$ (*black arrows*), for a matrix A estimated via regression during a single iteration of the bootstrap; (*right*) the same ensemble (*gray dots*) after transforming into rescaled principal coordinates (q_1, q_2) that have isotropic variance. In the *right plot*, the eigenvectors were calculated from a new matrix A estimated from the transformed data. Also shown in both figures is the goal equivalent manifold (*GEM*) (*dark gray line*) in the local coordinates, and the variance ellipse (*dashed line*). We observe that while the variability is radically changed by the transformation, the local geometry of the inter-trial dynamics is fundamentally preserved

Figure 9.9 shows the effect of this transformation on a typical geometric stability analysis, carried out using the data from one subject. In Fig. 9.9 (*left*), we see the results for the data in the original position–velocity fluctuation coordinates. For this figure, the eigenvectors $\hat{\mathbf{e}}_w$ and $\hat{\mathbf{e}}_s$ were computed from a single, typical matrix A, as would be estimated during a single bootstrap iteration. Also included in the figure is the standard variance ellipse, which, as would be expected from the results of Fig. 9.8, is not particularly well aligned with the GEM. However, the weakly and strongly stable subspaces are oriented in a way that helps understand how control is organized around the GEM. In Fig. 9.9 (*right*), we see the same data, however transformed into (q_1, q_2) coordinates, together with the eigenvectors. These eigenvectors *were not* merely transformed from Fig 9.9 (*left*), rather, the transformed data were used to estimate a new matrix A, and a new eigenanalysis was then performed. In the transformed picture, it is clear that the variability cloud provides no useful information about the location of the GEM since, by design, its variability ellipse is circular. However, the new eigenvectors continue to define weakly and strongly stable subspaces that correctly demonstrate how control is organized about the GEM.

9.8 Discussion

In this chapter, we have described a dynamical approach to the experimental analysis of inter-trial variability in skilled movement tasks. Our approach combines consideration of task manifolds, in the particular form of GEMs, with optimal control concepts, to formulate experimentally testable models of inter-trial fluctuations.

Because of this fundamentally dynamical perspective, we are not forced to make inferences about control based solely on the "static" structure of variability observed in some body-level state space, but rather can characterize the way variability, at both the body and goal levels, is organized and generated in time.

While the general GEM-based framework discussed in this chapter can be used to create mathematical models suitable for theoretical analysis, our approach is phenomenological and experimentally oriented. Thus, the primary significance of the theoretical discussion presented here is that it allows us to arrive at a set of quite generic hypotheses on the structure of variability observed with skilled performers: namely, that we expect to see strong evidence of dynamic anisotropy in the inter-trial fluctuations near a GEM. Furthermore, while motivated by both the MIP and the UCM hypothesis, consideration of our relatively simple mathematical models in the light of available experimental evidence leads us to the conclusion that neither can be true in an ideal form, since "perfect" MIP controllers would result in nonlocalized fluctuations that drift randomly along the GEM. Thus, our hypotheses include the assumption of a generalized MIP for which control along the GEM is not zero, but weak. This seemingly minor observation has an important experimental consequence: while this weakly controlled direction might be expected to be nearly tangent to the GEM, it will not, in general, be perfectly so.

To illustrate the theory, as well as its experimental implementation, we applied our analysis approach to study the variability observed in a virtual shuffleboard experiment. We found that all of our general hypotheses regarding dynamic anisotropy were supported by the analysis results. In particular, we found that subjects exhibited strong control of fluctuations in a direction transverse, but not typically normal, to the GEM, whereas they only weakly controlled fluctuations in a direction nearly, but not exactly, tangent to it. The assessment of control "strength" in these two directions was not determined by the relative magnitude of variances, but was provided both by local stability analysis and DFA. In both of these cases, the differences between the weakly and strongly stable directions were found to be as predicted and highly significant.

We compared our dynamical analysis with a non-temporal, variance-based analysis carried out using PCA. We found that the orientation of the variability cloud did not help identify how inter-trial control was organized around the GEM. Furthermore, we showed that our dynamical approach is robust to coordinate changes that result in isotropic variability. Under such circumstances, variability alone provides no information about the GEM, whereas the orientation of weakly and strongly stable subspaces still helps explain how variability is structured around a GEM, as well as how control is temporally organized.

The theoretical discussion in this chapter, together with the experimental demonstration that the weakly stable directions are not exactly directed along the GEM, suggest that while goal-level error minimization is likely a dominant cost being minimized by the human motor system, it is not the only one. In particular, our work suggests that there are relatively small additional costs—such as might be related to ergonomic, physiological, or even psychological needs of the performer—that need to be considered in combination with error reduction so that we might completely characterize experimentally-observed motor variability. It is hoped that dynamical data analysis methods like those presented here might help us to identify such costs in future experiments.

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Chapter 10
Motor Control in Action: Using Dance to Explore the Intricate Choreography Between Action Perception and Production in the Human Brain

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10.1 Introduction

Cue the crescendo: An audience watches as a ballerina takes center stage and precisely executes 32 *fouettés en tournant*—*en pointe*. Each revolution is performed with athletic deftness, spatial precision, and corporeal poise. Underlying the smooth delivery, the dancer's mind and body reach an apex: maintaining balance with arched feet, pointed toes, grounded core muscles, and postural stability. She generates impetus for the turns while coordinating her arms, shoulders, and hands, to appear light and effortless, with a smile on her face and perfect synchronization with the music. Complex coordination in a dance context extends well beyond the movement vocabulary of classical ballet dancers. It is cultivated among the many cultures of the world and their respective dance traditions. For the purposes of the present chapter, we define dance as bodily movements—whether choreographed or impromptu, rhythmic or asymmetric, with or without musical accompaniment—as a medium for artistic expression for individuals or groups. The ubiquity and purpose of dance have been examined in scientific contexts for over a century. First postulated by Darwin and corroborated by recent research, the origins of dance are speculated to be displays of courtship and mate selection, including indicators of symmetry, testosterone exposure in males, and synchrony with partner(s) (Fusani 2008; Shuster 2009).

Scientific investigation of dance can illuminate more than just its origins or the evolutionary function of coordinated movement, however. Of interest in the present chapter is how the behavioral and brain sciences are using dance paradigms in experimental contexts to better understand the neurophysiological substrates supporting

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links between the physical or affective experience of an observer and how the observer perceives a movement. We have chosen to focus on two particular points of convergence between dance and neuroscience, namely (1) how dance informs our understanding of action expertise, and (2) how dance advances our understanding of neuroaesthetics.

Nearly as many dance styles and traditions exist as there are human cultures: from the highly stylized, minimalist movements of Kabuki dancers in Japan to the rigorous, structured movement vocabulary of classical ballet, or the dramatized isolation of the eye muscles, neck, and knuckles in the Indian dance form of Kathakali, to the whole-body, poetic articulation of the dances of the Yoruba people in West Africa, humans all over the world create, perform, and watch dance. Only recently have scientists turned to this art form as a resource for research into motor control and aesthetics. In the first section of this chapter, we consider how early neurophysiological work with nonhuman primates gave rise to the notion of neural mechanisms that link action with perception, and how recent work with dancers has helped to refine our knowledge of how physical experience and expertise shape perception. In the second section, we delve into the realm of empirical aesthetics, specifically into the budding field of neuroaesthetics, to explore how this nascent field seeks to link subjective appraisals of stimuli with the neurobiological foundations that support such appraisals. Here as well, we highlight how research with dance and dancers is helping to move forward our understanding of the biological substrates of action perception and appreciation.

10.2 How Dance Informs Research Into Action Expertise

A question that has been of particular interest to philosophers for centuries, and to psychologists and neuroscientists ever since the advent of their fields, is how we are able to integrate physical and perceptual experiences to learn new movements. Such abilities are quite pronounced in professional dancers, whose livelihoods depend on rapid and adept movement, reproduction, and refinement. Before discussing how research with dancers advances our understanding of complex action learning and perception, it is first necessary to ground these questions within a broader, historical context. With the advent of cognitive psychology in the late nineteenth century, William James introduced the idea that action and perception processes likely converge or overlap in the human mind (James 1890). Neurophysiological investigation into the ability of the brain to use perceptual information to shape movement began in the mid-twentieth century, when information-processing explanations proposing complex transformations from perception to the organization and execution of action gathered momentum (Welford 1968; Sanders 1967, 1983; Mountcastle et al. 1975; Massaro and Friedman 1990). In the mid-1970s, Mountcastle and colleagues began the first investigations into putative neurophysiological mechanisms linking action with perception (Mountcastle 1975; Mountcastle et al. 1975; Yin and Mountcastle 1977). Through these seminal studies, Mountcastle and colleagues determined that neurons in parietal cortex respond to visual cues associated with specific actions.

Mountcastle and colleagues suggested that parietal cortex is a likely candidate for cross-modal convergence of action and perception, and established the foundation for the next several decades of further research into how these modalities interact (Andersen et al. 2004).

In the 1990s, research into the interface between action perception and production experienced an extraordinary surge in interest that was sparked by the discovery of so-called mirror neurons within the ventral premotor cortex of the macaque monkey. These neurons fired in a similar manner both when a monkey performed an action and when it observed another monkey or a human perform the same action (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996). A similar firing pattern when perceiving or performing actions was subsequently observed in the inferior parietal lobule (Fogassi et al. 2005), which suggested that perceiving others' actions engages a similar fronto-parietal circuit as executing actions.

One dominant explanation of these response profiles is tied to the notion of motor simulation (Jacob and Jeannerod 2005; Jeannerod 2001). The concept of motor simulation is consistent with other forms of mental simulation, which involve the reenactment of mental processes associated with previously experienced states (Barsalou 2008). Such states can be perceptual, motoric, or introspective. Hence, motor simulation is an instance of a more general concept of mental simulation (Jacob and Jeannerod 2005). Many researchers implicitly or explicitly hold that the mirror system is a key neural substrate for processes of motor simulation (e.g., Decety and Grezes 1999, 2006). In addition, motor simulation accounts of action comprehension have proposed that perceiving and understanding the action of another might involve the observer's brain simulating observed movements using their own motor system (Fadiga et al. 1995, 1999; Grafton et al. 1996; Rizzolatti et al. 2001). Thus, it is argued that through a process of motor simulation, action comprehension occurs by engaging specific parts of the motor system that would be used to perform the same action that is being observed (Rizzolatti et al. 2001).

Interest in mirror neurons has sparked hundreds of studies and an ongoing debate among researchers regarding the specific parameters, scope, and limitations of a possible action simulation system within the human brain (Gallese et al. 2011; Gallese and Sinigaglia 2011). While an exhaustive review of the past two decades of research performed in this domain is beyond the scope of this chapter (for reviews, see Grosbras et al. 2012; Molenberghs et al. 2012; Rizzolatti and Sinigaglia 2010), what a burgeoning corpus of research demonstrates is that neural tissue found within parietal and premotor cortices of the human brain is engaged when actions are performed and when they are observed. This work has given rise to the notion of a human mirror system, which consists of multiple cortical regions and shows evidence for behaving in a similar manner to individual mirror neurons found within nonhuman primate brains (Molenberghs, et al. 2012). A schematic representation of the human mirror system is depicted in Fig. 10.1.

The implications of a neural link between perception and action are broad-reaching and have been explored by scientists from disciplines and perspectives beyond neurophysiology and cognitive neuroscience, including the sport sciences, cognitive psychology, philosophy, and physical and occupational therapy (Johnson-Frey 2004;

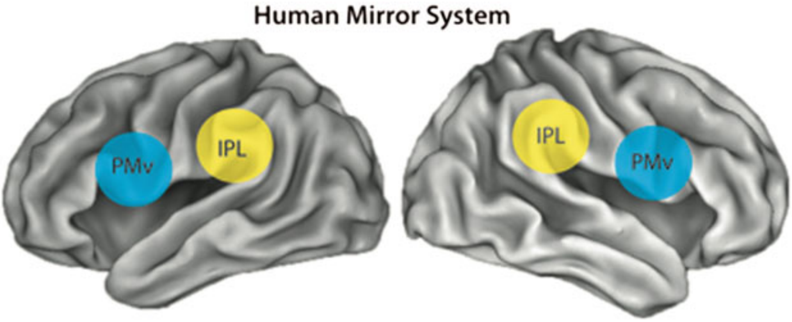

Fig. 10.1 Schematic representation of the human mirror system. The core nodes of the human mirror system are bilateral ventral premotor cortex (*PMC*) and inferior parietal lobule (*IPL*). While other regions within the human brain have been reported to show mirror-like properties, the strictest definition of the human mirror system includes only those brain regions where so-called mirror neurons, or cells that respond when performing an action or watching another perform an action, have been reported through neurophysiological investigations in the nonhuman primate brain

Braun et al. 2006; Jacob 2008; Goldman 2009; Yarrow et al. 2009; Guillot and Collet 2010; Moran et al. 2012). Moreover, some researchers have found that experimental paradigms that borrow from the arts, namely dance, offer an ideal means for advancing knowledge of how action and perception are linked (Bläsing et al. 2012). Paradigms incorporating dance training or the study of professional dancers have shed light on how motor expertise is manifest in the human brain, as evidenced by the two original studies to approach questions of action expertise using expert dancers as participants.

The first study to investigate how physical expertise with a particular dance style shapes neural activity when watching dance was conducted by Calvo-Merino et al. (2005). The authors studied a group of expert male capoeira dancers, expert male ballet dancers, and a group of age and sex-matched control participants. In this functional magnetic resonance imaging (fMRI) experiment, participants from all three groups watched 12 different 3-s videos depicting capoeira movements, and 12 different 3-s videos depicting ballet movements. The task was to indicate via a button press how tiring they thought each movement was. The authors found strong evidence in support of the idea that one's individual motor repertoire strongly shapes perception of others in action. Specifically, they found that when ballet dancers watched ballet or when capoeira dancers watched capoeira, they showed greater activity across brain regions associated with the mirror system, including left dorsal and ventral premotor cortices and posterior superior temporal sulci and bilateral intraparietal sulci. This finding is illustrated by the parameter estimates that quantify the relative amplitude of brain responses to watching the different kinds of dance videos among the three groups of participants. Crucially, no differentiation between the dance styles was seen in these regions within the brains of control participants. The authors concluded that long-held motor expertise markedly shapes perception, such that brain regions implicated in linking up performed with perceived actions are more active when an observer watches a particular movement he or she is physically familiar performing.

The study by Calvo-Merino et al. (2005) forged new territory in understanding how highly complex action and perception are linked in a number of ways. First, the data suggested that the mirror system codes complete action patterns, as opposed to individual movements. This was evidenced by the fact that movements from each dance style contained similar elements (such as swinging arms or jumping), yet the brains of capoeira and ballet dancers responded preferentially to their embodied movement style. The authors interpret this as evidence that neural architecture linking action with perception is sensitive to abstract levels of organization (such that two different dance styles can be distinguished). The findings are also important, in that they demonstrate the sensitivity of mirror system representations to *learned* movements, as opposed to innate action patterns that might be performed more or less by different groups of people.

A subsequent experiment more closely investigated this latter point in a longitudinal training study performed with a company of contemporary dancers (Cross et al. 2006). In this study, the authors scanned the brains of ten expert contemporary dancers once a week across 5 weeks of the rehearsal process as they learned a new piece of choreography that was rhythmically complex and lasted 25 min. The dancers rehearsed the new choreography for 4–5 days each week, and on each weekend, they underwent fMRI while watching 18 short-movement sequences from the work they were learning, or 18 kinematically similar control movements (all performed by the same dancer). While the dancers were in the scanner, their task was to watch each movement, imagine themselves performing it, and to evaluate how well they could perform each movement segment. At the end of each video clip, dancers reported on a 1–4 scale how well they thought they could physically perform the sequence they just watched.

The authors found that across the testing sessions, how the dancers rated their performance ability for the rehearsed movements significantly increased while their performance ability ratings for the (unrehearsed) control movements did not change. In terms of the neuroimaging findings, when the dancers watched movement that they had physically practiced compared to the kinematically similar control movement, more activity was seen within bilateral mirror system regions. This finding provided a clear replication and extension of what was reported by Calvo-Merino et al. (2005) with the ballet and capoeira dancers, demonstrating that de novo learning also results in marked differences in how similar movements with different experiential profiles are perceived. The most novel finding from this study, however, is what the authors found when they ran a parametric analysis querying brain regions whose activity increased with higher ratings of performance proficiency. This analysis revealed two small foci—left inferior parietal lobule and left ventral premotor cortex, which showed the strongest responses when dancers watched the movements that they were (individually) best at performing. What this finding suggests is that the better a dancer is at performing a movement he or she is watching, the more he or she simulates the observed action, and core mirror system regions within the left hemisphere are engaged by such processing.

These two highlighted studies using expert dancers to explore the neural signatures of physical expertise have been joined by a small but growing number of subsequent studies also using dancers to further knowledge on the impact of expertise on the brain (cf. Calvo-Merino et al. 2006; Orgs et al. 2008; Fink et al. 2009; Hänggi et al. 2009). Taken as a whole, these studies demonstrate how combining brain-imaging approaches with populations in possession of a highly specialized and skilled motor repertoire can advance our understanding of how action perception and performance are linked at behavioral and brain levels. However, the utility of dancers and dance paradigms for understanding how we perceive others is not limited to questions of motor expertise. In the following section, we explore how the dance domain can inform other aspects of the psychological and brain sciences, such as our affective appraisal of the movements of others.

10.3 How Dance informs Understanding of Aesthetics at Behavioral and Neural Levels

Another way in which research with dancers and the use of dance-based experimental paradigms has advanced understanding of how the brain perceives others in action is via empirical aesthetics. Classically, the study of aesthetics is associated with scholars in the humanities, such as philosophers, visual artists, and performing artists. For this reason, it is useful to define what, precisely, we mean by "aesthetics" when we discuss it in a scientific context. In consideration of the breadth of meanings and ambiguities the term "aesthetics" may carry, Brown and Dissanayake (2009) suggested that "aesthetics" has been used in two ways. In one sense, "the aesthetic" has been used to account for emotional responses that emerge when perceiving works of art, wherein art works (i.e., paintings, sculptures, sketches, dances, music) and the arts (i.e., corresponding activities or expressions) are fundamental to this usage. Another use of "aesthetics" is in reference to any system of valuation for the appreciation of beauty; the sensory preferences that humans and/or animals hold, with positive emotional responses towards objects resulting from selective attention (Orians 2001; Voland and Grammer 2003).

For this chapter, we will consider the term "aesthetics" as a heuristic for considering the experiences that result from the perception, appreciation, and/or creation of an artistic work. Aesthetics are studied and appreciated across myriad contexts including (but not limited to) faces, landscapes, music, dance, sculpture, food, paintings, mate selection, and machinery (Jacobsen 2006). For thousands of years, the only way in which aesthetic processing could be studied was to directly ask an individual about his or her experience with a stimulus, or observe their overt behavior toward a stimulus (Jacobsen et al. 2004, 2006). With the advent of cognitive neuroscience, new tools and techniques have enabled scholars from the psychological and brain sciences to explore the neurophysiological underpinnings of aesthetic perception. As such, neuroaesthetics offers another means of investigation into one's experience of the sublime. By simply being in the world, humans are in a constant state of aesthetic appraisal of ordinary objects, people, and experiences. The domain of neuroaesthetics aims to shed light on the nature of the aesthetic experience; that is, the relationship between the observer and the object, and the aesthetic processes that coalesce to create a rich relationship between stimulus and perceiver. As neuroaesthetics is a relatively new discipline, only a small number of empirical studies yet explored the affective relationship between an observer and a stimulus. Moreover, most of the work to date has focused on aesthetic responses to (static) visual artworks or music (cf. Cinzia and Gallese 2009; Blood and Zatorre 2001), with just a handful of studies that have explored the aesthetic responses in brain and behavior to dance. To place the dance neuroaesthetics research within a broader context, we first consider what we learn from the wider literature on empirical aesthetics and neuroaesthetics.

When a spectacle and its spectator meet, what the spectator beholds can vary from a fleeting sublimity to a sense of humdrum to a mere, neutral acknowledgment of an artwork. Each experience is, of course, personal to the beholder; one's personal preferences, expertise, and exposure, for example, may reflect in the evaluative judgments that follow, giving rise to inter-individual variability (Palmer et al. 2013). Underlying the aesthetic processing of a stimulus is an assortment of neural processing, including (but not limited to) activity within the medial orbitofrontal cortex (mOFC), a brain region associated with decision making, affective judgments, and expectation (Kawabata and Zeki 2004; Vartanian and Goel 2004; Kringelbach 2005). It thus appears that beauty is not so much in the eye, but instead the brain, of the beholder. In one recent study (Ishizu and Zeki 2011), volunteers drawn from a range of cultural/ethnic backgrounds were asked to rate a series of works—paintings or segments of music—as belonging to the categories of "beautiful", "neutral," or "ugly" while undergoing fMRI. The goal of the study was to determine where in the brain cortical activity correlated with experiences that participants rated as beautiful or ugly. The most striking finding from this study was that a portion of the mOFC was active when participants experienced a musically *or* visually beautiful stimulus. Of note, the intensity of activation within this region was correlated with ratings of the intensity of beauty. This region is thought to make rapid assessments as to the reinforcing properties of a stimulus, offering one possible pathway between reward, judgment and aesthetic pleasure upon perception. The authors concluded by offering a brain-based theory of beauty wherein the mOFC codes the aesthetic or rewarding value of a stimulus, regardless of its modality.

When further considering the relationship between the observed and the observer in an artistic context, a number of scholars have argued that understanding the role of empathy is crucial. Robert Vischer (1873; as referenced in Mallgrave and Ikonomou 1994) initially discussed empathy and its role in aesthetic experience as the notion of *Einfühlung,* which refers to the physical response when observing forms within art works (primarily paintings). This notion has subsequently been defined as "aesthetic empathy," and naturally applies to the dance domain as well, in what has been termed kinesthetic empathy (Hagendoorn 2004). In distinguishing from a passive mode of "seeing" and an active mode of "looking at," Vischer described how certain depicted forms, i.e., bodily postures or the function of muscles and limbs, could arouse certain feelings in response. Such nonpassive perceiving was proposed to involve a profound response of empathy. As a result, the body of the observer would resonate with the observed or depicted forms in the work. In turn, certain forms should evoke certain emotions. Hildebrand (1893) elucidated upon this idea, suggesting that in order to decipher a work, one has to implicitly grasp its creative process. Warburg proceeded to acknowledge this in his notion of *Pathosformel,* or form-evoking Pathos, wherein certain gestures, bodily forms, actions and expressions can be consistently detected throughout art history (Warburg 1999).

The array of dimensions involved in an aesthetic response of the observer is reflected by the body of research addressing the structure of this experience. One seminal theory that attempts to draw together notions of mirroring between the artist's work and the observer, grounded within contemporary neuroscientific understanding of the human mirror system, was proposed by Freedberg and Gallese (2007). In this account, termed the embodied simulation theory of aesthetics, the authors suggest that embodiment plays a significant role in appraising an artwork. Somewhat surprisingly, in many formal art criticism circles, empathy towards or bodily resonance with a work of art was previously dismissed as entirely intuitive subjective phenomena (Collingwood 1938). Due to accumulating research on the function and scope of the mirror system, however, this claim has been convincingly challenged. For example, when an observer watches a particular body part of someone else being touched, activation is seen within the brain of the observer as if the observer's own body were itself being touched (cf. Keysers et al. 2004). Freedberg and Gallese (2007) suggest that empathetic simulation is evoked by the representation of figures in an image, and a high degree of sensorimotor resonance with an agent depicted in an artwork is what leads to an aesthetically pleasing experience for the observer. The authors go on to propose that such resonance between an artwork and observer need not end at figural representations. Instead, an observer might experience some kind of somatic resonance with the artistic medium or technique used in the work. For example, an observer might be drawn in on a visceral level by the artistic gestures used to create a work, such as the brisk brushstrokes of Pollock, or the slashed cuts of a Lucio Fontana piece. This is what allows an observer to, as described by Freedberg and Gallese (2007), "[feel] the movement behind the mark" (p. 201).

Following on from the proposal that embodiment processes play a role in aesthetic appraisal, several research groups have turned to dance paradigms to further explore the role of kinesthetic empathy between the observer and artwork (in this case, the work of art is the movements performed by a dancer). The first study to do this was performed by Calvo-Merino et al. (2008) with a group of dance-naïve participants watching short-dance segments while undergoing fMRI. Several months after the fMRI experiment, the participants returned to the laboratory and rated the individual movements on a number of established aesthetic dimensions (after Berlyne 1974). In contrast to the mOFC findings that have been reported by experiments looking at aesthetic appraisal of static works of art and music (cf. Kawabata and Zeki 2004; Ishizu and Zeki 2011), the brain regions found to track with increasing aesthetic ratings of dance were located within bilateral occipital cortices and right premotor cortex. Thus, it appears that visual and sensorimotor cortices are more engaged when watching aesthetically pleasing dance, a finding that fits well with Freedberg and Gallese's (2007) embodied simulation account of aesthetics.

A subsequent study by Cross et al. (2011) sought to tie together the findings discussed in the previous section on embodiment and physical experience with what was reported by Calvo-Merino et al. (2008) concerning the involvement of sensorimotor brain regions in the aesthetic appraisal of dance. In this study, dance-naïve participants watched a range of ballet and contemporary dance movements performed by professional dancers while undergoing functional neuroimaging. Participants were asked to rate each movement on how well they could physically reproduce it (same question/scale used by Cross et al. 2006), and also how much they liked watching each movement. Behaviorally, the authors found a strong negative correlation between perceived physical ability and liking, such that participants most enjoyed watching those movements they rated as the most difficult to physically perform (Cross et al. 2011). To analyze the brain-imaging data, the authors ran parametric analyses to query brain regions that showed increasing responses based on increasing (or decreasing) ratings of physical ability or aesthetic value. The most interesting finding emerged from the interaction between parameters of perceived physical ability and aesthetic value. This analysis evaluated brain regions showing a stronger response when participants rated a movement as difficult to perform, but highly enjoyable to watch. The authors found that bilateral occipitotemporal cortices and right inferior parietal lobule showed increasing responses the more a participant liked watching a movement, and the less he or she could perform it.

When the findings of Calvo-Merino et al. (2008) and Cross et al. (2011) are considered together, they begin to build a compelling case in support of Freedberg and Gallese's embodied simulation account of aesthetics (2007). It appears that when watching dance, even dance-naïve observers engage sensorimotor brain regions associated with action perception and action performance to a larger degree when they find the movement aesthetically pleasing. One might conclude from these findings that embodied simulation of a dance piece is integral to aesthetic experience, although this hypothesis has not yet been tested directly. Along these lines, however, recent work from our laboratory is seeking to more fully characterize the role and impact of physical experience on aesthetic experience in dance contexts (Kirsch et al. 2013; Kirsch et al., in preparation). One of the patterns of findings most relevant to consider in light of Freedberg and Gallese's embodied simulation account of aesthetics concerns the relationship between the perception of one's ability to perform a movement, or the inherent complexity of a movement, and how much an observer enjoys watching the movement. Figure 10.2 illustrates findings from dance-naïve observers who watched a series of dance movements and were asked to rate their physical ability to perform the observed movements (panel A; Cross et al. 2011) or the perceived complexity of the movements (panel B; Kirsch et al. 2013), as well as how much they enjoyed watching them.

The plot in panel A and the first plot in panel B illustrate that dance-naïve observers enjoy watching most of those movements that they perceived as difficult or complex to perform. This pattern of findings might suggest that complex dance movements

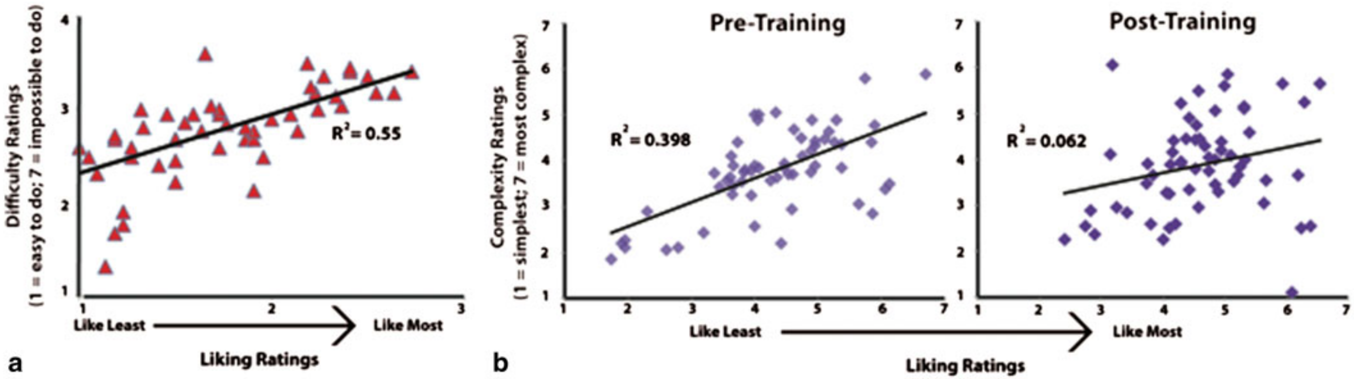

Fig. 10.2 Comparison of findings from Cross et al. (2011, panel A) and Kirsch et al. (2013, panel B) regarding the relationship between perceived ability to physically perform a movement or perceived complexity of a movement, and how enjoyable a movement is to watch. The relationship between perceived complexity/difficulty and liking is manifest as a positive correlation among dance-naïve observers, but once physical experience is gained, this relationship attenuates. (Figure adapted from Cross et al. 2011 and Kirsch et al. 2013)

engage observers more, perhaps by challenging them to embody the movement in a manner. However, the study illustrated in panel B (Kirsch et al. 2013) incorporated a training manipulation where participants learned to perform a subset of the movements they observed and rated before having any kind of dance training or experience. What the right plot in panel B illustrates is that after learning to physically embody a movement, the relationship between perceived complexity and enjoyment is no longer present. Of course, this finding raises more questions than answers, concerning how embodiment and aesthetic value are linked in the action perception and production domain. Ongoing work in our laboratory aims to further delineate the behavioral and neural consequences of the relationship between embodiment and affective processing of others' movement.

10.4 Conclusion

The aim of the present chapter was to illustrate the utility of dancers to scientists seeking to explore how action and perception are linked in learning, expertise, and aesthetics. We have attempted to place the action expertise and neuroaesthetics research with dance in a broader context that clarifies how and why scientists have worked with dance and dancers in their experiments. Neuroscientists initially turned to the domain of dance to use it as a means of addressing fundamental questions of action and perception, rather than to study its representation as an artistic medium in the human mind or body per se (Cross and Ticini 2012). With this being said, it is perhaps unsurprising that ever since the first neuroscience work with dancers started to emerge nearly a decade ago, many individuals in the dance community have been interested in what such research might reveal (or not) about the performance and perception of their art form. A number of cross-disciplinary forums and research projects are starting to emerge that attempt to find ways for artists and scientists to work together on research that mutually informs and benefits both the scientific and artistic domains (cf. Motion Bank (www.motionbank.org) and Watching Dance (www.watchingdance.org)). From a dance perspective, these endeavors have the possibility to illuminate factors that influence the performer–observer relationship, and to map the boundaries of an aesthetic experience. From a scientific perspective, such collaborations will undoubtedly reveal new ways of exploring fundamental aspects of human behavior and brain function with dance, both within and beyond the domains of action expertise and neuroaesthetics.

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Chapter 11
Apollo's Curse: Causes and Cures of Motor Failures in Musicians: A Proposal for a New Classification

Eckart Altenmüller, Christos I. Ioannou, Markus Raab and Babett Lobinger

11.1 Becoming a Horowitz: Challenges in Acquiring Superior Motor Skills in Musical Performance

Performing music at a professional level is one of the most complex human accomplishments. Playing an instrument requires integration of multimodal sensory and motor information, generation of appropriate action plans, selection, and retrieval of highly refined movement patterns from procedural motor memory, and initiation of the movement. In most instances, these movements are highly overlearned, and depend on feed-forward programming of the anticipated—mostly audible—results and on real-time feedback.

Auditory and kinesthetic feedback is needed to improve and perfect performance. Music making therefore relies primarily on a highly developed auditory–sensory–motor integration capacity, which has been theoretically conceptualized in the "common-coding" model by Prinz (1984). Simplifying this model, movements are represented as sound patterns, and sound patterns as movements (see for a review Zatorre et al. 2007). Subtle perturbations of this auditory feedback will have a major impact on motor control. For example, playing on a keyboard with slightly delayed sound production will compromise regularity of scale playing even in highly accomplished pianists (Cheng et al. 2013). Furthermore, the kinesthetic senses constitute

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another basis of high-level performance. They allow for control and feedback of muscle and tendon tension as well as joint positions enabling continuous monitoring of finger, hand, or lip position in the frames of body and instrument coordinates (e.g., the keyboard, the mouthpiece). Again, subtle changes in kinesthetic feedback result in alteration of the motor program, and long-term loss will cause, in some individuals, severe disturbances of the motor program and even focal dystonia (for a theoretical account and review on this topic, see Konzcak and Abruzzese 2013).

In order to acquire these specialized sensory–motor skills, extensive training periods over many years, starting in early infancy and passing through stages of increasing physical and strategic complexities, are necessary. This process of practicing involves assembling, storing, and constantly improving sensorimotor programs through prolonged and repeated execution of motor patterns under the controlled monitoring of auditory and kinesthetic senses. To attain a professional level, as a rule of thumb, 10,000 h in 10 years of deliberate practice are needed (Ericsson et al. 1993). Of course, time invested into the acquisition of motor skills is only a necessary, however, not a sufficient precondition of becoming an outstanding artist. Quality of practice as well as communication skills and expressive gesturing, rendering a performance "speaking," are equally important in the process of artistic perfection of publicly acclaimed and valued interpretations (Hallam in press).

In music, learning through experience and training is accompanied by remarkable plastic adaptations of the central nervous system (CNS), which are not only reflected in modifications of the neuronal networks of the brain, as a result of a strengthening of neuronal connections, but also in its overall gross structure. It is known, for example, that music practice enhances myelination, grey matter growth, and fiber formation of brain structures involved in the specific musical task (for a review see Münte et al. 2002; Wan and Schlaug 2010). For example, Gaser and Schlaug (2003) could demonstrate enhancement of grey matter density in cortical sensorimotor regions, auditory regions, the left dorsolateral prefrontal cortex, and in the cerebellum in professional instrumentalists as compared to nonmusicians and amateurs. Interestingly, these plastic adaptations depend on critical periods: Musicians, who start early, before age 7, do not display these adaptations of the brain structure at least in the sensorimotor cortices and the callosal fibers. However, they seem to have an "early optimized network," which allows superior performance of motor tasks without enlarged anatomical structures (Steele et al. 2013; Vaquero et al. 2014). In contrast, late starters, after age 7, do show the abovementioned structural adaptations accounting for the effects observed in many morphological brain imaging studies (e.g., Bangert and Schlaug 2006; Gärtner et al. 2013).

When discussing skilled motor behaviour in music performance and its deterioration or even loss, it should be emphasized what is unique to making music and what renders it particularly challenging and fragile in terms of motor control:

1. Musical training usually starts very early, sometimes before age 6, when the adaptability of the CNS is highest. This feature is not unique to music, since other skilled activities, for example classical ballet dancing also requires an early start.

2. Making music is linked to sound production. As in speech, the auditory system provides very precise feedback of the movement effects, with a temporal resolution superior to kinesthetic and visual feedback. Furthermore, in the frame of classical music, which is notated and available as sheet music, the target parameters, namely temporal accurateness (correct tempo, accuracy of rhythm, swing, beat, pulse etc.), and spatial accurateness (correct pitch on key or fingerboard, correct sound quality), are predefined. Therefore, a highly reliable reproduction of movements meeting these targets is required. This feature is unique to music, since for example in classical ballet, visual feedback is less critical in terms of temporo-spatial precision.
3. Most musicians work at the upper limit of their sensorimotor capabilities and strive to push their limits even further, in order to be faster, louder, and more expressive. Given the complexity of music, the demands of composers, especially in the past 100 years, and the role of outstanding peers as models, for example the Chinese pianist Lang Lang, or the "record breaking" violinist David Garrett, the theoretical limit of movement accuracy and speed is the temporal and spatial resolution of the auditory system. As musicians say "there is always a colleague who plays this piece faster, louder and more beautifully." This is in part also true for sports, but in music, fine motor skills predominate. Musicians therefore are colloquially frequently denoted as "small muscle athletes."
4. The societal pressure and expectancies concerning the quality of musical performances has definitely grown over the past centuries, due to the ubiquitous availability of music recorded in media such as YouTube and CDs, as well as due to collective learning processes leading to higher standards of music appreciation. This process augments anxiety, tension, and competition amongst musicians rendering their life increasingly stressful. Frequently even outstanding soloists have to cope with severe performance anxiety (Wilson 1997).

On the other hand, making music is frequently linked to highly positive emotions, to feelings of joy, satisfaction, and even to strong emotional reactions, known as "chill responses" (Altenmüller et al. 2013). These qualities are known to enhance plastic adaptations of the brain and can even lead to a sort of addictive behavior, causing younger musicians to over-practice and ignoring their bodily limits which are indicated by fatigue and musculoskeletal pain.

In the following section, we will focus on the loss of motor control in highly performing musicians and will argue that these problems need to be classified in a more refined manner.

11.2 Deterioration of Motor Control in Musicians: Towards a Refined Classification

In this section, we will not deal with problems of acquisition of new and refined motor skills. Instead, we will focus on the deterioration of skilled movements, which had been acquired previously through long-term practice and automation. The former is familiar to all music teachers: some students are simply unable to attain a certain tempo, to perform a certain articulatory technique (e.g., "double-tongue," in flute players), or to control the execution of phasic movements (e.g., the vibrato is too fast, or too slow etc.). Its causes are not well understood and will require substantial research in the future.

Furthermore, we will exclude disturbances of motor control due to tissue damage, be it peripheral, such as cervical root injury, trigger finger etc., or be it of CNS origin, such as stroke, brain hemorrhage, or tumors. We will not cover these topics here, but we will concentrate on proposing six different categories of deterioration or loss of motor control in musicians with intact neural substrates.

For classifying deterioration of motor control in musicians, based on the current state-of-the-art, we have applied the following classification criteria: (1) duration and development of the problem, (2) triggering mechanisms, (3) psychological profiles, (4) response to treatment, (5) accompanying symptoms, and (6) genetics.

11.2.1 Motor Fatigue

Most musicians know instances of loss of motor control when playing their instrument. Frequently this phenomenon is short-lasting and due to either lack of practice or overuse. It is accompanied by mental or bodily fatigue and obviously linked to reduced attention and insufficient movement monitoring. Usually these deteriorations of movement coordination are short-term, disappear overnight, and do not compromise overall performance. Although these incidents seem to be frequent, there is almost no scientific data available. A recent questionnaire study in German orchestral brass instrumentalists identified temporary crises of embouchure coordination in a percentage as high as 30 % of musicians (Steinmetz et al. 2013). In clinical practice, symptoms are lack of regularity in scales, trills and other fast repetitive movements, wind players complain of loss of sound quality and occasionally early fatigue. Usually, pain is not reported. There is no information available whether any medical intervention other than rest is useful to treat this condition.

11.2.2 Overuse Injury

In contrast to the former conditions, overuse in the narrow sense of the word should only be diagnosed when pain is a dominating symptom and a history of either prolonged or unaccustomed practice exists. Here, local inflammation of overstrained tissues, release of pain mediators, and spinal reflexes with increased or occasionally lowered muscle tone may lead to a deterioration of motor control, mostly accompanied by relieving movements (Szeto and Lin 2011). This condition may last a couple of days, and under rest subsides after a few weeks.

11.2.3 Choking Under Pressure

Another condition leading to deterioration of motor control is "choking under pressure." Choking under pressure (CuP) figures widely in the sports psychology literature but has not yet been adopted by experts in musician's medicine and performing arts psychologists. We therefore devote a longer section to this condition.

In sports, the current definition characterizes CuP as an acute performance failure due to a perceived mismatch between the individual resources of an athlete and the demands of the situation (Hill et al. 2009). CuP describes the situation in which the individual perceives a subjectively unmanageable situation that is accompanied by fear of failure, anxiety, and increased arousal, leading to reduced motor control and worse performance outcome. In musicians, CuP is a relatively frequent experience, especially in performing novices, and is usually subsumed under the term "performance anxiety." According to questionnaires, between 15 and 60 % of performing musicians occasionally suffer from this condition (Brugués et al. 2011a; Steptoe and Fidler 1987). It may lead to loss of agility, heightened muscular stiffness accompanied by increased co-contraction of antagonist muscles (Yoshie et al. 2009), and, as a consequence, reduction of temporo-spatial precision of movements and sound quality. In brass players, the so-called tongue stopper prior to an important cue is a typical manifestation.

In sports, different theories have been proposed to explain the appearance of a choke. They can be divided into drive theories and attentional theories (for a review see Hill et al. 2010). Drive theories are based on the assumption that increased arousal, resulting from striving to perform well under pressure, will have a detrimental effect on performance (Spence and Spence 1966). Drive theories account for the classical inverted-U model of performance anxiety. This model predicts that increased arousal will first lead to an improved performance; however, further increase will reduce performance quality (Yerkes and Dodson 1908). However, drive theories cannot explain why some athletes or musicians thrive but others fail under pressure.

Attentional theories try to account for individual differences. Attentional theories can be separated into distraction (Carver and Scheier 1981) and self-focus (Baumeister 1984) theories. Distraction theories assume that pressure-induced anxiety will occupy the performer's working memory, restricting the processing of task-relevant information (Eysenck and Calvo 1992). Self-focus theories propose that performance anxiety causes the performer to shift the focus of attention inward or to consciously monitor the skill, which detrimentally affects the well-learned automated skill (Baumeister 1984). Crucial for the occurrence of choking is the perceived control of a situation, which is influenced by both situational and personality factors (Otten 2009). Personality factors that increase the likelihood of choking include low self-confidence (Baumeister and Showers 1986) and high trait anxiety (Wilson 2008).

11.2.4 Dynamic Stereotype in Musicians

When motor incoordination and lack of motor control persist for more than 4 weeks, even though rest has been observed and careful rehabilitation under the guidance of a therapist or teacher has been attempted, one can assume a more grave alteration of sensorimotor networks leading to a deterioration of motor programs in the CNS. We have called this condition “dynamic stereotype” (DS), a term borrowed from the eminent Russian physiologist Ivan Pavlov (1951; for a critical review, see Windholz 1996). Originally, this condition can be understood as a reflection of fatal compensation strategies, which became automated. In the words of the exponents of Russian behaviorism, “dynamic stereotypes” are defined as a type of integral activity performed by the cerebrum of higher animals and man and manifested by a fixed, or stereotyped, succession of conditioned reflexes. The DS is influenced by external factors that are repeated in a certain order. Accordingly, the DS is the most vivid manifestation of the extremely subtle analyzing and synthesizing activity of the cerebral cortex and is the product of very complex interactions between the areas of the cortex. It can at least partly be conceptualized as a consequence of long-term CuP when these dysfunctional movements are stored in procedural memory traces, maybe as a consequence of conditioned reactions to previous choking experiences and procedural memory formation under stress (Klämpfl et al. 2013; Lobinger et al. 2014).

The phenomenology of DS resembles in many aspects focal, task-specific dystonia (see below). However, in contrast to the latter, it seems to be more modifiable and more fluctuating, especially during stressful performances. Sometimes, “islands” of well-being and complete motor control occur, although only for hours or a few days. It responds occasionally to trick sensory maneuvers, such as alterations of either tactile input from the body parts affected by dystonia or alterations of auditory input for example by delay of the produced sound. We could demonstrate that improvement of motor control, when playing with a latex glove is related to better outcome of retraining and behavioral therapies (Paulig et al. 2014). It should be mentioned, however, that responses to sensory tricks and objective improvement are rare and highly variable (Cheng et al. 2013). We therefore prefer to consider this phenomenon a “soft-sign” with respect to classification of problems of motor control.

11.2.5 Focal Dystonia in Musicians

The most severe movement disorder among instrumental performers is task-specific musician’s dystonia (MD; Altenmüller 2003), also known as musician’s cramp. Commonly, two major forms, focal hand dystonia (FHD) and embouchure dystonia (ED) are distinguished. It is a movement disorder characterized by persistent muscular incoordination or loss of voluntary motor control during task-specific highly trained movements, such as playing a musical instrument (Altenmüller 2003; Jankovic and Ashoori 2008). In most cases, pain does not accompany the disorder. Occasionally

Fig. 11.1 Typical patterns of dystonic postures in a pianist, a violinist, a flutist, and a trombone player suffering from musician's dystonia

some muscular strain can occur due to attempts of compensating for the dystonic movement by over-activation of the antagonist muscles. However, the lack of pain distinguishes it from the abovementioned overuse injury. It is important to make this distinction bearing in mind that prolonged pain syndromes may lead to symptomatic dystonia. MD frequently terminates professional careers and is among musicians' most highly disabling condition (Altenmüller 2003; Brandfonbrener and Robson 2004; Lederman 1991; Altenmüller and Jabusch 2010).

Various symptoms can mark the beginning of the disorder: subtle loss of control in fast passages, finger curling (cf. Fig. 11.1), lack of precision in forked fingerings in woodwind players, irregularity of trills, fingers sticking on the keys, involuntary flexion of the bowing thumb in strings, impairment of control of the embouchure in woodwind and brass players in certain registers, are among the most frequent descriptions given by patients. At this stage, most musicians believe that the reduced precision of their movements is due to a technical problem or lack of practice. As a consequence, they intensify their efforts, but this reaction often exacerbates the problem. The loss of muscular coordination is frequently accompanied by a co-contraction of antagonist muscle groups. For example, in pianist's cramp, the co-activation of wrist flexor and wrist extensor muscles is frequently observed, and we have documented a case of a task-specific dystonia in the leg of a bass drummer, leading to pronounced co-activation of ankle flexor and extensor muscles (Lee and Altenmüller 2014).

There are special cases of task-specific loss of motor control in musicians, which should be mentioned here since they are strongly related to MD or even constitute subgroups: Dystonic tremor is characterized by task-specific tremulous movements of the supporting arm in woodwinds or in the bowing arm of string players (Lee et al. 2013). A very rare condition is a task-specific inability to recruit motor programs required for a specific overlearned movement, termed "negative dystonia" (Mezaki 2007).

According to recent estimates, 1 % of all professional musicians are affected (Altenmüller and Jabusch 2010). In contrast, in the general population, prevalence of focal dystonias, including writer's cramp, blepharospasm, and cervical dystonia, is estimated as 29.5 per 100,000 in the USA and 6.1 per 100,000 in Japan (Nutt et al. 1988; Nakashima et al. 1995). In comparison to other activities producing dystonic movements, such as writing, playing golf (the "yips"), or dart ("dartism"), classical musicians are at highest risk to develop focal dystonia (Frucht 2009).

Demographic data demonstrate a preponderance of male musicians with a male–female ratio of about 4:1 (Lim and Altenmüller 2003). Hereditary factors play a role in the etiology of MD, since a positive family history of dystonia exists in up to 36 % of affected musicians (Schmidt et al. 2009). According to epidemiological data, the probability of developing MD depends on the instrument played, with guitar players, pianists, and brass instrument players having the highest risk of developing dystonia (Altenmüller and Jabusch 2010). Repetitive use, controllability of motor actions, temporo-spatial demands, and extra-instrumental fine motor burdens, such as writing, are triggering factors (Altenmüller et al. 2012; Baur et al. 2011). Furthermore, those musicians who start later than age 10 with their instrumental practice are at a much higher risk to develop MD (Schmidt et al. 2013).

With respect to a differentiation of MD from the above-described DS, there is probably a certain overlap. Generally, focal dystonia is more severe and the dysfunctional movements are more obvious, and more resistant to any attempt to correct them voluntarily. Furthermore, movements respond to a lesser degree to the above-mentioned sensory tricks. Sudden spontaneous improvements are rare exceptions and psychological stressors do not influence the loss of motor control to a major degree. Finally, in contrast to DS, in MD there is a tendency to generalize from the specific movement when playing the instrument to other daily-life movements. For example, the problem may appear first only in the ring and little finger of the pianist when playing scales, as depicted in Fig. 11.1, but later extends to typing on a computer keyboard and to buttoning up a shirt, and in the end may lead to permanent cramping of the hand. In neurology, this condition is termed "dystonic cramp" and it seems to affect about 35 % of musicians suffering from primarily task-specific dystonia (Rosset-Llobet et al. 2007). In the same line, loss of motor control may progress from the forearm to the upper arm, leading in rare cases to segmental dystonia. When dystonia propagates from one hand to the other, which is the case in about 3 % of the musicians suffering from FHD, a bifocal dystonia has to be assumed (Rosset-Llobet et al. 2007).

11.2.6 Symptomatic Task-specific Dystonias in Musicians

Symptomatic task-specific dystonias in musicians are a rare heterogeneous group of dystonias. By definition, the leading symptom is isolated deterioration and loss of motor control when playing a musical instrument. In contrast to the abovementioned "idiopathic" focal dystonias, this disorder is caused by either an underlying neurological or psychological pathology. For example, in rare cases it may mark the beginning of Parkinson's disease, albeit we have to acknowledge that we have only seen two MD patients who developed Parkinson's disease several years later. When taking the numbers of our whole group of presently 850 MD patients into account, this is in the range of the incidence of Parkinson in the general population in Germany. In neurological textbooks, furthermore morbus Wilson, Huntington's chorea, and other neurodegenerative diseases have been mentioned as a cause of symptomatic dystonia; however, an isolated task-specific loss of motor control in these conditions, specifically when playing the instrument, has to our knowledge not yet been described.

MD is sometimes triggered by bodily trauma. Here, it is unclear whether the lesioning of peripheral nerves and the concomitant sensory degradation or the trauma-induced rest or change in practice schedules, playing postures, etc. constitute triggers. We have seen two flutist patients suffering from inferior alveolar nerve lesion and numbness of the lower lip who developed embouchure dystonia (unpublished clinical data).

Psychogenic dystonias in musicians are extremely rare conditions. We have never seen any musician malingering, probably due to the rewarding nature of music and the lack of secondary benefits when losing the ability to perform. However, fluctuating or longer-lasting loss of motor control when playing an instrument may occur in some psychiatric diseases, such as schizophrenia, obsessive–compulsive disorders, and constraint and anxiety disorders. In schizophrenia, long-term consequences of antipsychotic drugs have to be considered as a cause. In obsessive–compulsive disorder, dysfunctional working behavior and, as a consequence, motor fatigue and overuse may be the underlying pathogenic mechanisms. Anxiety has been frequently found as a risk factor in MD (see below). This might hypothetically be linked to chronic choking under pressure, as discussed above in the "DS" section.

Finally, psychogenic MD in the narrow sense of the word is, as far as our experience goes, extremely rare. The underlying theory assumes a conversion disorder, which in turn is caused by fundamental unresolved psychological conflicts, leading to subconscious alterations of motor behavior which may express the nature of the underlying conflict in a "converse" manner. It is very difficult to diagnose and therefore frequently subsumed under the term "unexplained medical conditions" (Lang and Voon 2011). As a rule of thumb, musicians suffering from psychogenic dystonia usually have a history of previous physical or psychological trauma or disorder, show the symptoms in an exaggerated, "speaking" manner, seem to be more emotionally distant to the motor disorder, and display less despair. Sometimes, a triggering event can be identified, and in the follow-up, very fluctuating symptoms with prolonged periods of complete remission or miracle healing are suspicious of a psychogenic cause (Czarnecki and Hallett 2012).

Summarizing this section, an outline of a provisional "classification tree" is sketched in Fig. 11.2. The idea is that motor disturbances in musicians are gradually developing under given circumstances, such as high workload, underlying anxiety, and stress.

Still, many details of this classification are hypothetical. Our thoughts were guided by clinical experience and our goal is to find a better diagnostic algorithm in order to improve client-tailored treatment.

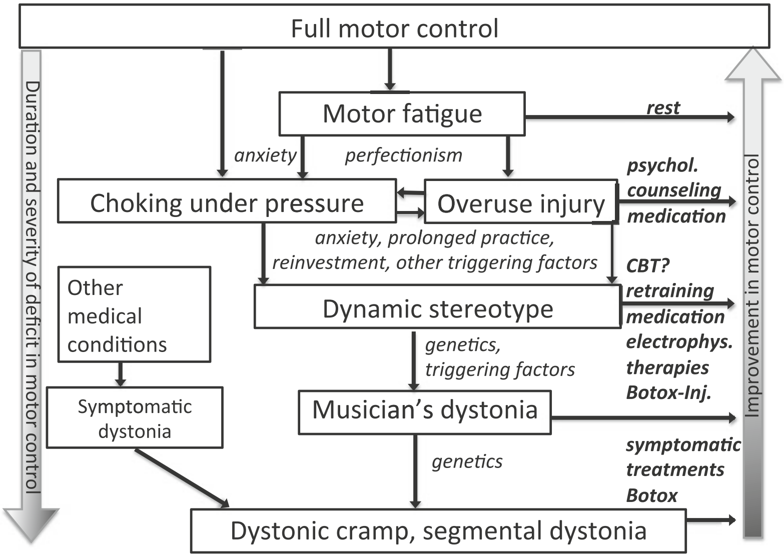

Fig. 11.2 "Flow chart," displaying the different types of motor disturbances sorted according to duration and severity of the motor deficit. Factors promoting the transition from one class to the next one are shown in *italics*, therapeutic strategies in ***bold italics*** at the *right* part of the panel. CBT stands for "cognitive-behavioral therapy"

11.3 Can Psychological Profiles and Neurophysiological Mechanisms Contribute to a Refined Classification of Motor Degradation in Musicians?

In the following section, we will examine how a classification based on phenomenology and underlying neurophysiological mechanisms may lead to client- tailored treatment. As outlined above, the six types of motor disorders can be classified according to the duration of motor degradation, the accompanying symptoms, the underlying neurophysiological mechanisms, and the response to treatment. In Fig. 11.3, we have depicted a heuristic model, assuming a continuous worsening of motor control from temporary subtle awkwardness to increasingly unstable motor control and finally, fully developed focal dystonia. Furthermore, we have added triggering factors, identified in our previous epidemiological studies (Altenmüller 2003; Altenmüller and Jabusch 2010).

In the beginning, motor fatigue may cause a temporary degradation of motor skills, or, in highly skilled experts, additional/alternative recruitment of muscles contributing to dysfunctional movements. This mechanism has been convincingly demonstrated in skilled table tennis players (Aune et al. 2008), and most probably also applies for instrumental musicians. For example, in skilled piano players, fatigue of the long flexor muscles in the forearm may be compensated by activation of the intrinsic muscles in the hand, which in turn results in dysfunctional movements in the

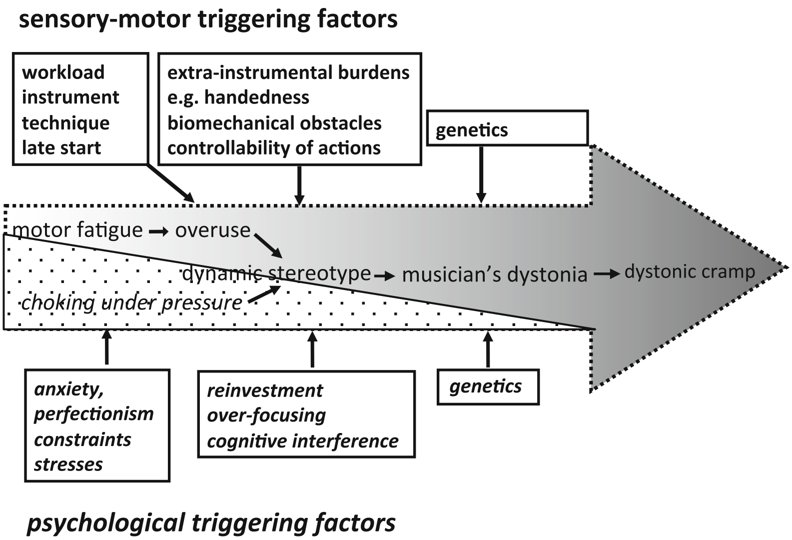

Fig. 11.3 Heuristic model demonstrating the proposed interplay of sensory–motor and psychological triggering factors and their contribution to the different motor disturbances. The assumed degree of "psychological" triggering factors is displayed as the *dotted space*; the increasing *grey shade* symbolizes the increasing degree of loss of motor control

metacarpophalangeal (MCP) joints with lack of fine control of touch and degraded sound quality. These changes are accompanied by central nervous adaptations, due to short-term plasticity, resulting in reduced amplitude of movement-related potentials and in an alteration of the topography of motor and premotor cortex activations (Dirnberger et al. 2004). Interestingly, in a study with musicians suffering from dystonia, a fatiguing muscular contraction significantly improved motor performance. In contrast, in healthy musicians, performance consistently worsened following fatigue (Pesenti et al. 2004).

In the overuse condition, dysfunctional CNS plasticity probably plays an important role in motor degradation (Byl et al. 1996; see also Flor 2012 for a review). Although in most instances prognosis is good and quick recovery is common, under conditions with heightened anxiety and other stressors, such as high professional workload, these dysfunctional motor patterns may stabilize in procedural memory. Here, psychological stress might induce the cascade of emotionally induced memory consolidation, which has been described previously for different forms of memory: It mainly relies on noradrenergic activation of the basolateral amygdala (BLA) (McGaugh 2000; Packard et al. 1994). The primary motor cortex, which is essentially involved in the storage of motor memories (Karni et al. 1998), receives a BLA projection (Sripanidkulchai et al. 1984). Thus, it may be assumed that consolidation of these dyscoordinated movements as dysfunctional motor programs is a BLA-mediated process in the primary motor cortex (Jabusch and Altenmüller 2004). This may also be the link to conditions discussed below, namely CuP and DS.

CuP is not uncommon in sports and has been investigated in golfers, suffering from the yips. This condition is defined as involuntary movements during the execution of putting strokes, resulting in a serious decrease in the success rate in putting. It has been classified by some authors as a task-specific focal dystonia (Adler et al. 2005); however, many authors believe that the yips is more related to CuP (Lobinger et al. 2014). Arguments against the classification as a focal dystonia are:

1. The yips occur not only in professionally trained golfers but also in golfing beginners. This renders a pathophysiological mechanism similar to that of MD very unlikely. In musicians, we could demonstrate that dysfunctional brain plasticity induced by prolonged practice leads to distorted topographies of receptive fields in the somatosensory cortex, which in turn leads the observed degradation in motor control, due to abnormal somatosensory feedback (Elbert et al. 1998).
2. The yips look more like a sudden jerk, or an anticipatory tremor prior to hitting the ball. In MD, reduced inhibition in the motor output is another proven cause of dysfunctional movements, leading to prolonged co-activation and typical dystonic postures, for example, the curling of fingers in Fig. 11.1.
3. The yips are relatively frequent in the golfing community with prevalence between 16 and 24 % (Klämpfl et al. 2013). This is unusual for any kind of dystonia. The most common task- specific dystonia up to now is MD, which affects 1–2 % of professional musicians.

In music, the term CuP has not been applied, but the phenomenon clearly exists. The abovementioned tongue stopper in brass players and the short-action bowing tremor in violin players playing soft notes with the tip of the bows are good examples. Here, most probably anxiety induced "reinvestment" leads to cognitive interference, resulting in dysfunctional movements due to the attempt to prevent or even correct feared errors. In an electroencephalography (EEG) study on highly trained professional pianists, we could demonstrate that their brain anticipates errors of motor execution, and that these "pre-error"-related brain waves arise about 50 ms prior to the wrong keystroke (Herrojo-Ruiz et al. 2009). Such a rapid error anticipating mechanism cannot be cognitively controlled. Rather, is highly susceptible to disturbances via cognitive control. Therefore, it is plausible that reinvestment and CuP may lead to a deterioration of motor control.

DS is characterized by a more permanent reduction of motor control. As outlined above, it differs from focal dystonia only gradually, but probably is more linked to psychological triggering factors as to underlying genetic factors (Ioannou and Altenmüller 2014). In terms of underlying neurophysiological mechanisms, we speculate that these musicians have a deficit in the so-called limbic loops of the basal ganglia, linking movements and motor control to emotions. However, this question remains to be addressed in future investigations in a patient population, which a priori is correctly classified (Ioannou and Altenmüller 2014).

MD can be distinguished from the former by the more pronounced worsening of motor control, the lack of "islands" of well-being, and the tendency to progress to dystonic cramps. The pathophysiological basis of MD can only briefly be summarized. For more details, we refer to a review by Altenmüller and Jabusch (2010).

Numerous studies are revealing abnormalities in three main areas: (a) reduced inhibition in the sensorimotor system, (b) altered sensory perception, and (c) impaired sensorimotor integration. In recent years, an increasing number of brain-imaging studies in musicians—and other focal dystonias—have demonstrated that these alterations are probably not task specific. Functional connectivity (Moore et al. 2012), cortical activation patterns (Haslinger et al. 2010), and basal ganglia anatomy (Walter et al. 2012) have proven to be abnormal, although behavioral tests are more in favor of task specificity when testing musicians in other skilled motor tasks (Rosset-Llobet 2007). We argue that musician's focal dystonia is the product of a hereditary susceptibility, probably related to a general lack of central nervous inhibition and the abovementioned triggering factors. This leads not only to task specific functional alterations of CNS networks—as we predict in patients suffering from a dynamic stereotype—but also to structural alterations found in the abovementioned studies.

In previous publications, we have emphasized psychological conditions as an underlying triggering factor. In several questionnaire studies, we found elevated anxiety and extreme perfectionism in MD patients (Altenmüller and Jabusch 2009; Enders et al. 2012). According to Jabusch et al. (2004), these psychological characteristics had already been present before onset of dystonia according to personal recall. We now argue that musicians with a major psychological burden most probably can be subsumed under the classification of a DS. We are presently conducting a study addressing the impact of stress and anxiety on motor performance in musicians suffering from loss of motor control who are demonstrating either high or low psychological burdens. Subsequently, we will apply specific interventions aiming at improving psychological conditions and preventing dysfunctional reinvestment in order to improve motor control in those musicians who suffer from dynamic stereotypes.

11.4 Consequences for Treatment of Motor Disturbances in Musicians

What do psychological and neurophysiological findings imply for the differential treatment of motor disturbances in musicians? We have already mentioned that motor fatigue should probably be best treated with rest, although no scientific data are available. For treatment of overuse injuries, besides rest, pain medication, muscle relaxants, and physiotherapy with gentle stretching exercises have proven to be useful (for a review see Helliwell and Trainor 2004). In these pain syndromes, a prompt intervention is required to avoid dysfunctional plastic adaptations of the CNS seen in chronic pain conditions (Jensen et al. 2013). CuP in musicians is probably best prevented by mental training and specific cognitive strategies, already applied in sports psychology (e.g., "hemispheric priming," Beckmann et al. 2013). Efficient treatment probably includes cognitive-behavioral therapy, mindfulness training, and various breathing and relaxation techniques (for a review, see Brugués 2011b). As medications, beta-adrenergic receptor blockers (such as propanolol) and benzodiazepines are potentially helpful. Both drugs act on preventing dysfunctional motor memory formation (Soeter and Kindt 2013).

As far as treatment of DS is concerned, we predict that psychological techniques such as prevention of dysfunctional reinvestment and cognitive interference will be helpful. The latter, for example, could be influenced by guiding attention from an internal (body-related) to an external (sound-related) focus as have been shown to be efficient in complex motor studies of normal and patient groups (Wulf 2007, for an overview). Furthermore, psychotherapeutic techniques reducing anxiety and perfectionism will probably improve the condition. Specific interventions are learning-based sensorimotor training (LBST) based on redefining spatial and temporal processing capacities in the sensory and motor cortices in order to restore task-specific skills (Byl and McKenzie 2002). Prolonged pedagogical retraining has been successfully applied in pianists suffering from loss of motor control (van Vugt et al. 2014). Useful medications include selective serotonin reuptake inhibitors (SSRIs; e.g., escitalopram) to overcome reinvestment, overfocussing, and depression, anticholinergic drugs to reduce dysfunctional motor memories, and finally as a symptomatic treatment, local injections of botulinum toxin into the cramping muscles (Schuele et al. 2005). These medications are also applied in MD.

Finally, treatment for MD is mostly symptomatic and depends on the type of dystonia. Psychological interventions seem to be less effective as compared to DS. Various oral medications have been used and the anticholinergic drug trihexyphenidyl has proven to be the most effective agent (Jabusch et al. 2005). Occasionally, patients may benefit from baclofen, or antiepileptic drugs such as phenytoin, primidon, or rivotril. Chemical denervation using botulinum toxin has been used for many forms of MD with considerable success. Botulinum toxin blocks the transmission of nerve impulses to the muscle and weakens the overactive muscles involved. Results in musician's cramp depend on the dystonic pattern, on the injection technique, and on the precise localization of the dystonic muscles. In our series, injections of botulinum toxin were applied in 71 musicians suffering from hand dystonia. Fifty-seven percent of patients reported long-term improvement (Schuele et al. 2005). A new promising therapy is bihemispheric transcranial direct current stimulation during execution of functional movements at the instrument. In a double-blind randomized prospective trial, we could demonstrate that stimulation with inhibition of the dysfunctional network over the "dystonic" motor cortex, and activation of the "healthy" network over the contralateral motor cortex improved performance significantly (Furuya et al. 2014).

Preventing MD is important, since successful treatment is still a challenge. With the refined heuristic model outlined in this article, assuming a progression of increasing motor disturbances from fatigue, pain, anxiety to dysfunctional motor memories, and finally to MD with structural memory consolidation and brain adaptations, we now have the theoretical means at hand to intervene at an early stage. From the first lesson on, music educators should strive to create a friendly, supportive atmosphere, introduce reasonable practice schedules, teach economic techniques, prevent overuse and pain by including mental practice, and vary movement patterns. Students should be encouraged to maintain motivation by avoidance of mechanical repetitions and frustration. They should be taught to adopt healthy living habits, including warm-ups and cool-down exercises, regular physical exercise, sufficient breaks, and sleep as the cornerstones of healthy musical practice.

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Chapter 12
Motor Control and the Injured and Healthy Artist

Roger M. Hobden and Samuel Tétreault

12.1 The Origin of Art

The origin of art is probably related to the origin of symbolic thought (Lorblanchet 2007). The human being, like other animals, is able to partly modify his environment and the objects contained therein. By modifying objects, human beings are able to increase the information contained in those objects (Schneider 2006; Koch 2014). These objects acquire information that they would have never been able to acquire by themselves by being exposed to the forces in the environment. Modified objects become tools that can be used by their creator and by other humans. The information contained within these objects is thus also transferred in part to other humans. Human beings can also create abstract objects, like words and symbols, which also can be used to transfer information. Some of these words and symbols can be used to describe the laws of nature, and thus there is a relation between art and science through the action of the creative mind.

Art is present in all aspects of life. Virtually all man-made objects that we interact with during normal life have a specific artistic stamp—the bed we sleep in, the shower we use, the clothes we wear, the plate and glasses we use to eat breakfast, the vehicle we travel with, the building where we work, the novels we read, the music we listen to, etc. Every man-made object in a city, town, or village has an artistic

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component. An artless existence is simply unthinkable. Art is part and parcel of the human existence. There is no human being that is untouched by art.

12.1.1 Lessons from Artists

In the area of neurophysiology, much progress has occurred from working with injured patients. Correlating damaged areas of the body with loss of function has led to many insights about function. The disadvantage of this approach is that documenting a lesion will only tell you that a specific area of the nervous system plays an important role in a specific disease, but not clearly what that role might be. To use an image: if you remove a transistor from a radio, and hear a screeching sound when the radio is turned on again, this does not mean that you have removed "the screech inhibitor."

The advantage of doing clinical and experimental research on high-level performers like elite athletes, dancers, musicians, circus artists, singers, etc., is that these performers have become experts in the mastery of their chosen discipline. As soon as something is "not quite to right," they are able to describe pain and loss of function that interfere with performance. These verbal descriptions and practical demonstrations are usually very accurate and precise (valid and reliable). Since high-level performing artists function at the extreme limits of human capacity, they can be a unique and useful source of information for the clinician and the researcher who wants to understand how the human body can work at an optimum level. We will recall that Nikolai Bernstein not only studied skilled workers but also elite pianists, for instance, documenting with kymocyclography that keyboard musicians could play hundreds of notes per minute (Kursell 2006).

The interest in the injuries of artists has a long history. The first textbook that mentions injuries in musicians is Bernardino Ramazzini's 1713 treatise, *Diseases of Tradesmen* (Ramazzini 1933). With the advent of the pianoforte in the nineteenth century, composers started taking advantage of the properties of this new instrument to create musical pieces that required increased speed, power, and sound intensity. With increasing performance requirements came increasing injury rates, and a few physicians started to develop an expertise in the treatment of these ailments (Poore 1887). Some of these injuries would now be recognized as tendinopathies, and others, known as musician's cramp, now fall under the heading of focal dystonias. Different medical approaches were devised to address these various ailments and obstacles to enhanced performance. For example, it was well acknowledged by piano teachers and students that the fourth finger had less mobility and power than the others and, eventually, physicians invented an "ingenious" solution to this problem: tenotomy (a surgical procedure) of the secondary tendons of the ring finger. A few surgeons specialized in this technique and traveled by invitation to practice their art on those who wished. The long-term results were less than convincing, however, and this practice was eventually abandoned (Sataloff et al. 2010). The famous Romantic piano composer, Robert Schumann, developed a hand injury that prevented him eventually from practicing his instrument. Current research indicates that this condition, affecting his third finger, may have been a focal dystonia (Garcia de Yebenes 1995). Indeed, in the early 1830s, Schumann created the Toccata in C Major Op. 7, an extremely difficult piece that can nonetheless be entirely played without the use of the third finger of the right hand (Alltenmüller et al. 2005).

The rapprochement between artists and health professionals has led to interesting discoveries. For instance, the technique of indirect laryngoscopy was invented by a professional opera singer, Manuel Garcia, who used a dental mirror to examine the vocal cords of his students. Garcia eventually presented his findings at the Royal Society of Medicine in 1855 (Sataloff et al. 2010). In the second half of the twentieth century, there was a major increase of scientific activities in relation to health, disease, and performance of the professional artist. There are presently annual conferences devoted to arts medicine in North America, Europe, and Asia. Some cover all of the performing arts, and others are more focused, for example, on the injuries of musicians or dancers. Scientific journals dedicated to health and disease in music, voice, and dance have been in existence for over a quarter of a century. Indeed, the effect of music on the brain is an area of research in neurology that has increased by many orders of magnitude since the early 90s.

The visual arts field also has not been left out, as more researchers are exploring the links between visual perception and artistic creation in the areas of painting and other visual arts (Conway and Livingstone 2007; Pinna 2011).

12.2 How Artists Learn and Train Depends on the Type of Discipline Considered

Let us take the example of dance. In dance, students will acquire very specific skills in classroom situations. For instance, ballet students will typically start training when they are 8 years old or even earlier. A teacher will demonstrate how to perform ballet movements correctly and the student will attempt to reproduce these movements, while the ballet teacher corrects the student until the proper movement has been achieved. In the case of ballet, the quality of movement is of the utmost importance. It is not simply a question of standing still with the feet turned out and of bending the knees. This action must be done in a very fluid and controlled way that appears effortless and flawless. The dance student must learn to minimize jerkiness by the fine control of the equilibrium of the posture of the body and the smooth activation of the muscles. The student first learns to do this on both legs, and then on one leg (the supporting leg), during which the other leg (the gesture leg) will describe different patterns in space. These patterns have different names and form part of the ballet vocabulary. There are a few variations in terminology, depending on which ballet method is used (Vaganova, Cecchetti, Bournonville, etc.), but in essence the similarities are greater than the differences. Learning in a ballet class depends a lot on visual cues and the ubiquitous presence of the mirror, which helps the student to self-correct the attempted movements.

The comparison of the ballet dancer's movement with those of others in the class can be stressful. Because of the values of perfectionism that are part and parcel of ballet, the student will always perceive herself as imperfect: too tall, too short, too fat, too slow, etc. One of the challenges of a good dance teacher is to convince the student that she must strive to be the best of what she is and not a failed copy of which she is not.

Eating disorders are commonly associated with the word "ballet," even though research has failed to demonstrate that anorexia and bulimia are more prevalent in ballet schools than in the general population. The scientific consensus at this time is that eating disorders are influenced by genetic and epigenetic factors, and family dynamics, but are triggered by specific psychosocial events and interactions (Treasure et al. 2010). An example of trigger would be a boyfriend or a dance teacher telling the student that it would be desirable for her to lose weight. One of the central aspects of certain eating disorders is that the individual has a distorted visual image of herself. This distortion is in fact an enhanced visual perception of the body that is associated with the notion of being overweight (Keizer et al. 2013). Any minute bulge of the skin will be detected with the eyesight of an eagle. The action–perception issues associated with this medical condition have recently started to attract the attention of researchers (Guardia et al. 2010).

One of the challenges of teaching ballet is that even though the ballet teacher demonstrates exactly the same sequence of movements to a dozen different pupils, each of these students will perceive what has been shown and explained differently. This perception will be based on the psychological and physical properties of the student (Gibson 1987). Thus, a sequence of movements will be seen as doable, partially doable, or not doable. This will depend on the state of the components of fitness of the student: coordination, flexibility, strength, endurance, power, etc., but also on the genetic potential of the student, similar to that of any other individual, to acquire the required performance level (Bouchard 2012).

One aspect, which differentiates ballet from sports training, is that there is no individualization of the training program. No block of time is set aside in the weekly schedule so that the student can work privately to improve her own specific motor skills. The dance student is never assessed individually to identify her training needs. Corrections are usually given "on the fly" within the framework of the dance class.

12.2.1 The Challenges of Effortless Appearance

Another aspect that differentiates dance from most sports is that the motor actions need to appear effortless. Let us take, for example, a "grand rond de jambe en l'air." The dancer starts the movement standing on one leg, with the other leg extended in front of her, parallel to the ground. Keeping the knee straight, the dancer will then gradually bring the gesture leg outwards towards abduction, and then bring the leg backwards, always staying in the same horizontal plane. At the beginning of the movement, the sole of the foot is facing the ground, and, at the end, it is facing the ceiling. What happens is that, as the leg travels from forward to backwards, the leg rotates so that the load is transferred, apparently without any effort, from one group of muscles to another, along the upper arc that is part of the cylinder of continuous muscles that extend from the thigh to the ankle. Naturally, all the muscle groups must be co-activated to maintain the shape of the leg, even though the greatest muscle activation will be provided by a band of motor units that are supporting the mass of the leg at any given time.

The appearance of effortlessness must also be maintained during ballistic movements. As the dancer performs a "grand battement devant," the leg must be shot high up in the air as fast as possible, yet the rest of the body must appear completely immobile. Rapid movements are more challenging because they require more kinetic energy. Kinetic energy is related to the mass and the square of the speed of an object. So if the leg is travelling at a speed of three units, the mass will be multiplied by nine, whereas if the leg travels at a speed of ten units, the mass will be multiplied by 100, which is an order of magnitude higher than a movement three times as slow. The body of the dancer must not only be able to generate such high kinetic energy but must also be able to control, as the movement is taking place, the exact trajectory of the leg according to the demands of the piece.

Naturally, the dancer must be able to simultaneously mobilize all necessary forms of energy to stabilize the rest of the body and give this appearance of perfect immobility of the trunk and the standing leg. All dance students have different characteristics (power, flexibility, endurance, etc.), and so the movement solutions chosen by the dancer must be "good enough" to accomplish the task according to the demands of the teacher, and not necessarily "optimal." As the student learns to handle movement of all her body parts as an integrated whole, less energy will be wasted to stabilize limb trajectory and body shape, and more attention can be focused on decomposing a global movement into the smaller details that make the dance piece more interesting for the spectator, including the possibility that the movement is voluntarily jerky, if wished for by the choreographer.

12.3 Differences and Similarities Between Artists and the General Population

The professional artist needs to be performing at the highest skill level. His employability depends essentially on this characteristic. Artists have to be different from the rest of the population. The saying that "it's the little differences that make the big difference" applies especially well to the arts world. The artist can be seen as an ideal model of what can be accomplished by the human body with specialized training. Motor coordination will develop slowly based on exercise and experimenting with the task at hand. At the early stages of training, the artist will be overwhelmed with the excessive number of degrees of freedom related to the task: playing this note versus that note, landing on this space and not another, putting the hand here instead of there to catch the ball, etc. Sensory feedback given by the outcome of a determined movement will permit self-corrections and stabilization of the intended task. Overcoming peripheral indeterminacy by coordination of movement will lead to relative stability of goal-directed performance, accompanied by a sense of self-confidence (Bernstein 1967; Reppa et al. 2012).

When the artist has achieved mastery of his given discipline, the motor impulses used to control movement will have become more efficient and will be used to guide the passive elements (bone, water, fat, cells, etc.) of the limbs and digits in the direction of the intended goal. The inertial properties, reaction forces, and interaction torques of these passive elements then cease to be a problem, and in fact become part of the solution of the required movement. All this is accomplished by online constant afferent feedback from the mechanoreceptors (Bernstein 1967; Silva 2012). The information that arises from the periphery is also transmitted through the body by mechanical waves that travel at the speed of sound through the various tissues of the organs. These waves travel much faster than that of neural transmission. To what extent this mechanical information can be utilized by the central nervous system (CNS) is as yet unknown. Certainly, most of the cells of the human body, including neurons, are equipped with primary cilia (Anderson et al. 2008). Many of these primary cilia have a role in mechanical perception at the cellular level (Tobin and Beales 2009). The existence of such primary cilia may also explain in part the favorable effects of strength and aerobic training on health and disease (Trilk and Phillips 2014).

12.4 Circus Disciplines

In contrast to dance, voice, and music, up until now, the circus disciplines have not attracted a lot of attention on the part of health and fundamental researchers, and the existing studies are mostly of an epidemiological nature (Shrier et al. 2009; Wanke and Hamilton 2012). This may be in part due to the fact that many circus injuries are also commonly found in various sport disciplines, and thus the transfer of basic and clinical knowledge can be made more readily.

Still, the unique blending of motor and psychological skills with the goal of activating an artistic effect on the audience adds a new layer of complexity to the accomplishment of the circus movements. Contrary to his athletic counterpart, the circus artist cannot afford to be in a psychological cocoon, oblivious to the reactions of the spectators. Quite the opposite, the successful circus artist must be able to reach out and connect with each person in the audience.

In this section, we will review the main circus disciplines and the motor control issues that arise within each of them. Circus disciplines can be classified into five main families: aerial disciplines, equilibristic disciplines, acrobatic disciplines, juggling and object manipulation, and clowning disciplines.

Fig. 12.1 Aerial hoop. (Photo: Lionel Montagnier, artist: Alexandra Royer in Sequence 8 by Les 7 Doigts de la Main)

12.4.1 Aerial Disciplines

Aerial disciplines require specific abilities and motor skills. They require a predominance of upper body work and pulling against gravity. The construction of these movements could be addressed by motor control levels A and B, as proposed by N.A. Bernstein (Bernstein et al. 1996). Examples include aerial hoop (Fig. 12.1), static trapeze, flying trapeze, swinging trapeze, and vertical rope. A high level of proprioception and spatial orientation is required. These disciplines present a significant level of danger and risk, and psychological issues including the fear of falling.

Fig. 12.2 Hand balancing. (Photo: Louis Ducharme; artist: Samuel Tétreault)

12.4.2 Equilibristic Disciplines

Equilibristic disciplines require, in contrast, the ability to push against gravity. Constant postural corrections are required on the part of the stabilizing muscles. These might correspond to Bernstein’s levels B and C1. Examples include hand balancing (Fig. 12.2), tightwire, high wire, slack rope, rola bola, and hand to hand. The perfect balance that is required is not immobility but rather a dynamic balance (active correction of posture and the ability to perform a task while maintaining a stable position). Psychologically, this type of discipline requires from the artist the ability to sustain concentration at every instant.

Fig. 12.3 Chinese hoop diving. (Photo: Valérie Remise; artist: William Underwood in TRACES by Les 7 Doigts de la Main)

12.4.3 Acrobatic Disciplines

Acrobatic disciplines require explosive movements (fast-twitch fibers are more in demand than slow-twitch fibers) and are characterized by a predominance of lower body work. These might be assigned to Bernstein's levels C2 and D. Examples of these disciplines include Chinese hoop diving (Fig. 12.3), Korean board, Russian bar, and Chinese pole. Spatial orientation and proprioception are very important, and there is a high level of risk, so fear of injury needs to be addressed.

12.4.4 Juggling and Object Manipulation

Juggling and object manipulation requires excellent hand–eye coordination skills. These skills would be an example of control level D according to Bernstein. There

Fig. 12.4 Cigar box juggling. (Photo: Sylvie-Ann Paré; artist: Eric Bates in Sequence 8 by Les 7 Doigts de la Main)

is a high demand on upper limb dexterity. Examples of these disciplines include cigar box juggling (Fig. 12.4), club juggling, and diabolo. Juggling can also be done with partners. A large amount of practice is necessary to accomplish juggling acts. Jugglers tend to have mathematical and musical types of mind (patterns, precision, timing; Polster 2003). Indeed, the first recorded mathematician-juggler is believed to have been Abu Sahl al-Quhi, a mathematician living in Baghdad in the tenth century (Buhler et al. 1994).

12.4.5 Clowning Disciplines

Clowning disciplines find their origins in the grotesque characters of ancient cultures and in the early forms of theatre such as commedia dell'arte. Both classical and contemporary circus clowns very often combine their specific artistic performance with other circus disciplines and therefore there are no specific motor control skills or body types required.

12.5 Training in the Circus Arts

Learning is more a question of differentiation rather than a question of enrichment (Gibson and Gibson 1955). There is no reason to believe that artists use different strategies to learn than other human beings. Based on experience, coaches are adept in identifying those individuals with enhanced motor-perceptual skills that are "trainable" within a specific discipline. The existence of individuals with distinct or exceptional qualities is well-recognized, and even if there are many competitive descriptive frameworks that address this (see, for example, Gardner 1983), satisfying explanations from a neurophysiological, biomechanical, and biochemical point of view are still lacking. Naturally, some disciplines, like contortion, require a genetic and epigenetic makeup that is truly exceptional. Identifying to what extent these super-flexible individuals are similar or different to the majority could enhance our understanding of the interaction between gene expression and training with regard to flexibility in the general population, and could lead to insights about injury prevention in sports and in the workplace.

While the artist trains, he or she compares qualitative differences (Verri and Poggio 1989) such as bigger than, farther than, faster than, etc. For instance, when a juggler tries to catch a ball that is thrown in the air, the optical flow to his eye is compared with previous experiences of watching movable objects transiting in every manner possible. The immediate perception he has of his own body will tell him instantly if he has even the remotest possibility of catching that ball. This is based not only on the relative speed and direction that the ball is traveling but also on his training and how his body perceives the state of health of his limbs (injury in the shoulder, etc.). Eventually, these tasks will become well-learned habits that the circus artist can count on to be accomplished nearly automatically, whether the artist is immobile, or traveling along a well-known trajectory. When confronted with the new situation, more areas of the brain will be solicited to be able to compare known experiences versus the necessity of inventing new tasks. As the circus student becomes a professional, the possibilities afforded by the environment and its objects will be modified because the artist's capabilities have been modified. This training process entails an updating of the brain's active operative representation (modeling) of the external world (Bernstein 1967). Whether this process is qualitative or quantitative is presently the object of much debate (see, for example, Ostry and Feldman 2003). When exposed to the same array of objects (ropes, balls, ladders, etc.), a nonartist will perceive different affordances from a circus artist.

General principles of circus training include physical preparation in strength and flexibility, basic acrobatic classes and biomechanics (floor and trampoline), decomposition of complex movements into simpler ones, progression using educative movements, use of safety lines and crash mats, repetition until patterns and sequences become integrated, consistency, and endurance.

Psychological issues are also very important, as the artist must learn to plan near into the future the complex movements related to his or her discipline. "Death defying" acts have always been part and parcel of the traditional circus trademark

Fig. 12.5 Swinging trapeze. (Photo: Yann Boyenval; artist: Danica Plamondon in PSY by Les 7 Doigts de la Main)

while in the contemporary circus arts the focus is less on sensationalism and more on the artistic research and individual expression. Commonly, especially during the first half of the twentieth century, many aerial artists boasted about their capacity to work without a safety net. Current research is now looking into these and other psychological skills (Shrier and Halle 2011). Learning to master the fear of death is intimately tied with the human capacity to plan ahead (Bernstein 1967).

12.5.1 Training in Aerial Disciplines

Morphological qualities include a smaller and lighter body type, good flexibility, and good lines, and the proportion of slow-twitch versus fast-twitch fibers depends on the type of aerial discipline. Psychological skills include being comfortable with heights, courage, a high tolerance to pain (for instance, caused by the friction of the rope or twine), the capacity to visualize complex sequences of movements and thereby their mechanics, risk management (security), and rigging knowledge. Action and perceptual skills include hanging and suspension postures (from hands, knees, feet, heels, etc.), spatial orientation without contact with the ground, swinging on a trapeze, for example, (Fig. 12.5) and tempo movements, feeling the "dead point" (moment of weightlessness), and flipping and twisting movements.

12.5.2 Training in Equilibristic Disciplines

Morphological qualities are believed to require a preponderance of slow-twitch muscle fibers, and the ideal body type will depend on the discipline. For example, good shoulder and elbow flexibility is required for hand balancing or hand-to-hand actions (Fig. 12.6). Psychological skills include attention to details, being meticulous, having the capacity to concentrate over long periods of time, patience and perseverance, calmness, understanding the biomechanics of balance, and the capacity to visualize shapes and postures in terms of balance structures. Motor control skills include consciousness of the base (anchor) points and extremities, consciousness of body alignment, posture and muscle tone, proprioception accuracy, standing and balancing postures using different body parts as anchors (hands, feet, head, knees, etc.), dynamic balance (active correction of posture), isolation of movement within a fixed shape, and steady movement.

12.5.3 Training in Acrobatic Disciplines

Morphological qualities include a shorter, muscular body type with fast-twitch fiber predominance. Psychological skills include a courageous and daredevil spirit, the capacity to visualize complex sequences of movement and their biomechanics, greater attention to the whole and less detail-oriented, and risk management (security). Motor control skills include jumping and landing from and to different surfaces, spatial orientation and fast movement combinations, quick trajectory and velocity corrections, initiating and stopping rotation, explosive movements, and flipping and twisting movements such as those seen in Fig. 12.7 on the Korean board.

12.5.4 Training in Juggling and Object Manipulation

No specific morphological qualities are required for this discipline (body type, flexibility, muscle type). Psychological skills include patience, perseverance to the point of obsessiveness, a mathematical/musical mind type, and the capacity to visualize complex patterns of intricate upper limb movement (Beek and Turvey 1992). Of note, there is a predominance of male jugglers. Motor control skills include a high level of hand–eye coordination and dexterity; relation with objects in space and time; throwing, catching, and manipulating objects of different shapes and weights using different body parts; and consistency in highly repetitive movements.

Fig. 12.6 Hand to hand. (Photo: ODC Photo; artists: Sebastien Soldevila and Émilie Bonnavaud in La Vie by Les 7 Doigts de la Main)

Fig. 12.7 Korean board. (Photo: Sylvie-Ann Paré; artists: Maxim Laurin and Ugo Dario in Sequence 8 by Les 7 Doigts de la Main)

12.5.5 Training in the Clowning Discipline

What mostly defines the clown artists is found on a psychological level: A great sense of humor and self-derision is an essential personality trait to any good clown. Clowns often provoke laughter by exposing their own flaws and vulnerabilities, appearing

Fig. 12.8 Russian bar. (Photo: Lionel Montagnier; artists: Eric Bates, Tristan Nielsen and Alexandra Royer in Sequence 8 by Les 7 Doigts de la Main)

clumsy or failing in what they attempt. They are a mirror for what we usually do not want to see in ourselves or try to hide from others and therefore clowns need to have an acute sense of observation for their own behaviors and those of others. It is not rare to see some of the funniest clowns on stage being rather moody or even depressed off stage.

12.5.6 Partnering and Group Disciplines

In terms of morphological quality, a "flyer" (the acrobat who is being carried, thrown, and caught) will usually have a shorter and lighter body type, while the "base" or "catcher" has a taller and stronger body type (Fig. 12.8). Psychological skills include the capacity and interest for teamwork, capacity to put one's trust in someone else and to be trustworthy, verbal and nonverbal communication skills, and the capacity to visualize movement sequences involving the simultaneous movement of others. Motor control skills include the capacity of throwing and catching people using different body parts (hands, feet, shoulders, back), giving and taking weight and counterweight, letting go of the automatic reflex of balancing yourself (flyer) and letting the "base" balance you, developing synergistic movement with someone (synchronized "tempo") to combine pushing actions, high adaptability, and requiring quick adjustments (the other person is a variable you cannot control).

12.5.7 *The Live Performance Has Specific Issues of Its Own*

The artist has to deal with psychological factors like the stress of performing in front of the public, the fear of failing or falling, mishaps, and last-minute changes. Outside factors include the conditions of the show: lighting, musical cues, different stage sizes, floor types and ceiling heights, etc. This is where experience and training allow the artist to transcend the acrobatic elements and motor skills and to reach a sense of freedom in his artistic expression.

12.6 Basic Considerations About Motor Control and Injury

In the past 150 years, much progress has been made in the area of motor control. In particular, the area of synergies and their origin have been the object of many publications and discussions, including the proper definition of the word itself (Latash 2012; Turvey 2007). The creation of a neologism that captures exactly "what is meant" might contribute usefully to the standardization of motor control terminology. For the moment, let us consider that there may be three kinds of synergies: inorganic synergies like those of the lattice that unites the molecules of a rock, organic synergies characterizing the structure and metabolism of living things, and action synergies, which are the goal-directed movements of living things and their interaction with the environment. The last two categories may be corollaries of each other. Action synergies are driven by the demands of the organism and its interactions with the environment. The similarities between the goals of a unicellular organism and those of a complex animal like a mammal are obvious. All living organisms need to consume molecules to generate energy, need to gain access to sources of energy, need to maintain their structural integrity, and need to reproduce themselves (Pross 2012). Indeed, it may even be hard to draw the line between metabolism and structure. For instance, the cytoplasm also contributes to the mass, shape, and structure of the cell, through both osmotic and hydrostatic pressure (Myers et al. 2007). Another consideration is that all living organisms are constrained by physical factors like pressure (the pressure of water or of the atmosphere), temperature (molecular agitation and the threat of loss of information), electromagnetic waves, mechanical waves, and gravity.

What the CNS seems to learn are correlations between changes of body sensation and visualization of body movement, so that a given dynamic image of the change of the body configuration is associated with a change of body perception. The unit of control of the CNS is probably not the muscle, but rather the motor unit. Muscles do not seem to exist as far as the controller is concerned. The controller would seem to recruit, through threshold modification, the number and location of the motor units necessary to accomplish the required task. The elementary component of movement confined in the organism is most probably the motor unit and its feedback loop (motor loop). It is through this motor loop that the animal probably perceives part of the environment, and notably deformation of matter, which is interpreted as "force." It is thought that similar loops are related to the existence of consciousness in humans and animals (for a review, see Dehaene 2014; see also Tononi 2008; Koch and Tsuchiya 2012; Koch 2014).

Injury is a structural breakdown of the normal components of the organism. This breakdown can affect the metabolism, the external or internal mechanical structure, the communication system, and any or all of the above. Inflammation, a common component of injury, will create localized changes in pressure, volume, and temperature. These localized inflammatory changes will disrupt the organic synergies of the animal or human. For instance, thermodynamic measurements indicate that native proteins are only marginally stable under physiological conditions (Voet et al. 2012). These localized inflammatory changes may also disrupt action synergies.

Injury can also be accompanied by structural hypermobility, hypomobility, or both. The coexistence of both is not at all rare: For instance, in the case of a severe injury to the knee, the joint may have not only an increased mobility because of a partial ligamentous tear but also a decreased range of motion because of a torn meniscus.

The existence of organic synergies is not trivial. The proper way that each mechanical part of a living animal will interact is already included in the way that the animal is constructed. This greatly simplifies motor control, as movements that are forbidden and movements that are permitted are already built into the biomechanical structure of the animal. For instance, the knee is constrained to mostly perform flexion and extension, and the healthy artist does not have to think about producing "impossible" movements. Indeed, if an injury affects the normal length or tensile properties of the ligaments, fasciae, etc. of the knee, the artist, because of his enhanced training, will become very worried because he can instantly tell that "something" is not quite right, and that he cannot count on his knee or leg to perform flawlessly. Quite often, the instability can be very subtle, and there is a real risk that the injury will be dismissed out of hand by an examiner who is not used to dealing with dancers and circus artists, for instance.

This does not contradict the fact that action synergies are probably controlled only at the most distal part of the motor arc (or motor circle), the muscle activation threshold of the muscles of the body (Feldman 2009). According to Bernstein, "the co-ordination reflex is not an arc but a closed circle with functional synapses at both ends of the arcs." Recent studies have supported this point of view (Mattos et al. 2013).

Naturally, the bones that meet at the knee joint have, in reality, six degrees of freedom, like every other bone of the body, if viewed on a sufficiently small scale. The debate between those who see the helical axes of the knee as more ligament-controlled or more muscle-controlled (Blankevoort et al. 1991; Zatsiosrky 1998) is probably artificial, as the tensegrity (Ingber 2008; Swanson 2013) model, based on the concept of pre-stress within biological entities (cells, organs, etc.), apparently reconciles these seemingly opposing viewpoints.

12.7 Injuries in the Artistic Disciplines

The causes of injury in the artistic disciplines are very similar to those in sports. Injury is usually multicausal. Let us take yet again the example of dance. It is useful to parse the causes of injury into intrinsic and extrinsic risk factors (Emery 2003; Liederbach 2010; Ojofeitimi and Bronner 2011).

Intrinsic factors of injuries can be subdivided into modifiable and nonmodifiable factors. Examples of nonmodifiable factors include sex, age, genetic, epigenetics training history, and previous injury. Modifiable factors include fitness level, flexibility, strength, stability, proprioception, nutrition, total workload, and psychosocial factors.

Extrinsic risk factors can also be subdivided into nonmodifiable and modifiable factors. Some of these nonmodifiable factors would include type of dance, dance level, and unpredictable accidents. Modifiable factors include the disregard of sound training principles, predictable accidents, temperature, surface, and choreography. The modifiable character of this last factor depends naturally on the goodwill of the choreographer. Indeed, in more than a few instances, one would be excused in believing that the definition of a choreographer is “someone who creates new ways of getting injured.”

12.7.1 Injuries and Their Impact on Motor Control of an Artist

Let us take, for example, the case of an artist with an ankle sprain (Gehring et al. 2013a, b; Hubbard-Turner et al. 2013; van der Wees et al. 2006). When a person sprains his ankle, common clinical findings include the following: (1) inflammation and swelling, (2) hypermobility of the ligaments, (3) loss of mobility of the ankle joint, (4) pain, (5) loss of muscle strength, and (6) loss of proprioception. In fact, most of the injuries of the various joints of the body will generate the same clinical findings. These findings can be used as outcome variables to help therapists determine when the injury has resolved. In the case of an ankle sprain, the sprain will be healed when there is no more inflammation; the ligaments have healed with a length and stiffness that is as close as possible as the pre-injury state; the range of motion of the ankle has been restored; the pain is gone; the strength, speed, and endurance of the muscles are back to normal; and proprioception has been restored.

Let us consider the effect of these six variables on normal motor control.

1. Inflammation will cause abnormal neural messages to be sent to the nervous system through two main types of stimuli: chemical stimuli, caused by specialized molecule, and physical stimuli, caused by abnormal increases of volume and pressure on the nerve endings (Pongratz and Straub 2013). This array of abnormal stimuli caused by inflammation will serve as a negative feedback loop to inhibit muscle activity.

2. Hypermobility between two bones will have an inhibiting effect on muscle action through a different pathway than the previous one. Recall that the relative length of muscles is regulated through muscle spindles and their relative strength through the Golgi tendon organ (Kistemaker et al. 2013). The laws of mechanics tell us that the array of mechanoreceptors measure not only the "action" (force) of the muscles involved but also the "reaction" (including the inertial properties (heaviness) of the bones and other tissues) on which the muscles act. Recent research suggests that perceived heaviness is related to mass, volume, and symmetry of the perceived object (Turvey et al. 1999).

   When excessive (abnormal) mobility is perceived between two bones, the nervous system will send instructions to the muscles to protect the body from this excessive mobility. Thus, muscles will not be allowed to stretch to their maximal length. The same muscles will also not be allowed to exert their maximal force. Based on his clinical experience, one of the authors has found that trained artists (circus, dance, music) are able to sense these effects in great detail and can give very useful feedback to the health professionals that treat them.

   These changes may be triggered because the body perceives that the combined inertial properties of the bones and other attached structures have changed. Naturally, at the cellular level, the array of Golgi tendon organs involved probably does not measure "force," but rather sends out signals in proportion to the deformation of their physical and chemical structure, signals that are interpreted qualitatively ("heavier than," "lighter than," etc.).

   How simultaneous loss of strength and loss of maximal muscle length are mediated can be predicted and explained by the equilibrium point theory of motor control (Feldman 2008). The equilibrium point theory (or threshold control theory) seems to be the only theory that is presently capable of explaining why the same muscle can be measured as being weak at one end of the range and spastic at the opposite end of the range, in stroke patients (Levin et al. 2000).
3. Hypomobility is often also accompanied by a loss of strength and a loss of maximal muscle length. If the muscle is directly damaged, the cause of both the loss of mobility and of strength is readily apparent. However, there are common injuries that are accompanied by a misalignment between the bones in the joint space. Surprisingly, this can coexist with the fact that the joint is not necessarily painful, yet the muscles seem to be "switched off" or "toned down." In these cases, restoration of anatomical congruence by the means of manual treatments is accompanied by an instantaneous return of maximal muscle length and strength (Cibulka et al 1986; Suter et al. 1999). Research is ongoing as to the local and regional effects of these treatments (Dunning and Rushton 2009). Again, the equilibrium point theory brings a neurophysiological explanation to this common response, which is observed by health professionals on a daily basis in the clinical setting. Because of their heightened proprioceptive awareness, artists are able to guide the therapist in a step-by-step manner during the treatment session to restore proper mobility of each joint as required for optimal performance.
4. Pain in the tendon or in the muscle (due to a muscle tear, for instance), despite the pain component being a "subjective" sensation created by either increased focal

pressure or tissue damage (Moayedi and Davis 2013), will directly generate a loss of strength and resistance to lengthening through "nociceptive" stimuli (antalgic paresis).

5. Loss of strength and endurance can be caused either directly through damage of the muscles or tendons or indirectly through damage of the nerves, or through inhibition caused by inflammation, hypermobility, or hypomobility.
6. Loss of proprioception can be caused either directly through damage of the nerve endings (mechanoreceptors) or indirectly, because of inflammation, hypermobility, or hypomobility.

   All the joints of the body generate the same reactions to tissue damage. These phenomena are scale invariant, whether the damage involves a joint of a finger, the knee joint, or the intervertebral segments. In the case of a microscopic tear of the intervertebral disc, even without any bulging or change of shape of the disc, inflammation and disruption of the nerve endings within the annulus fibrosis will affect muscle function. Certain muscles will lose their maximal strength and maximal length, and this will disrupt the overall synergies of the trunk muscles.

12.7.2 The Special Properties of the Spine

If the joints of the locomotor system are all the same, as they are indeed histologically, being composed of bone, cartilage, synovial fluid, joint capsules, ligaments, enthesis (Benjamin et al. 2004), tendons, muscle, nerves, and skin, why is the spine perceived to be somehow different?

Yet, the trunk is indeed different, for three main reasons. These reasons are physical, anatomical, and neurological.

1. Neurologically, the spine and trunk muscles are the oldest part of the locomotor system, from a phylogenetic point of view. Human consciousness does not have a clear image of the mobility of the vertebrae, compared to the consciousness that we have of our upper or lower limbs. With our eyes closed, it is easy for us to visualize the motion between the phalanxes of the finger, or the motion between the thigh and the leg. If we try to visualize the rotation of the vertebra L4 versus L5, we are incapable of doing so. When we turn the trunk to the right, we will only have a general idea of the motion that takes place between the vertebrae. Obviously, part of us knows which muscles to activate and how, but our consciousness does not have access to that information. When we injure a knee, for instance, it is possible for us to adopt a strategy to reduce nociception, such as deciding to walk with the knee extended to avoid painful flexion. When we injure the joint space between L4 and L5, however, there is no way we can have conscious access to muscle strategies that permit us to dissociate the movement of L4–L5 from that of the rest of the trunk.
2. From an anatomical point of view, all the trunk movements are multi-muscle movements that are united through synergies between agonists and antagonists

(Robert et al. 2008; Vora 2010). We would be tempted to say that the trunk muscles are enslaved to one another, in a similar way and for the same reasons as the muscles of the fingers (Zatsiorsky et al. 2000). When there is an injury between L4 and L5, all of the 20 or so muscles that attach to these vertebrae on each side of the body are affected by whatever is taking place at the joint space. Thus, all the muscle synergies of the trunk will be affected by this very localized injury at only one level. Some muscles will receive instructions telling them to activate less strongly and to not lengthen to the maximal length, but other muscles will receive the usual instructions they would get to accomplish the given task. This conflict between normal functioning muscles and abnormal ones will create, for instance, the so-called spasm that takes place because a muscle is extended beyond its minimized range, trying to follow its companions. The spasm caused by palpation is due to the same mechanism: The palpating finger lengthens the muscle beyond its permitted range, generating a painful reaction.

3. Physically, the trunk is where the center of gravity of the body is situated when the human being is standing. The gravity line passes through the trunk and the center of mass projects between the feet. As the body moves around in space, so does its center of mass (Roussouly and Pinheiro-Franco 2011). Each displacement in space will require activation of the trunk muscles and mobility of the intervertebral spaces, possibly triggering an increase of inflammation, increase of hypermobility, etc. It is not possible to physically isolate these vertebral joints in the same way that one can isolate an injured knee or ankle during locomotion. Every movement of the whole body requires necessarily a movement involving all of the vertebrae of the body.

So, for these neurological, anatomical, and physical reasons, spinal dysfunctions are much more debilitating than injuries of the upper and lower limbs. These are probably the main reasons why spinal injuries are intuitively perceived by patients and health professionals to be different from limb injuries, even if the basic histological structures and physiopathological mechanisms are similar.

Circus artists and dancers develop an exquisite sense of body awareness of their spinal movements. This enhanced spinal proprioception makes them ideal subjects to study the normal and abnormal function of the trunk, as they are able to pinpoint exactly the intervertebral segments that are not functioning correctly. In the situation where manual treatments are required, they are able to give immediate feedback as to the effectiveness of a given manipulation. Through the course of a half-hour- or an hour-long treatment, all the intervertebral segments that are hypomobile can have their proper motion restored. This is accompanied by a gradual and significant increase in mobility of the gross movements of the trunk (flexion, extension, rotation, etc.) throughout the treatment session. Naturally, if there is an underlying segmental hypermobility associated with deep muscle weakness, this will need to be treated by an appropriate series of exercises.

In addition, undiagnosed inflammation is a common finding that may lead to failure of treatment if not addressed correctly. The role of the nervous system at the level of the joint has been identified as a significant factor in the modulation of the inflammatory response (Schaible and Straub 2014). In particular, the intravertebral disc has attracted a lot of attention, and many recent publications demonstrate the ongoing interest in this area (Adams and Dolan 2012; Rajan et al. 2013; Ulrich et al. 2007).

The experience of one of the authors is that practically all dancers and circus artists affected by common spinal dysfunctions ("low back pain") are able to return to performance with no functional limitations whatsoever, even after being off work and in treatment for 1 or 2 years. Even taking into account the "well-worker effect," understanding the reasons for this may lead to a better understanding of how to treat spinal dysfunctions in the general population.

12.8 The Healthy and Injured Artist as an Object of Study

As was discussed initially, arts and science are related to each other like both sides of a piece of paper. In the same way, understanding injury and disease is another way of understanding health and performance. Both go hand in hand. Developing research projects to understand how high-level artists achieve the mastery of their art form and how injury or disease interferes with artistic performance has the potential to lead to better insights about how the human body works in general.

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Chapter 13
Adaptations to Neck/Shoulder Fatigue and Injuries

Julie N. Côté

13.1 Neck/Shoulder Musculoskeletal Disorders: A Considerable Societal Problem

In the past three decades, the incidence of musculoskeletal disorders (MSDs) has grown to affect a large portion of the population, accounting for considerable amounts of compensation claims, lost time, and health-care costs in most industrialized countries (Feuerstein et al. 2003). In many countries, MSDs consistently cause more work absenteeism or disability than any other group of diseases (Badley et al. 1994; Feeney et al. 1998; Leijon et al. 1998; Woolf et al. 2010), even though the proportion of the workforce working in sectors characterized by heavy physical work has steadily declined (Madeleine 2010). Although there can be various causes for MSDs, repetitive work has often been cited as one of the leading causes for reporting symptoms. For instance, it has been previously reported that 55 % of MSD attributed to repetitive movements were thought to be caused by work-related activities (Tjepkema 2003). Among the European workforce, it has been shown that the two highest exposures to physical risks are a painful/tiring position and repetitive movement (Fourth European Working Conditions Survey 2007). Indeed, these statistics show that the proportion of workers exposed to repetitive hand or arm movement for at least one-quarter of the working day has increased over the past 5 years, reaching 62 % of the working population. Further, 45 % of the population indicated experiencing painful, tiring positions for at least one-quarter of the working day. While many studies have focused on MSDs of the low-back or distal upper limb, MSDs affecting the neck and/or shoulder region have substantial socioeconomic consequences in

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many countries (Silverstein et al. 1998; Bongers 2001; Hamberg-van Reenen et al. 2007). Although distinctive risk factors have been associated with either neck or shoulder MSDs, most studies agree that complaints often affect the neck/shoulder area as a unit (Visser and van Dieen 2006), especially in the case of low-load, work-related symptoms, so that the etiology of neck/shoulder MSDs is thought to revolve around one common mechanism that is not yet fully understood (Andersen et al. 2003). Neck/shoulder MSDs have been linked to the development of chronic pain, dysfunction, and a high prevalence of secondary health problems (Nordlund and Ekberg 2004). Studies have suggested that neck/shoulder MSD can be caused by highly repetitive work, forceful exertions, highly prolonged static loads, static or extreme postures, and combinations of these factors (Larsson et al. 2007). One of the most important occupational risk factors for neck/shoulder pain is prolonged repetitive upper limb movement. A study showed that working with neck and/or body bent forward, arms above shoulders, precision work tasks and female gender were predictors of neck/shoulder MSDs (Wahlstedt et al. 2010). Despite the frequency, high cost, and range of initiatives implemented to prevent neck/shoulder MSDs, little is known about which interventions are the most effective, so that neck/shoulder MSDs remain a considerable problem (Buckle and Devereux 2002).

13.2 Towards a Model of Neck/Shoulder MSD Production

It is generally agreed that the mechanisms of MSDs are multifactorial, as suggested by the International Classification of Functioning (ICF) model of the World Health Organization (www.who.int/classifications/icf/), and few theoretical models succeed in conceptualizing the pathways by which injury can occur. With the goal of focusing more specifically on factors that can lead to the development of work-related neck/shoulder MSDs, we have developed a simple conceptual model (Fig. 13.1). In this model, personal factors combine with work-related risk factors to determine the level of exposure to damage of some selective neck/shoulder structures, which can result in injury if a balance between tissue damage and repair mechanisms is not met. Whereas force is a known MSD risk factor that can in itself have a direct effect on injury risk (Karsh 2006), in low-force tasks, the balance of personal and work-related factors is highly sensitive to the accumulation of damage caused by sustained efforts, which suggests a link between fatigue and the development of muscle injury.

13.3 Fatigue as a Precursor to MSD in the Injury Trajectory?

One of the most often studied risk factors for MSD, especially in association with repetitive work, is fatigue. Enoka and Stuart (1992) define fatigue as a decrease in functional capacity associated with an increase in the perceived difficulty in maintaining force production. In low-force tasks, fatigue is an ongoing process, which may not necessarily result in a decline in target submaximal force, but is typically

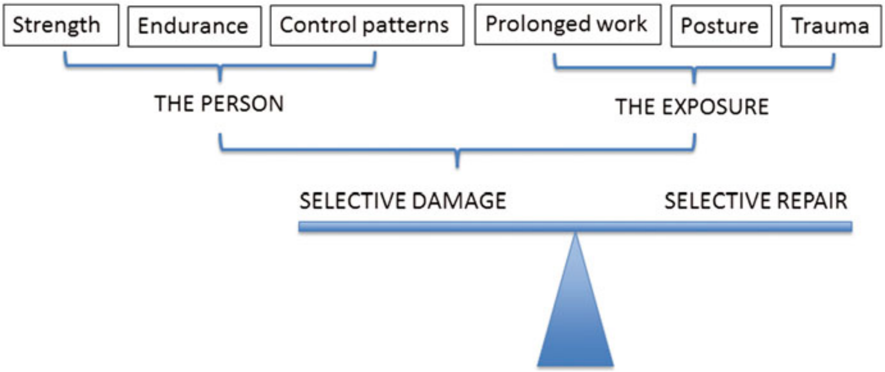

Fig. 13.1 General theoretical model of potential physical risk factors for neck/shoulder injury production. Injury to musculoskeletal structures can be caused by a combination of factors in the first row, affecting the person or his/her exposure to a risk of injury. Ultimately, injury production will depend on whether the balance between selective damage (caused by person- or exposure-related factors) and selective tissue repair processes can be maintained

manifested as an increase in perceived effort (Jones and Hunter 1983) and a reduction in the maximal force generating capacity of the neuromuscular system that occurs during sustained activity (Bigland-Ritchie et al. 1983; Vollestad 1997). Previous research shows increased amplitude of the electromyographic (EMG) signal (e.g., root mean square, RMS) and decreased mean power frequency (MPF) as fatigue develops during submaximal contractions (Vollestad 1997). Changes encumbered by the motor apparatus as fatigue develops may be attributable to impairment at any point in central or peripheral neuromuscular pathways involved in muscle contraction (Stokes et al. 1989). For instance, fatigue may be caused by changes at the central level, due to impaired motivation or failure of motoneuronal drive, or by peripheral changes, due to impairment at or beyond the motor nerve, including the neuromuscular junction and the contractile apparatus itself (Edwards 1983). When the task involves a submaximal contraction, an individual is able to increase the central motor command to counteract the reduction in force resulting from peripheral fatigue mechanisms (Maton and Gamet 1989), supporting the idea that fatigue is a mechanism that develops over time and that involves the coordinated action of many elements of the neuromuscular pathway.

Figure 13.2 shows a schematic representation of the temporal progression that could lead a worker exposed to a new work task to eventually develop MSD and associated disability. When first exposed to a new task, a worker or athlete would initially improve as a result of repetition and learning to attain a higher level of performance. If the worker continues to work beyond this optimal level and/or experiences insufficient recovery time, somewhat manageable symptoms such as fatigue and discomfort may lead to the development of less manageable and more debilitating and threatening ones such as delayed-onset muscle soreness (DOMS) and lesion-causing microtrauma, which can in turn cause permanent damage. Indeed, several

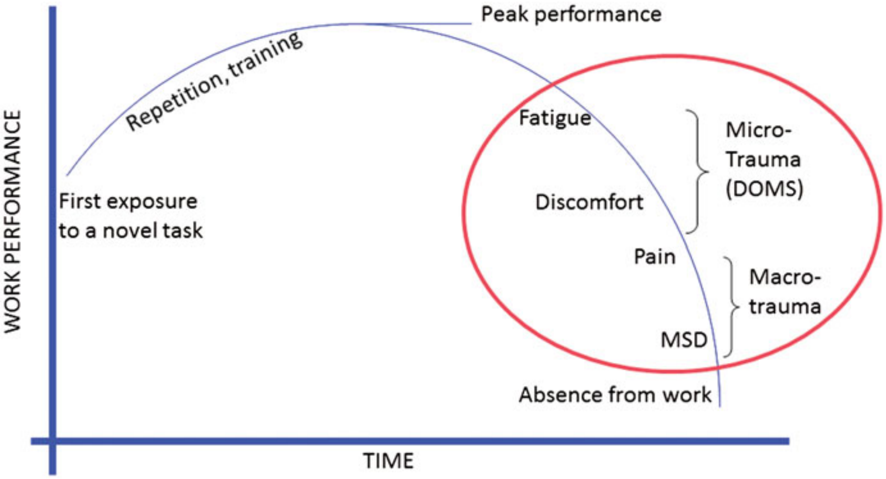

Fig. 13.2 Temporal sequence of events that can lead a worker to develop a musculoskeletal disorder and absence from work. The time scale can represent weeks to months to years

authors have suggested that muscle fatigue plays an important triggering role in neck/shoulder MSD (Rempel et al. 1992; Sundelin and Hagberg 1992; Hermans and Spaepen 1995; Takala 2002). The exact pathophysiological mechanisms by which fatigue can trigger pain and injury has been thought to involve the sensitization of nociceptors caused by a release of mediators from the free nerve endings (FRNs), which in turn may be due to peripheral mechanisms such as lowering of the firing threshold of the nociceptors (Madeleine 2010). However, the way in which sustained or recurrent fatigue, discomfort, and pain episodes may lead to chronic symptoms and impairment remains poorly understood. It is well known in the sports training world that a certain level of fatigue is necessary to trigger a training and tissue modeling effect, so that the difference between "effective" and "threatening" fatigue is a puzzle that has posed a challenge to many coaches and therapists. Moreover, what distinguishes the trajectory of one worker over that of another, impacting on the speed of this downward slope displayed in Fig. 13.2, remains in large part a mystery and likely depends on the balance between damage and repair mechanisms, which in itself may depend on many work- and nonwork-related factors.

13.4 Low-Force Efforts and MSD: The Cinderella Hypothesis

Even though it is conceivable that injury can be avoided with low-force efforts interspersed with sufficient rest, it is difficult to predict the exact work–rest regimen that can effectively achieve this goal. Even efforts as low as 10 % maximum effort have documented endurance time limits, in the order of 1 h (Fallentin et al. 1985). In such cases, the primary physiological mechanism leading to fatigue is largely unknown (McLean and Goudy 2004). It has been argued that since there is little blood flow occlusion at this low-force level (Parker et al. 1984), muscle fibers involved in this action should theoretically be capable of sustaining this force nearly indefinitely. However, evidence suggests that even such low-force activities, when sustained and/or repeated, may contribute to muscle injury (Winkel and Westgaard 1992; Kilbom 1994; van der Windt et al. 2000; Sluiter et al. 2001). To resolve this issue, over the past decades, a number of theories mention unfavorable motor control strategies as a risk factor in the etiology of MSD (van Dieen et al. 1993; Sjogaard et al. 1986; Mathiassen and Aminoff 1997), and recent prospective studies have provided evidence for the link between some motor control patterns and the development of MSDs (Veiersted 1994; Madeleine et al. 2003).

The most recognized hypothesis for neck/shoulder MSD associated with low-force efforts is the Cinderella hypothesis (Hagg 1991). This hypothesis points to the behavior of the low-threshold motor units (MUs) and their associated type 1 fibers as a central aspect of the mechanism of injury associated with sustained, low-intensity efforts (Visser and van Dieen 2006). Cinderella fibers are the type 1 (slow, fatigue-resistant) muscle fibers connected to the lowest recruitment threshold MUs that, according to the size principle of MU recruitment (Henneman 1957; Bawa and Murnaghan 2009), are the first ones to be recruited and remain activated for the longest periods of time during sustained low-force efforts. Muscle injury would result from overload, accumulation of calcium ions preventing muscle relaxation, and structural damage to these fibers (Lexell 1993; Hagg and Astrom 1997), implying insufficient regenerative processes at the injury site (Hagg and Suurkula 1991; Visser and van Dieen 2006; Voerman et al. 2007). These mechanisms would then trigger secondary ones, including stimulation of nociceptors, triggering of sympathetic nervous system responses and alterations in blood flow (Larsson et al. 2004; Shiro et al. 2012). Finally, sensitization would trigger injury chronicity. Some biopsy studies lend support to the Cinderella hypothesis (Lindman et al. 1990; Hagg 1991, 2000) and as such, it is one of the few MSD injury hypotheses linking experimental evidence with tissue damage mechanisms. Another prediction of the Cinderella hypothesis is that the injury trajectory is dependent on the duration of use but could also be accelerated by deficits in normal MU rotation and load-sharing mechanisms (Visser and van Dieen 2006). Indeed, it has been shown that some derecruitment of low-threshold MUs can take place during low-intensity sustained muscle contractions (Westgaard and DeLuca 1999). As such, the neck/shoulder muscles, particularly the trapezius, often display continuous activity of some MUs over a wide range of tasks (Thorn et al. 2002; Zennaro et al. 2003), but some studies have shown that some subjects display less derecruitment than others (Westgaard and DeLuca 1999). Moreover, these particular patterns do not seem to be related with any known specific injury risk factor, suggesting that their presence could predispose certain people to develop overload and injury in an unpredictable way.

The Cinderella hypothesis has mostly been used as a framework for studies of low-load repetitive upper-limb tasks targeting output from the neck and upper limb musculature. For instance, studies of trapezius muscles of cleaners showed experimental evidence for the predictions of the Cinderella hypothesis with the presence of presumably overloaded type 1 necrotic, "ragged red" fibers in workers with symptoms (Sjogaard and Sogaard 1998). Two notable characteristics of this work situation are (1) the involvement of the complex neck/shoulder musculature, encompassing many muscles that can theoretically produce force in many directions, and motion of considerable amplitude, (2) the prolonged, repetitive nature of the associated upper limb task. These two characteristics can be generalized to two aspects of motor behavior that can be linked to the risk of tissue overload and injury: motor abundance and motor variability. We illustrate these two concepts within the Cinderella hypothesis by suggesting that motor abundance, through the potential contribution of many muscles to one given action, can be used as a way to provide help to vulnerable Cinderella fibers, whereas motor variability, through variation of one movement to the next, can be used to provide Cinderella fibers some breaks.

13.5 Give Cinderella Some Help: Abundance

13.5.1 The Concept of Abundance

One movement can be accomplished in many different ways. At the mechanical level, this concept can be modeled as a system taking advantage of its redundant degrees of freedom (Bernstein 1967). At the control level, redundancy can be considered as a consequence of having many muscles, having many MUs that can be triggered separately to produce a motor action. How does one select a "motor solution" in a given condition? In recent years, this apparent "problem" has been reformulated by introducing the concept of abundance (Gelfand and Latash 1998). In this view, the redundancy of the human system does not pose a problem but rather offers a theoretically rich set of solutions that can be used when accomplishing a motor action (Latash 2000). The concept of abundance is particularly attractive when applied to tasks related to neck/shoulder MSD, since as stated previously, the neck/shoulder musculoskeletal system has a high degree of structural complexity that can easily be underestimated by simple mechanical models (Hill et al. 2008). Thus, it is conceivable that in tasks involving a highly abundant system, even more so for tasks that allow for the contributions of other additional muscles and joints beyond those of the neck/shoulder region, taking advantage of this motor abundance could have implications on overload, and therefore injury risk, on the neck/shoulder musculoskeletal structures. More specifically in association with the Cinderella hypothesis, having access to the contributions of many joints and muscles to produce a task could help reduce the burden on a particularly vulnerable set of neck/shoulder Cinderella muscle fibers.

13.5.2 Abundance at the Level of the Neck/Shoulder Musculature

The most widely documented illustration of the concept of abundance has been shown to occur at the individual muscle level, with selective recruitment, derecruitment and substitution of MUs during the prolonged performance of a task.MU substitution typically describes a mechanism whereby higher-threshold MUs are recruited to replace lower-threshold fatigued units that have stopped firing (Westgaard and DeLuca 1999). Using this definition, MU substitution would be consistent with Henneman's size principle (Henneman 1957); however, MU substitution is often used synonymously with MU rotation (Sale 1987), which describes cyclical activity between MUs, such that substitution of one MU for another would be followed by back substitution of the original unit. While MU substitution is well described, MU rotation is controversial in that it suggests that a violation of the size principle of MU activation may occur. Moreover, MU substitution was previously believed to be more plausible in muscles that are anatomically subdivided (e.g., quadriceps femoris); however, recent evidence for the ability to control subdivisions of individual muscles can be used to argue against this suggestion and as such, MU substitution has been shown to occur within the upper trapezius muscle (Mathiassen and Winkel 1990; Westgaard and DeLuca 1999; Zennaro et al. 2003). Westgaard and DeLuca (1999) studied the activity of the human trapezius muscle during contractions lasting 10 min and found that low-threshold MUs showed periods of inactivity during which they were substituted by MUs with higher recruitment thresholds. It has been suggested that a purpose of MU rotation could be to maintain a desired level of muscle output, such as force (Sjogaard et al. 1986).

Few have attempted to relate phenomena of MU rotation with other pathological mechanisms related to injury. Sjogaard et al. (1986) investigated myoelectric signal activity during isometric knee extension performed continuously for 1 h at 5 % of maximal voluntary effort. It was found that blood flow was distributed heterogeneously throughout the muscle during the entire duration of the task, and EMG recordings suggested that this heterogeneity was related to the alternating recruitment of muscle fibers. However, currently there is little evidence related to the mechanism through which MU substitution occurs. In most studies, MU substitution was not seen during the first few minutes of a contraction, even among units that later displayed this phenomenon. It may be that a target force can be maintained while particular MUs (or even muscle fiber bundles) experience periods of inactivity to allow for the replenishment of metabolic needs (Sjogaard et al. 1986; Westgaard and DeLuca 1999). Indeed, the concept of MU substitution has long been postulated to offset the effects of fatigue (Person 1974), and researchers have reported the observation of substitution activity of MUs within a muscle that was performing a sustained, low-level static contraction (Sale 1987; Westgaard and DeLuca 1999), and have speculated that this is a natural strategy to resist fatigue. Van Dieen et al. (1993) even noted that muscles of subjects who demonstrated MU rotation had longer endurance times. However, in some studies, substitution and rotation were observed in muscles of some, but not all subjects (McLean and Goudy 2004), suggesting an individual predisposition for this mechanism that could be dependent on the ability to detect a need to trigger tissue regeneration mechanisms. In turn, this mechanism could be related to one's predisposition to develop MSD (Veiersted and Westgaard 1993). This is supported in studies from Thorn et al. (2002) and Zennaro et al. (2003) who used long-duration MU decomposition techniques to show that in a minority of subjects, at least one single MU remained continuously active over the duration of the contraction.

Other multisite EMG spatial distribution techniques have recently been developed to illustrate within-muscle changes in activation patterns with fatigue and with experimental pain. Previous studies have documented relative changes in the EMG amplitudes of different sections of the trapezius muscle after sustained isometric contractions and in response to experimental pain (Madeleine et al. 2006; Falla et al. 2007a). A recently developed technique quantifies the amount of shared information contained between two EMG time series, accounting for both linear and nonlinear signal characteristics (Madeleine et al. 2011), with the assumption that high levels of shared information illustrate functional connectivity between both time series. Indeed, within-trapezius functional connectivity has been observed to increase with DOMS (Madeleine et al. 2011). However, in another study of asymptomatic men and women accomplishing a prolonged repetitive upper-limb task, no effect on task time was found (which could be explained by a lower level of fatigue induced by the task). Moreover, women displayed a higher level of functional connectivity than men in two of the three muscle subdivisions studied (Johansen et al. 2013), confirming previous studies showing gender differences in trapezius muscle behavior (Falla et al. 2008).

13.5.3 Abundance and Multimuscle Patterns During Tasks Targeting the Neck/Shoulder Musculature

To this day, the description of patterns of multi-muscle behavior poses a significant methodological challenge, even despite recent advances in instrumentation and data processing capabilities (Hug 2011). This could explain why comparatively fewer studies have described patterns of groups of agonist, antagonist, and synergist muscles, even less so across many joints, during the production of complex upper limb movements. For one, cocontraction of single-joint agonist–antagonist muscle pairs has been well documented in situations of fatigue and pain (Psek and Cafarelli 1993). These patterns have been explained as an attempt to stabilize and protect vulnerable body areas from further damage, in line with the pain adaptation model (Lund et al. 1991). Moreover, findings from recent studies of low-back pain show that elevated coactivation patterns displayed by initially asymptomatic people were associated with the development of low-back pain, suggesting a causal injury mechanism (Nelson-Wong and Callaghan 2010). A few studies have also documented modifications of inter-muscle coordination among agonist and synergistic muscle groups of individual joints (Danion et al. 2000, 2001) and reduced trans-joint inhibition of synergistic muscles (Aymard et al. 1995) in prolonged tasks. In addition, Falla and colleagues showed that healthy subjects with experimental pain, and groups with whiplash and idiopathic neck pain showed increased use of accessory neck/shoulder muscles when performing repetitive upper-limb tasks (Falla et al. 2004, 2007b). We recently showed higher activity in stabilizers of the shoulder girdle in people with neck/shoulder pain performing a repetitive upper-limb task (Lomond and Côté 2011). We also applied the mutual information technique (Madeleine et al. 2011) to describe functional connectivity in neck/shoulder synergistic muscle pairs, to show decreased connectivity among the neck/shoulder group as fatigue developed during the repetitive task, and that this was more noticeable in men (Fedorowich et al. 2013).

Even fewer studies have extended their analyses beyond the level of individual joints. Some studies conducted in our lab showed that fatigued, noninjured people seemingly take advantage of multijoint abundance during the performance of whole-body tasks. (Côté et al. 2002, 2008; Fuller et al. 2009). In studies in which fatigue was induced by repetitive hammering, sawing, and pointing, subjects showed reduced hammering and sawing force output and movement amplitude, and increased activity of the fatigued upper limb muscles, in parallel with increased multidirectional movement amplitude of the trunk, whole-body center of mass (CoM) and center of pressure (CoP), and trunk EMG activity. Together, these changes seemed to target an increased contribution of trunk to endpoint motion; indeed, an increase of only a few degrees of trunk flexion, or even rotation could increase the amplitude of the upper limb endpoint by several centimeters. Trunk movement could be used to compensate for changes encumbered by fatigue at the neck/shoulder region. Moreover, most of the observed whole-body changes began to occur about halfway to exhaustion, suggesting an ongoing fatigue adaptation strategy (Fuller et al. 2011). Despite these many changes developing in parallel with fatigue, here again, as with overall muscle force despite MU rotation shown previously to occur during knee extensions (Sjogaard et al. 1986), some general task characteristics such as endpoint motion amplitude and timing, were kept constant, suggesting adaptations tailored to the perceived task goals. As summarized in Côté and Hoeger Bement (2010), studies of three low-force tasks performed to exhaustion provides evidence for (1) fatigue in areas mainly involved in each task (e.g., increased muscle activity, decreased motion amplitude at the elbow and shoulder), (2) increased involvement and contributions toward the overall task from adjacent body segments such as the trunk (e.g., increased muscle activity, increased motion amplitude), and (3) maintenance of the consistency of some overall task characteristics (e.g., endpoint movement amplitude and movement speed). Taken together, these findings not only provide evidence that changes in whole-body movement patterns occurred with low-force muscle fatigue but also suggest that these adaptations involve the use of the overall abundance of the musculoskeletal system even in areas remote to the one directly fatigued. The observation that global task measures remain largely unaltered after low-force fatigue despite the many kinematic changes occurring across the body, supports the hypothesis of a task-specific global adaptation strategy, of which parts can be modulated, but as a whole, remains largely unaffected by low-force fatigue. This was further challenged and confirmed in recent studies where we showed that most of the global task-specific adaptations that can compensate for localized fatigue also occur in the presence of a second perturbing factor added on top of fatigue (i.e., sudden support surface translations (Fuller et al. 2013), wearing an added external weight (Cantu et al. accepted). It should be noted that the task-specific characteristic that is thought to be used to guide the choice of motor solutions can also be related to the concept of synergies, defined as neural organizations that ensure task-specific covariation of elemental variables providing desired stability properties of important output, or performance variables (Latash 2012; see also Latash, this volume). According to this concept, synergies would serve to simplify the organization and selection of a given motor solution that would satisfy, with more or less room for variation from one trial to another, what are perceived to be important task goals.

In situations of experimental or acute pain, previous studies have documented similarities in whole-body adaptation patterns displayed by healthy fatigued people (Madeleine et al. 1999; Latash and Anson 2006). In comparison, the range of whole-body adaptations to repetitive movements seems smaller in people with MSD. We have previously shown that there was a significant correlation between scores of the shoulder pain and disability index, and reductions in kinematic (motion, speed, acceleration) amplitudes at the upper limb joints during hammering (Côté et al. 2005). Participants in the symptomatic group also displayed reduced trunk as well as overall endpoint motion amplitude. To challenge this finding, we performed a study where the task required subjects to maintain a specific endpoint motion amplitude during repetitive reaching between two targets, and found that in this case, patients again show less upper limb joint motion, with significant negative correlations between initial pain level and shoulder range of motion (Lomond and Côté 2010). However, in this case, participants developed a strategy of increasing whole-body CoM motion amplitude, suggesting a prioritization of compensatory strategies, with perhaps the most cost-effective ones prioritized over the least cost-effective ones and/or the most painful ones (Lomond and Côté 2011; see also Levin, this volume). Figure 13.3 shows previously unpublished data on the same repetitive reaching task, but this time accomplished in the seated position, further reducing the abundance of movement solutions to accomplish the repetitive task under the same spatial (i.e., moving the finger forward between the two targets adjusted for height and distance, while maintaining the elbow above a barrier adjusted to force the entire arm to move in a horizontal plane) and temporal (moving at one movement per second) constraints. The data shows that in the seated position, the symptomatic group took less advantage of trunk (in this case, head, arms, and trunk CoM) compensatory strategies, possibly to avoid destabilizing the upper body or placing additional load on the extensors of the upper trunk. This reinforces the notion that (in this case, mechanically) more advantageous solutions are prioritized, especially when dealing with repetitive motions in the presence of pain.

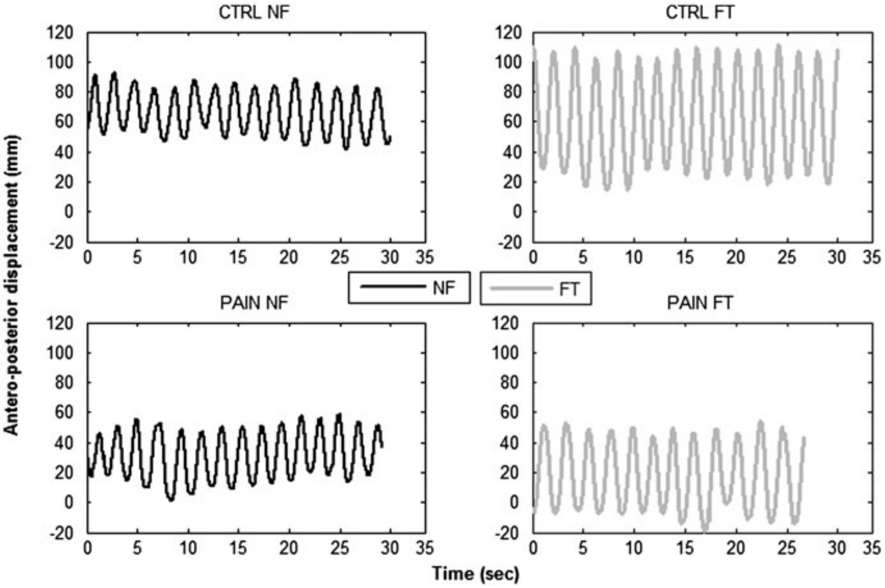

Fig. 13.3 Head, arms and trunk center of mass trajectory (mm) in time (s) during repetitive forward–backward reaching at shoulder height, in the sitting position (representative subjects). *CTRL* asymptomatic, *PAIN* chronic neck–shoulder pain, *NF* during the first minute, *FT* during the last minute right before exhaustion

13.6 Give Cinderella a Break: Variability

13.6.1 Defining the Concept and Scope of Variability

While abundance, as defined here, addresses the various ways in which the system can produce a given sensorimotor action, the concept of variability addresses the repeatability of these patterns from one action to the next. Variability, the variation of behavioral outcomes over repetitions or time, is an inherent feature that plays a role in the central organization of voluntary movements (Latash et al. 2002). The amount of variability in any characteristic of posture or movement can be estimated using simple statistics such as standard deviation (SD), coefficient of variation (CV), or interquartile range (IQR) (Srinivasan and Mathiassen 2012), each measure providing a slightly different illustration of variability (e.g., CV is impacted by the mean measurement taken over repeated trials, whereas SD is not). In motor learning research, variability has been considered not just as undesirable noise (Newell and Slifkin 1998) but also as an indicator of motor development and skill acquisition (Bartlett et al. 2007). In this paradigm, skill acquisition does not merely imply developing an adequate movement pattern but also developing a certain optimal variability of that pattern, that is neither too low (stereotypical) nor too high (unstable) (Stergiou et al. 2006). Motor variability, in turn, ensures that new motor solutions can be explored in response to changes in the external environment or the internal physiology (Dingwell et al. 2001; Riley and Turvey 2002). One important issue to keep in mind when navigating through the literature is that variability has been studied as various levels of the motor output (Newell and Corcos 1993; Stergiou 2004; Davids et al. 2006). For instance, variability in performance outcome measures may have important implications on the quality of performance and in fact may not easily be modified in real-life situations such as during work at an imposed rhythm. Variability in joint or segment kinematic characteristics displayed while performing a task may be more easily manipulated without affecting performance outcome; however, these adjustments may be limited by the inherent mechanical constraints associated with the architecture of the human body (Newell and Slifkin 1998). Variability in activity patterns and in more elemental control variables may also operate. Ultimately, the system must account for the possibility that some level of variability exists at all of these levels to produce adequate actions. A large body of literature related to the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; Latash and Scholz 2007; Martin et al. 2009) has focused on the structure of variability, distinguishing between variability that does not affect performance quality ("good variability") and variability that (negatively) does ("bad" variability). Recent contributions to this literature notably further highlight good variability as beneficial towards overall performance stability (Rosenblatt et al. 2013). While the UCM literature undoubtedly provides an important contribution to the literature on variability in motor control, it is extensively reviewed elsewhere (see Latash, this volume) and is thus not expanded upon further in this chapter, which will focus on the amount, and not the structure, of motor variability.

13.6.2 Variability as a Strategy to Find Solutions to an Acute Problem

Repetitive tasks imply the potential development of fatigue, and fatigue has been shown to have an effect on movement variability. For instance, Cignetti et al. (2009) examined variability of gait during cross-country skiing and found arm and leg movements to become more variable with fatigue. However, other studies suggest that motor variability may have a positive effect on mitigating fatigue development. In an examination of a target-tracking task, Selen et al. (2007) showed that despite increased kinematic variability with fatigue, overall task performance (accuracy) was maintained. In a repetitive reaching study (Fuller et al. 2011), movement-to-movement variability of the shoulder and elbow joints and the CoM average position increased with fatigue, but these were not associated with any deterioration in performance. What is more, some studies have associated variability in movement patterns with high endurance. Studies of repeated knee extensions (Skurvydas et al. 2010) and back muscle exertions (van Dieen et al. 1993) show associations between joint and muscle pattern variability in the nonfatigued state with high endurance during

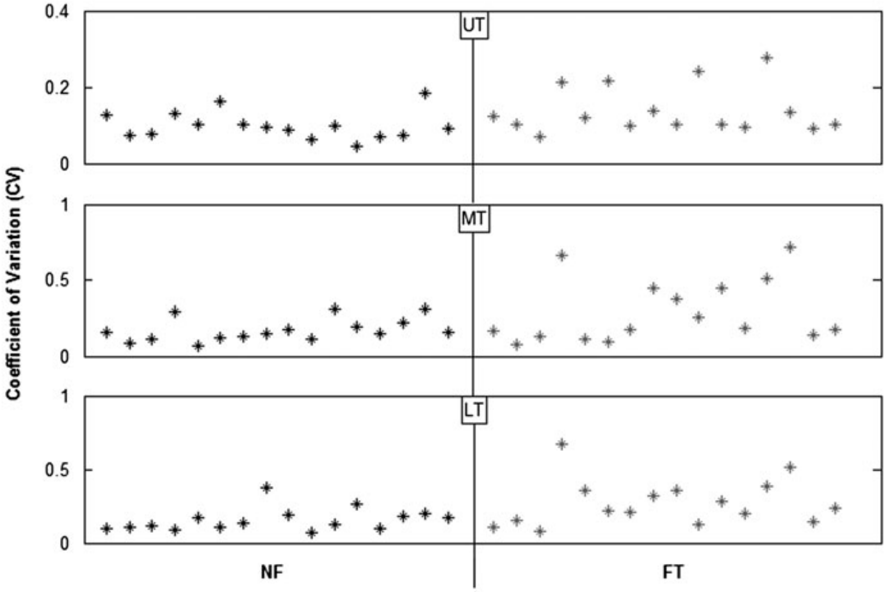

Fig. 13.4 Movement-to-movement variability (coefficient of variation, *CV*) in trapezius EMG RMS between consecutive forward-reach movements at shoulder height, accomplished in the seated position, in asymptomatic participants. Each symbol represents the CV of one participant, in each trapezius subdivision (*UT* upper trapezius, *MT* middle trapezius, *LT* lower trapezius), at each of the nonfatigued (*NF*) and fatigue-terminal (*FT*) states

the performance of tasks engaging the respective muscles and joints. Similar findings were shown recently by our group, with initially higher variability in trapezius muscular patterns showing a positive association with longer endurance time during the repetitive reaching task, but with this association being significant only in our female subsample (Fedorowich et al. 2013). This study was, to our knowledge, one of very few documenting movement-to-movement variability of electromyographic (EMG) characteristics of muscles of the neck/shoulder region, including muscle (trapezius) subsections. These findings were confirmed in a recent (unpublished) study (Fig. 13.4) where subjects performed the same task in a seated position, further targeting the load during the repetitive upper-limb reaching task on this musculature. Here again, we observed significant increases in reach-to-reach variability in the fatigued state in all three subsections of the trapezius muscle despite the fact that frequency and trajectory of reaching were still preserved.

The preservation of overall performance despite increased variability with fatigue implies that some level of proficiency may be required in order to develop such compensatory strategies (Bosch et al. 2011). This is supported by studies that have shown that only expert table tennis players were able to increase variability and still maintain a high level of performance (Aune et al. 2008), and other studies that have shown that increased variability with fatigue negatively affected the performance of complex upper-limb tasks (Huysmans et al. 2008; Missenard et al. 2008). As a whole however, most studies agree that during repetitive, fatiguing tasks, where some level of performance can theoretically be maintained over a certain number of repetitions, variability in some movement characteristics can be useful to manage fatigue. Yet, we still have little understanding of the mechanisms underlying these observations. It has been suggested that whole-body compensatory strategies could be triggered by the detection of time-related changes at the muscle level, such as increased muscle activity, decreased proprioception, or accumulation of metabolites. Since these localized changes have been shown to occur well before exhaustion in low-force tasks (Fuller et al. 2011), and consistently with the notion that variability could be used as a compensatory strategy, we could expect to observe fluctuations in variability characteristics over the duration of a task performed to exhaustion, although this has not been well-documented to date. Nevertheless, this would have the advantage of providing fatiguing muscles with windows of opportunity to rest, or at least with some degree of load variations (Visser and van Dieen 2006), which in itself has been shown to promote derecruitment of MUs (Westad et al. 2003), thereby favoring intermittent recovery during prolonged tasks. These observations feed beliefs held by practitioners in occupational health that biomechanical variation decreases the risk of developing MSDs as well as in sport biomechanics in a formulation of the "variability-overuse hypothesis" (Bartlett et al. 2007). It should also be noted that the hypothesis that increased variability during repetitive tasks illustrates a search for solutions to an acute problem, up to now in this section represented as fatigue, is supported by similar findings in situations of experimental pain induced during a simulated cutting task (Madeleine et al. 2008) and during a prolonged, discomfort-provoking sitting task (Søndergaard et al. 2010).

13.6.3 Variability in People with Musculoskeletal Disorders

The association between chronic pain conditions and reduced motor variability has been shown in several studies. In their series of studies on butcher work, Madeleine et al. showed that as opposed to acute pain, chronic pain was associated with decreased variability. In subjects with unilateral knee impairment, the injured limb exhibited less motor variability than the intact one (Hamill et al. 1999; Heiderscheit et al. 2002; Georgoulis et al. 2006). Recently, it was shown that people with low back pain exhibited reduced trunk movement variability during gait in comparison to a control group with no pain (van den Hoorn et al. 2012). In interpreting their findings, authors suggest that less variable patterns illustrate protective strategies where one, or a small set of motor solutions, representing the least amount of pain and/or smallest risk of aggravation or injury, is found and maintained. However, some authors suggest that more stereotyped (i.e., less variable) movement patterns may actually represent a greater risk of injury (Mathiassen et al. 2003; Madeleine et al. 2008), either by reducing the adaptability of the system to suddenly changing conditions or by posing a risk of overload and injury to the consistently loaded structures (Côté and Hoeger Bement 2010).

The above-cited studies likely would lead to the assumption that low variability would emerge as a consequence of experiencing pain or injury. This is further supported in a study on low gait variability in a pain group that showed increased variability to almost that of a healthy group when pain was temporarily reduced by the application of patellar taping (Heiderscheit 2000). However, other studies have provided evidence to argue that variability may be a part of one's inherent motor pattern and as such would have an impact on one's predisposition to pain maladaptive strategies. This hypothesis is supported by the observation that initially larger movement variability was associated with higher probabilities of returning to normal postural strategies after experimental pain (Moseley and Hodges 2006).

Even more so than in studies of variability with fatigue or acute pain, findings from studies of variability between healthy groups and others with chronic pain are largely impacted by the choice of metrics to quantify variability. For instance, given the same amount of movement-to-movement variability (SD) in degrees of joint motion amplitude, the finding that people with chronic pain usually show smaller ranges of motion would mean that as a result, their coefficient of variation would be larger. This was observed in a previous study of our group (Lomond and Côté 2011) and is replicated with new data below on variability patterns displayed during the repetitive pointing task performed in the sitting position (Fig. 13.5). This observation has two major implications: first, at the methodological level, this implies that great care should be taken when interpreting findings based on different ways to compute variability. Second, at the theoretical level, this plays in favor for a recommendation to consider both concepts of abundance (which has a direct impact in the contribution of a specific joint or muscle towards the production of a task) and variability together, so as to draw a more complete picture of whole-body adaptations, especially in chronic pain.

13.7 Cinderella Versus Cinderello: A Quick Word on Gender Differences

Most research agrees that in general, both the work conditions and the worker's personal features may predict the likelihood of developing MSDs (Messing et al. 2003; Messing and Stellman 2006; Théberge 2012). As such, both may potentially explain why women report MSDs more often. Indeed, recent statistics in Quebec show that work-related MSDs affect 16 % of men and 25 % of women (Stock et al. 2011). Higher reports of neck/shoulder MSDs in women are especially well-documented in the literature (Hooftman et al. 2009). A more detailed understanding of these gender differences may help tailor more effective injury rehabilitation and prevention approaches. Moreover, in the context of this chapter, a greater understanding of factors underlying this difference could help gain a better understanding of the role played by motor control mechanisms in the initiation and aggravation of MSDs.

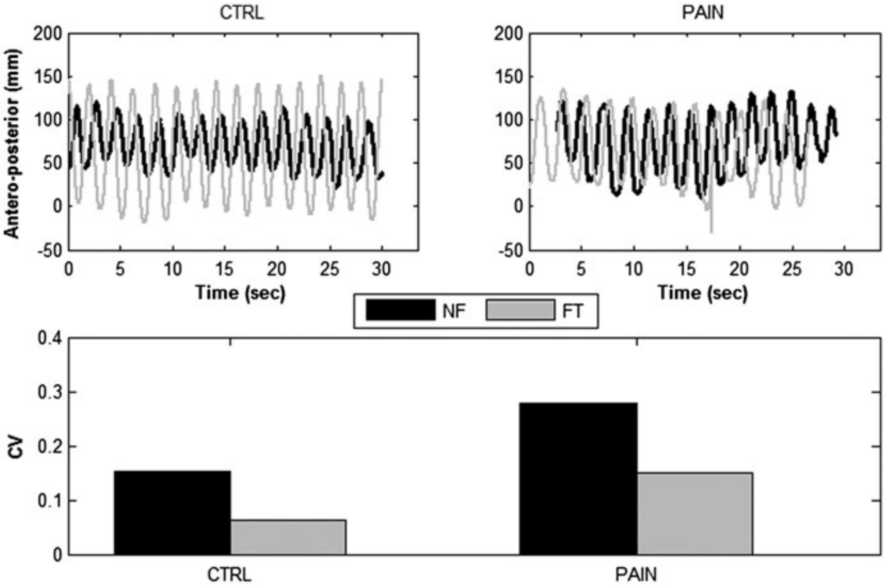

Fig. 13.5 Anteroposterior shoulder amplitude and variability characteristics during the performance of a repetitive reaching task at shoulder height, in the seated position. *Upper panels*: 30-s traces, representative asymptomatic (*CTRL, left*) and chronic neck–shoulder injured (*PAIN, right*) participants. *Bottom panel*: Variability index (coefficient of variation, *CV*) computed for each subject, during the first (*NF, black*) and last (*FT*) minutes of the task. Despite the largest motion amplitude displayed by CTRL at FT, their variability, computed using CV (SD/mean), is the smallest

This was the approach taken in a recent review (Côté 2012), which led to a first attempt at conceptualizing a model based on anatomical and neuromuscular factors to explain why the incidence and prevalence of neck/shoulder MSD is consistently higher in women. With recent data on gender differences that can be related to the concepts of variability and abundance, we propose a new version of this evolving model (Fig. 13.6).

The main elements of this conceptual model have been described previously (Côté 2012), and the additions in this current version of the model were introduced in previous sections of this chapter. To summarize briefly: a few studies have shown a reduced ability to modify muscle activity patterns in women (Ge et al. 2005), notably with women showing continued use of the same regions of the trapezius muscle even in the presence of experimental pain, whereas men responded by using different ones. Similar results were shown in our recent study on neck/shoulder patterns during fatigue adaptation (Fedorowich et al. 2013). However, recent studies show higher functional connectivity among neck/shoulder muscle parts during a low-fatigue task (Johansen et al. 2013). This rather suggests that the reason for the seemingly lower adaptability in women may be due to higher baseline functional connectivity. In other words, it could be that for the same task, women initially already make optimal use of abundance, such that their adaptability margin is lower. However, other studies

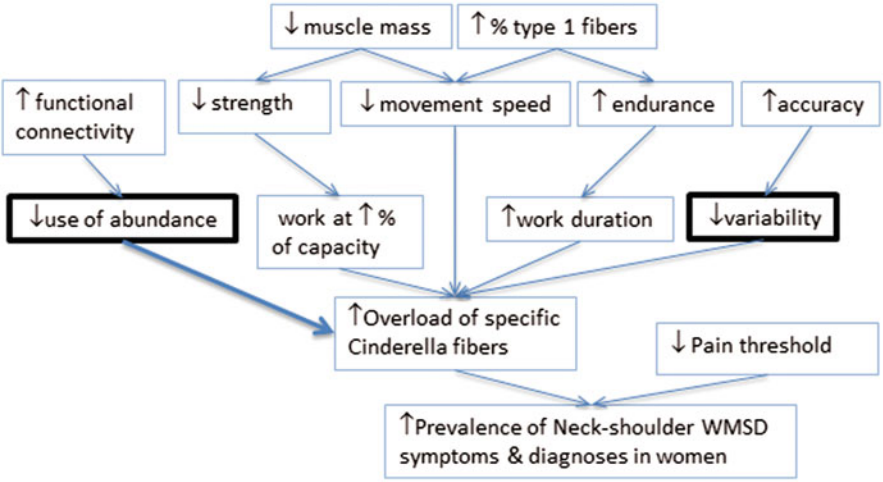

Fig. 13.6 Conceptual model to explain mechanisms underlying the physical basis for sex/gender differences in the prevalence of neck/shoulder MSDs. Based on a previously published model (Côté 2012), this new version integrates the concepts of abundance and variability at the core of this chapter

are needed to confirm or disprove this hypothesis. Nevertheless, this line of findings does shed an original light on the concept of abundance: similarly to findings from the literature on synergies, the key could be the flexibility in creating and breaking down synergies (Latash 2010), and in making use of abundance, that could predict effective MSD prevention. Conversely, in a few recent studies, it was shown that women displayed lower movement-to-movement force variability (Svendsen and Madeleine 2010), which can be linked to reported higher accuracy in women (Côté 2012). However, a recent study from our group showed a positive association between initial variability and endurance time in women (Fedorowich et al. 2013), further reinforcing the importance of benefitting from flexibility to optimize the response to stimuli such as fatigue and pain. The next logical step could then be to determine what predicts the higher flexibility and adaptability in women compared to men? Again using the gender comparison as a theoretical model, starting with the underlying premise that there are well-documented differences in anthropometric and strength characteristics between men and women, the key could lie in the size of the margin between one's capabilities and the demands of the task.

13.8 Conclusion: The Concept of Motor Repertoire

The notions of safety margin, leeway, and margin of maneuver have been introduced in relation to health and performance, with slight distinctions according to their field of application (Côté 2012; Durand et al. 2011; Côté et al. 2013). Generally, all of these refer to some ability to perform a task, and this ability is introduced here as a motor repertoire. The idea is that the possibility to benefit from a comparatively large motor repertoire is desirable, we argue, for two purposes: safety and performance. Let us compare the human body to a large orchestra displaying some musical repertoire. This repertoire can be constituted of simple and complex pieces involving the contributions of varying numbers of musicians. Similarly, at least some pieces of this repertoire can be produced to some degree of quality even in the absence of some musicians. The repertoire can be enriched with the introduction of some variations of musical pieces, as long as they satisfy the overall quality requirements of the orchestra. All of these characteristics can find parallels with what we know about the functioning of the human body, including the notions of abundance and variability. In turn, one objective pursued by ergonomists and therapists alike, could be to build a motor repertoire as large as possible within the existing capabilities, which could in turn serve to produce safe, durable, effective, and flexible motor performance. As such, one last important element to address is the task-dependency characteristic of this repertoire development. For instance, it is conceivable that equal instructions (e.g., move the finger as fast as possible; perform a data entry job for 40 h a week) can be perceived differently from one person to the next, depending on the person's (possibly changing) disposition and the (possibly changing) conditions in which the task is to be performed. Ultimately, the key could lie in creating a repertoire as large as possible between the perceived capabilities and the perceived task demands (Fig. 13.1), while accounting for flexibility for the capabilities and demands to evolve through time. For instance, this repertoire could be smaller for a woman compared to a man if the performance is related in any way to force capabilities, but this difference could be smaller if performance was rather associated with high accuracy demands. Still, despite these documented guiding principles that help understand how motor capabilities can differ between two individuals, ergonomists and therapists can design job modifications and training interventions to impact on health and performance. Interventions based on the concepts of abundance and variability can in turn have a positive impact on reducing and preventing MSDs.

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Chapter 14
Deficits in Spatial Threshold Control of Muscle Activation as a Window for Rehabilitation After Brain Injury

Mindy F. Levin

14.1 Background

14.1.1 The Problem of Spasticity and Disordered Motor Control

Spasticity is associated with an upper motor neuron lesion affecting recovery of motor function (Kim and Park 2011; Sunnerhagen et al. 2013). It is estimated that spasticity affects over 12 million patients worldwide who have had a stroke, spinal cord injury, head trauma, multiple sclerosis, cerebral palsy (CP) or other disorder of the central nervous system (CNS; Burke 1988; www.aans.org). At the root of the motor deficit after stroke is hemiparesis characterized by a diminished capacity to recruit agonist muscles (Hammond et al. 1988; Gemperline et al. 1995; Chang et al. 2013), or the use of abnormal recruitment patterns (Bourbonnais et al. 1989; Dewald et al. 1995; Kamper and Rymer 2001; but see Gowland et al. 1992; Fellows et al. 1994a, 1994a) and weakness (Kamper et al. 2006; Chang et al. 2013). Agonist–antagonist coactivation may be responsible for a reduced ability to selectively activate arm and hand muscles (Lang and Schieber 2004). This disability can also be associated with abnormal timing of agonist and synergist muscle activation, and failure to deactivate antagonist muscles (Hoffman and Strick 1995).

Spasticity, weakness, and motor impairments have traditionally been considered as separate phenomena (Fig. 14.1). However, the idea that they are interrelated was alluded to in the definition suggested by Lance in 1980. This definition, now frequently cited in the literature, describes spasticity as "a *motor disorder* characterized by a velocity-dependent increase in stretch reflexes (muscle tone with exaggerated tendon jerks) as one component of the upper motor neuron syndrome." Lance's definition suggests that spasticity and motor deficits are related to problems in stretch

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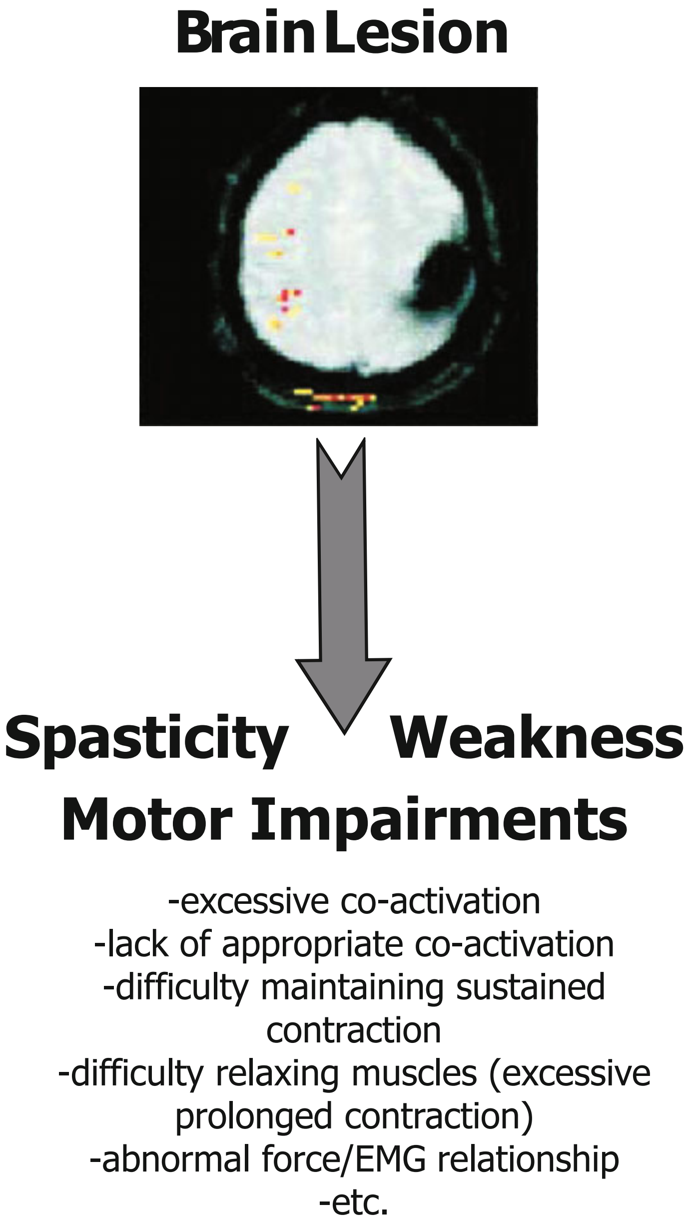

Fig. 14.1 Schematic diagram of the interrelationship between spasticity, weakness, and disordered motor function after a brain lesion

reflex excitability. However, the precise relationship between spasticity, hyperactive stretch reflexes, and the abnormalities in the production of voluntary movement remains unclear.

Studies attempting to determine the degree to which altered muscle tone and stretch reflex hyperexcitability may influence voluntary motor control have yielded equivocal results. Corcos et al. (1986) studied ballistic ankle dorsiflexion movements in subjects with spasticity of mixed etiology and showed that deficits in voluntary calf muscle activation were related to hyperactive stretch reflexes. However, other studies of upper limb hemiparesis reported that the disorder in voluntary motor control may not be related to spasticity or hyperactive stretch reflex activity (Sahrmann and Norton 1977; O'Dwyer et al. 1996; Burne et al. 2005; Chang et al. 2013). The controversy is associated with a lack of a coherent view of the relationship between spasticity and disordered voluntary muscle activation.

A major problem in the understanding of this relationship is the method used to quantify spasticity. Although the presence or absence of spasticity can be identified using current clinical scales (Malhotra et al. 2009), such clinical scales are insufficient to determine the relationship between spasticity, deficits of voluntary movements, and functional ability (for reviews, see Elovic et al. 2004; Wood et al. 2005; Calota and Levin 2009). There is general agreement that current scales of spasticity, even if objective, measure biomechanical variables (e.g., the resistance to imposed muscle stretch) that are *effects*, rather than *causes* of spasticity (Malhotra et al. 2009), and that various physiological measures (e.g., inhibition/facilitation mediated by cutaneous and muscular afferents) do not provide a comprehensive understanding of the nature of spasticity and disordered movement (Malhotra et al. 2008, but see Levin et al. 2000, Krakauer 2005; Musampa et al. 2007; Mullick et al. 2013).

Different components of spasticity have been identified using physiological measures (e.g., disorders of reflex pathways, Mazevet et al. 2003), biomechanical measures (e.g., deficits in interactive joint torque control, Dewald et al. 1995; Beer et al. 2000), or a combination of both (e.g., reflex and nonreflex components of ankle spasticity, Zhang et al. 2013); based on the assumption that these components are controlled separately. However, there is increasing evidence to suggest that not only spasticity and movement impairments but also muscle weakness and loss of dexterity (skilled muscle actions) are all consequences of the same underlying control deficit. It is proposed that this common control deficit is the specification and regulation of spatial thresholds (STs) of the stretch and other proprioceptive reflexes (Levin and Feldman 1994; Feldman and Levin 1995; Musampa et al. 2007; Feldman 2011).

14.1.2 ST Regulation in the Healthy Nervous System

The ST corresponds to the muscle length or joint angle (R) at which muscle activity begins. This expresses the muscle activation threshold in the spatial (angular) rather than the temporal (e.g., in terms of latencies) domain. The ST is the position of a body segment at which postural reflexes begin to act—such that postural reflexes are "centered" at the ST (Levin and Feldman 1994; Feldman 2011). Associated with the ST is a torque/angle characteristic representing the dependency of muscle reflex force on muscle length for a given threshold. The angular range through which the ST and its associated torque/angle relationship can be regulated is shown as a horizontal band in Fig. 14.2a. In the healthy nervous system, ST can be regulated throughout and beyond the biomechanical range of the joint (shown as the physical limits of joint flexion and extension lying between θ_- and θ_+, which correspond to the minimal and maximal biomechanical muscle length, respectively). The limits of ST regulation are shown by R_- and R_+. By shifting ST, the brain resets ("re-addresses") posture-stabilizing mechanisms to a new limb or body position. When the ST is shifted entirely to the left as shown in Fig. 14.2a (the lower limit, R_-), the muscle is activated even at very short muscle lengths. When it is shifted beyond the biomechanical range to the upper limit (R_+), the muscle cannot be activated and is fully relaxed. By regulating ST and its associated torque/angle characteristic (diagonal line in Fig. 14.2a) within these limits, the CNS can produce any physiologically possible combination of muscle activity, torque, and position without the need to specify these variables directly (Levin et al. 2000; Feldman 2011). Resetting of ST is also associated with the conversion of movement-resisting to movement-producing forces, providing a solution to the fundamental posture-movement problem; originally formulated by von Holst (1954; see also Ilmane et al. 2013 and Feldman, this volume).

ST regulation is an important mechanism explaining motor control in the healthy nervous system (Feldman and Levin 1995; Feldman 2009, 2011). ST control of stretch reflexes (in cats and humans) and intentional movements (in humans) is well established (Matthews 1959; Asatryan and Feldman 1965; Feldman and Orlovsky 1972; Nichols and Steeves 1986; Capaday 1995; Raptis et al. 2010; Sangani et al. 2011; Ilmane et al. 2013). The ST of a given muscle is controlled by descending inputs directly or indirectly influencing the membrane potential or electrical threshold of α-motoneurons (pre and postsynaptically via interneurons or γ-motoneurons; Matthews 1959; Feldman and Orlovsky 1972; Nichols and Steeves 1986; Hultborn and Kiehn 1992; Capaday 1995; McClelland et al. 2001). Changes in ST can be mediated by cutaneous afferents or those responsible for reflex intermuscular interactions, including reciprocal inhibition of agonist–antagonist muscles (Matthews 1959; Feldman and Orlovsky 1972). Segmental mechanisms including presynaptic and reciprocal inhibition are themselves modulated by biomechanical factors leading to the recruitment of different subsets of motoneurons (Ter Haar Romeny et al. 1984; van Zuylen et al. 1988) as well as by task-related descending influences mediated by neuromodulators, such as serotonin and norepinephrine, which change motoneuronal intrinsic properties, thus causing depolarization, plateau potentials, and shifts in their electrical thresholds (Lundberg 1967; Hultborn et al. 1987; Hultborn and Kiehn 1992; Meunier and Pierrot-Deseilligny 1998; McPherson et al. 2008). These mechanisms combine to regulate STs in a multi-muscle system according to the configuration of the system and specific task demands (Nichols and Steeves 1986; Feldman and Levin 1995; McClelland et al. 2001).

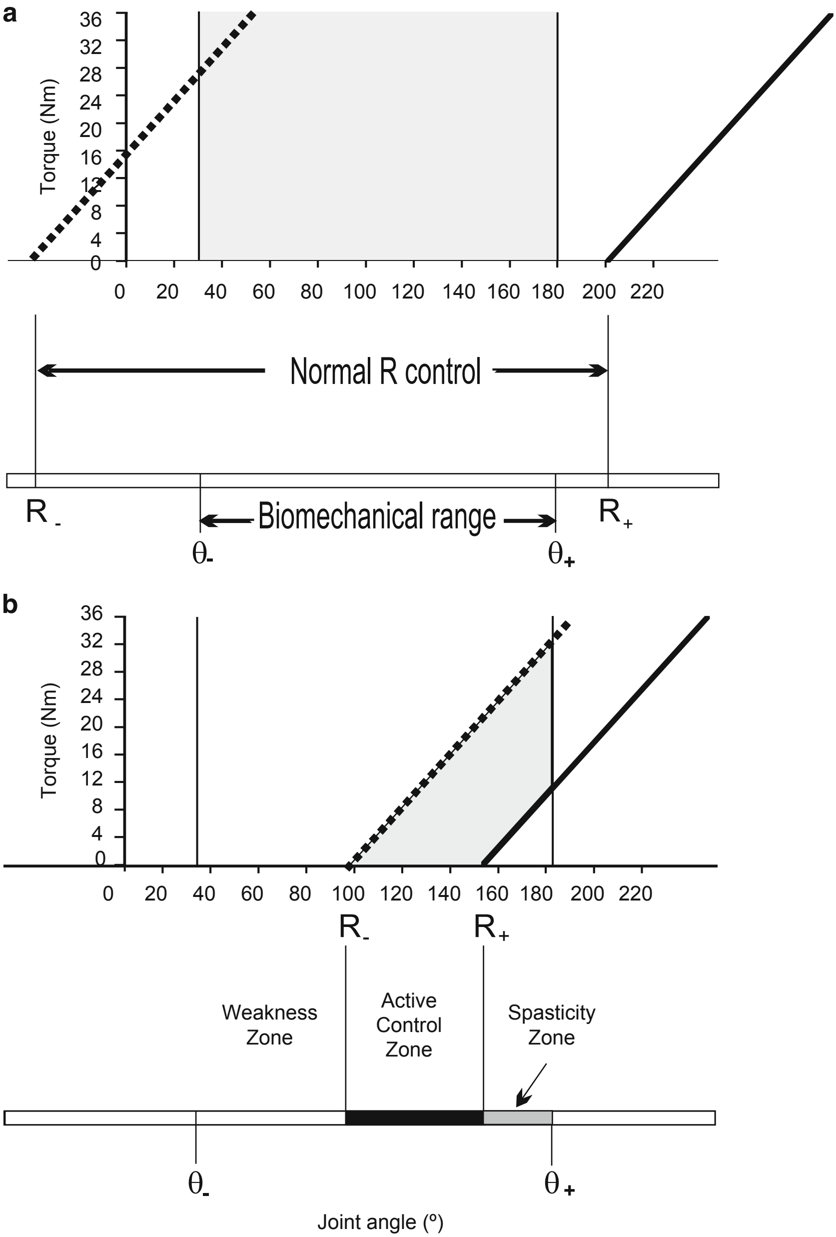

Fig. 14.2 Schematic diagram of central control of spatial thresholds (*STs*) of proprioceptive reflexes and motor deficits resulting from impairments of ST control. In this scheme, it is assumed that flexor muscles lengthen and extensor muscles shorten with increasing joint angle. **a** Normally, the range (R_-, R_+) of threshold regulation exceeds the biomechanical range of the joint (θ_-, θ_+), thus enabling the system to relax (when R_+ is shifted to the right beyond θ_+) or to activate muscles at any angle (when R_+ is shifted anywhere between θ_+ and R_-) to generate motion within the

14.1.3 ST Regulation After CNS Lesions

As reviewed above, in healthy subjects normal muscle activation is associated with an ability to regulate the ST in a range that exceeds the biomechanical joint range. Consequently, a decrease in the range of ST regulation following CNS injury or disease would result in motor control deficits (Fig. 14.2b and 14.2c). Deficits in descending and spinal mechanisms resulting from CNS injury, possibly together with changes in intrinsic motoneuronal properties such as in chloride reversal potentials and properties of serotonin receptors, in combination and isolation may contribute to limitations in ST regulation and the appearance of spasticity (Nielsen et al. 2007).

Empirical support for a common deficit in ST regulation underlying spasticity and motor control problems in single- and double-joint systems has been described in subjects with stroke (Lee et al. 1987; Powers et al. 1989; Levin and Dimov 1997; Levin et al. 2000; Mihaltchev et al. 2005; Musampa et al. 2007) and in children with hemiplegic CP (Jobin and Levin 2000). In particular, poststroke subjects with spasticity have deficits in the regulation of STs within the physiological joint range (Fig. 14.2b). Figure 14.2b shows what would occur if the lower and upper physiological limits of ST regulation (R_-, R_+) were reduced so that they lie within the biomechanical range of the joint. This would result in a narrowing of the range in which movement can be produced using "typical" reciprocal muscle innervation patterns. This range is called the "active control zone" since it is characterized by muscle activation patterns observed in people without neurological injury or disease. In the joint range between R_+ and the end of the joint excursion, muscles would be unable to relax at rest and the amount of muscle activation would be related to the velocity of stretch. This spatial joint range is called the "spasticity zone," which is not usually observed in people without neurological injury. Conversely, when the lower ST limit (R_-) is increased (i.e., shifted to the right of θ_-), the spatial zone between θ_- and R_- would be characterized by muscle weakness ("weakness zone") due to inadequate muscle activation (Levin et al. 2000). A combination of changes in the regulation of the upper and lower limits of R can result in different deficits occurring in different joint ranges (zones) accounting for abnormal muscle activation patterns observed when patients attempt voluntary movement (Levin et al. 2000; Lang and Schieber 2004).

Patterns of spasticity, weakness, and active control zones in flexor and extensor muscles around the elbow joint from 12 subjects with chronic stroke ($>$ 0.8–7.1 years post stroke) and different levels of arm paresis ranging from mild to severe

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biomechanical range. **b** Following a brain lesion, the upper limit (R_+) of threshold regulation can abnormally fall within the biomechanical range, resulting in an inability to relax flexor muscles at joint angles exceeding the position of R_+. Clinically, this deficit in poststroke subjects is identified as spasticity. **c** Following a brain lesion, the lower limit (R_-) can also fall within the biomechanical range, resulting in an inability to activate flexor muscles if the joint angle is less than the R_- (weakness zone)

(Fugl-Meyer Arm Assessment Score 15–65 out of 66; Fugl-Meyer et al. 1975) are shown in Fig. 14.3 (Levin et al. 2000). Zones were determined by stretching passive muscles at different velocities to identify STs of elbow flexors R_{f+} and elbow extensors R_{e+} and then by identifying patterns of agonist and antagonist muscle coactivation during slow full-range voluntary elbow extension and flexion. Each subject had a unique pattern of active control (blue), spasticity (black/yellow), and coactivation (black) zones within the biomechanical joint range. The range of movement in which active movement was possible is indicated from M_- to M_+. The range of M could extend beyond the active control zone, but movements made in this angular zone would be characterized by agonist/antagonist muscle coactivation. The figure shows that different patients had different angular ranges in which active movement was accomplished using reciprocal muscle activation (blue zones) and further movement was possible only with muscle coactivation (black zones). In all cases, the borders between reciprocal and coactivation zones coincided with STs identified in flexor (R_{f+}) and extensor (R_{e+}) muscles, shown for the first four subjects in Fig. 14.3.

14.1.4 Methodology Used to Identify the Range of Regulation of STs

In a series of studies, we sought to determine the upper limit of ST regulation for flexor and extensor muscles of the elbow in patients with spasticity. However, by definition, the tonic ST is the value of the threshold when the system is at rest (e.g., at zero velocity of stretch) and thus cannot be measured directly. Therefore, we developed a method to determine the velocity-dependent or *dynamic* stretch reflex thresholds (DSRTs), and then to extrapolate the value of the tonic stretch reflex threshold (TSRT) from these values. Each DSRT is the joint angle and velocity corresponding to the onset of the EMG in the stretched muscles at each stretch velocity. A regression line is plotted through the set of DSRTs and the intercept of this regression line with zero velocity is the TSRT (Fig. 14.4b and 14.4c; Mullick et al. 2013). The TSRT thus corresponds to the ST for this muscle. In nondisabled individuals, DSRTs can usually only be evoked in noncontracting muscles if the stretch is performed at very high velocities ($>300°$/s; Thilmann et al. 1991; Levin et al. 2000). However, in adults with stroke and children with CP, muscle stretches at speeds as low as 8°/s, applied to the elbow joint, can generate DSRTs.

Previous studies in patients with spasticity due to stroke or CP have shown that (1) the TSRT lies within the physiological range of motion of the elbow; (2) the TSRT value may or may not be correlated with the degree of resistance produced by the same muscles when they are stretched; (3) the TSRT may be a better measure of spasticity than muscle resistance measures (Jobin and Levin 2000; Levin et al. 2000).

Jobin and Levin (2000) measured TSRTs in elbow flexor muscles of children with CP and tested the reliability of this value as an estimate of clinical spasticity. Fourteen children with CP and eight typically developing children participated in the

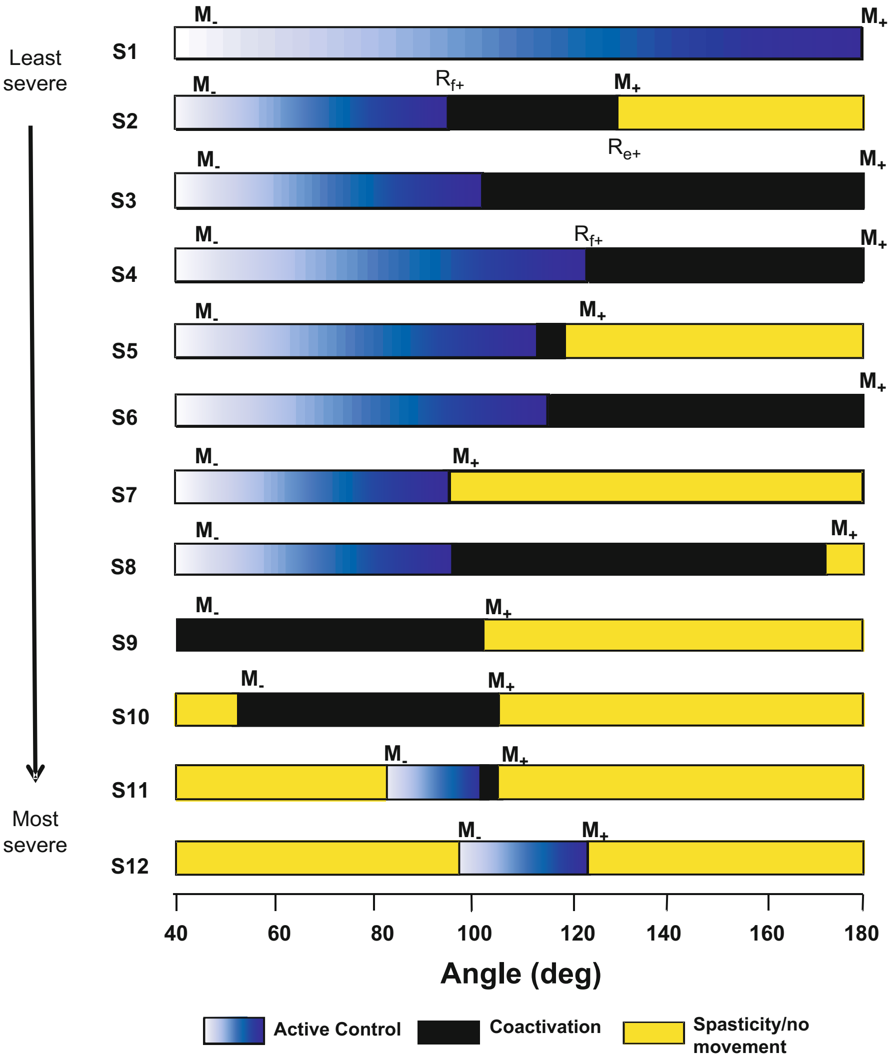

Fig. 14.3 The profiles of active control (*blue*), spasticity + coactivation (*black + yellow*) and spasticity + weakness (*yellow*) zones in 12 patients with chronic stroke (> 0.8–7.1 years post stroke) and different levels of arm paresis ranging from mild to severe (Fugl-Meyer Arm Assessment Score 15–65 out of 66). Each subject had a unique pattern of disability. Subject 1 (*S1*) had full range of movement with typical muscle innervation patterns. All other subjects had limited active control zones, while *S9* and *S10* had no active control zones throughout the entire joint range. Movements were still possible in these two subjects, but these were accomplished with muscle coactivation (*black zones*). (Adapted with permission from Levin et al. 2000)

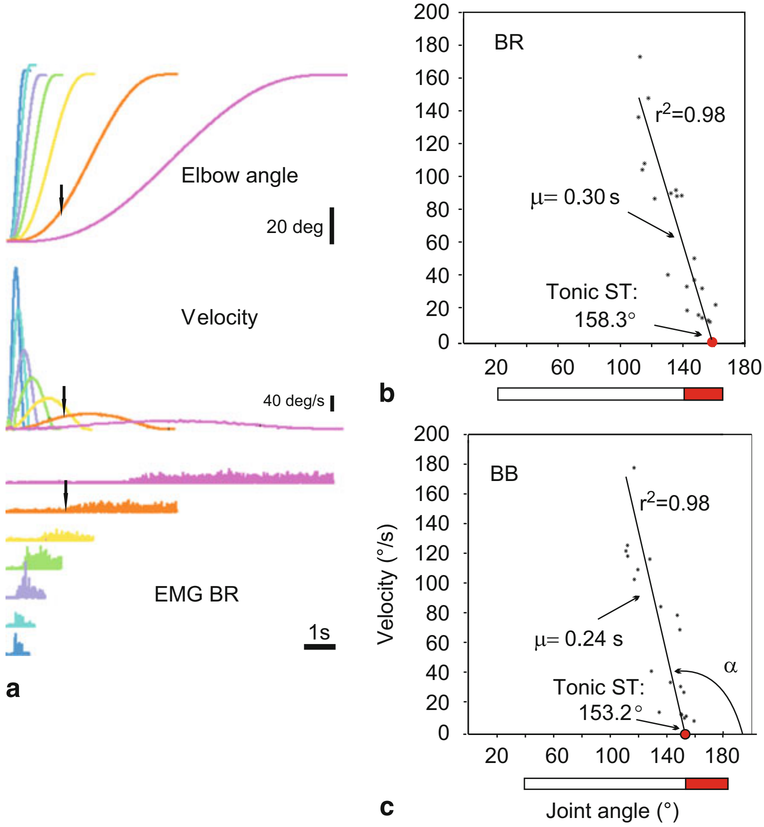

Fig. 14.4 Spasticity in a poststroke subject is associated with the presence of velocity-dependent threshold angles beyond which the muscle cannot be relaxed. **a** Single traces of elbow displacements (*top*) through a 90° range of extension at seven different velocities (*middle*) ranging from 8°/s (purple) to 160°/s (*dark blue*). Stretches were applied by a torque motor. EMG activity from Biceps Brachii (*BB*) evoked by each stretch is shown in bottom traces. Dynamic stretch reflex thresholds (*DSRTs*) are defined as the angle and velocity values at which EMG activation in the stretched muscle begins (arrows). **b, c** Example of dependencies of reflex spatial thresholds (*STs*) on velocity for two elbow flexors (*BR*, Brachioradialis; *BB*) in stroke subjects. Each point on the graphs represents the *DSRTs* for different velocities of stretch. The intercept and slope of the regression line through the *DSRTs* are the tonic stretch reflex threshold (*TSRT*) and dynamic sensitivity (μ) of the system, respectively. *Horizontal strips* below each graph show the flexor spasticity zone (*red*) and active control zone (*white*). (Adapted with permission from Mullick et al. 2013)

trial. DSRTs were evaluated by performing eight sets of stretches at seven, randomly selected velocities between 8 and 160°/s using a torque motor. For the elbow flexors, TSRT angles occurred later (closer to full elbow extension) in children with less-severe spasticity and TSRTs were only weakly correlated with clinically measured resistance to stretch of the passive muscle ($r = 0.39$). The test–retest reliability of the computed TSRTs was estimated as good (ICC = 0.73, $p < 0.001$).

14.1.5 TSRTs in Multi-Joint Muscles and Double-Joint Systems

Although the range of regulation of TSRTs can predict the location of ranges of spasticity and normal and abnormal movement patterns in a single joint, everyday gestures involve movements of more than one joint. Indeed, the TSRT value in a given muscle can be modulated by reflex interactions between muscles crossing adjacent joints (Matthews 1993; Bonasera and Nichols 1994; Ginanneschi et al. 2006; Musampa et al. 2007; Roberts et al. 2008). Interjoint interactions include autogenic facilitation; recurrent inhibition; presynaptic inhibition; reciprocal inhibition and facilitation; and heteronymous inhibition and facilitation (Cavallari and Katz 1989; Gracies et al. 1991; Katz et al. 1991; Cavallari et al. 1992; Créange et al. 1992). Interjoint reflex interactions have been identified in arm muscles in healthy subjects (Marchand-Pauvert et al. 2000; Archambault et al. 2005) and may lead to changes in net motoneuronal excitability of the stretched muscle from the convergence of information from afferents of heteronymous muscles via spinal, propriospinal, and/or transcortical pathways. In the intact nervous system, intermuscular reflex interactions have been reported for double-joint elbow muscles (Biceps Brachii and Triceps Brachii) when muscles were preactivated and placed in three different positions (McClelland et al. 2001).

In patients with poststroke spastic hemiparesis, Musampa et al. (2007) evaluated the influence of intermuscular interactions on TSRTs in uni and biarticular muscles of the double-joint elbow–shoulder system using a similar methodology as described above. They characterized the relationship between muscle length, TSRTs, and voluntary muscle activation patterns in elbow flexors and extensors and identified spasticity zones in the space of elbow–shoulder configurations from three initial positions of the shoulder (Fig. 14.5a). They also investigated how the presence of spasticity zones influenced voluntary arm movement. Similar to the previous identification of spasticity zones in a single joint (elbow; Levin et al. 2000), the limitations in the regulation of TSRTs in the double-joint arm system were shown to result in a subdivision of all-possible arm configurations into spatial spasticity zones and no-spasticity zones (Fig. 14.5b). All patients had ranges of shoulder–elbow arm configurations in which muscles could not be relaxed (spatial spasticity zones), which in some patients covered a substantial part of the biomechanically defined range of all possible arm configurations. It was also observed that these zones were practically the same for synergistic muscles and could overlap for antagonist muscle groups, such that there could be a zone in which both flexor and extensor muscles would show spasticity.

When patients attempted to voluntarily extend or flex their arm into the spasticity zones, significant abnormal agonist–antagonist muscle coactivation patterns occurred. Of note is that the angular value of the TSRTs evoked by stretching of passive muscles and the borders of the spasticity zone identified by active movement were highly correlated ($r = 0.64–0.86$), indicating a relationship between spasticity and disordered movement confined to specific areas in joint space. Thus, during active elbow extension, when the elbow reached the specific joint angle associated with the elbow flexor TSRT, elbow flexors became active and coactivation occurred. This relationship was less marked in the extensors during active flexion.

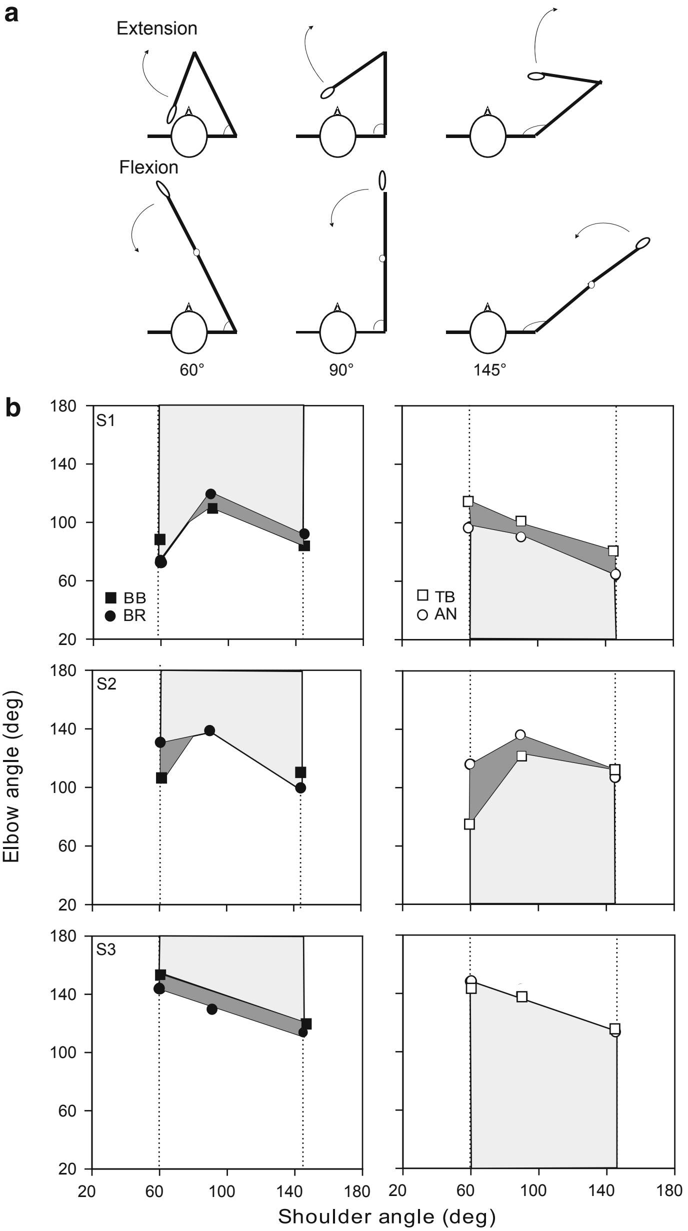

Fig. 14.5 **a** Methodology used to stretch single- and double-joint elbow muscles in order to identify the influence of initial muscle length (changes in initial shoulder position) on evoked responses. Initial position of the shoulder was varied from 60° to 145° before stretching elbow flexors (*top row*) and elbow extensors (*bottom row*). **b** Spatial thresholds (*STs*) evoked in four elbow muscles (Biceps Brachii, *BB*, *black squares*; Brachioradialis, *BR*, *black circles*; Triceps Brachii, *TB*, *white squares*; Anconeus, *AN*, *white circles*). Spatial spasticity zones are shown separately for the flexor muscles (*left panels*) and extensor muscles (*right panels*). Data from three patients with stroke-related upper

In summary, our studies have shown that limitations in the ranges of regulation of the TSRT correspond to the appearance of abnormal muscle activation patterns, such as excessive coactivation, when patients attempt to make voluntary movements (Levin et al. 2000; Musampa et al. 2007). In addition, ranges in which typical patterns of muscle activation can occur, such as reciprocal activation, have also been described using the TSRT approach. The use of this fundamental concept of threshold control based on equilibrium-point theory has led to a new and more in-depth understanding of the mechanisms underlying motor control deficits in patients with CNS lesions. Considering these findings, it may be inappropriate to view spasticity independently from the motor control deficit. Indeed, the concept of threshold control allows us to account for the spatial structure of deficits in the regulation of muscle activation and reflexes by indicating where in the biomechanical range, descending control of movement is mostly affected. Thus, it describes the control deficit in a functional context. This spatial structure of motor deficits is usually not taken into account in clinical evaluations and research on spasticity and disordered motor control, which may explain the heretofore elusive explanation of the relationship between them. Accounting for the spatial structure of motor deficits may benefit both researchers and clinicians by advancing the understanding of the mechanisms underlying unimpaired and impaired motor control. Based on this understanding, clinicians may more accurately measure these phenomena and establish more effective medical and physiotherapeutic interventions for their management.

14.2 Corticospinal Origin of Spasticity and Disordered Motor Control

In the healthy nervous system, cortical descending fibers mainly cross at the pyramidal decussation and project to muscles on the opposite side of the body (Kuypers 1985). Uncrossed fibers from the ipsilateral corticospinal tract mainly innervate axial and proximal muscles (Chen et al. 1997; Harris-Love et al. 2007). Previous studies using transcranial magnetic stimulation (TMS) in healthy subjects have shown that the corticospinal system exerts control over STs (Raptis et al. 2010; Sangani et al. 2011; Ilmane et al. 2013). Other crossed and uncrossed descending systems, such as the reticulospinal, rubrospinal, and tectospinal tracts, have also been shown to regulate STs in animal models (e.g., Feldman and Orlovsky 1972; Nichols and Steeves 1986). Of particular interest is that the crossed corticospinal tract is involved not only in the production of intentional movements but also in muscle relaxation in the entire biomechanical joint range (Raptis et al. 2010) and in anticipatory preparation of muscles to perturbations (Petersen et al. 2009; Sangani et al. 2011).

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limb hemiparesis are shown (*S1*, *S2*, *S3*). The *STs* are points on the border in shoulder–elbow joint space beyond which muscles are activated abnormally at rest. *Dark shaded areas* indicate joint space where flexors or extensors are activated. *Light shaded areas* indicated joint spaces in which only one of the two flexor or extensor muscles is active. (Adapted with permission from Musampa et al. 2007)

Stroke-related damage to cortical and subcortical systems results in an imbalance of excitatory and inhibitory activity at different levels of the CNS (Ward 2011). The presence of a tonic stretch reflex response within the biomechanical range (ST) at rest in spastic muscles implies that the resting membrane potential of α-motoneurons innervating the muscle is higher than normal (> -70mV; i.e., closer to threshold). This is supported by findings that TSRT excitation and inhibition are altered in motoneuronal pools due to interruption of the inhibitory cortico-reticulospinal pathway (Lance 1980; Powers et al. 1989) and due to changes in other descending pathways from the brainstem (e.g., Fedirchuk and Dai 2004).

With respect to voluntary movement, deficits in muscle activation result from damage to the same descending pathways mentioned above. Indeed, transmission in cortical (Shimizu et al. 2002; Bütefisch et al. 2003) and spinal (Zehr et al. 2012) neuronal circuits is impaired after stroke. The uncrossed corticospinal, rubrospinal, and reticulospinal tracts all could provide alternate routes for motor cortical output to reach the contralateral spinal cord and may result in the appearance of motor compensations (Lawrence and Kuypers 1968a, 1968a; Woolsey et al. 1972; Kuypers 1985; Fisher 1992; Fries et al. 1993; Cao et al. 1998; Belhaj-Saif and Cheney 2000). The motor cortex also sends uncrossed corticospinal projections to the spinal cord (Colebatch and Gandevia 1989; Kuypers and Brinkman 1970; Nirkko et al. 2001). Alterations in rubrospinal and reticulospinal pathways influence predominantly the proximal musculature (Nathan and Smith 1982; Nathan et al. 1996). In addition to spinal and muscle mechanisms, damage to the corticospinal system leads to an imbalance in afferent influences ascending to different brain areas, including sensory and motor cortices in ipsi and contralateral hemispheres (Lindberg et al. 2009). After stroke, greater ipsilateral corticospinal tract involvement is associated with greater compensations and poorer recovery (Perez and Cohen 2009) and an imbalance between projections from both hemispheres due to altered interhemispheric inhibition (Misawa et al. 2008).

14.2.1 Functional Consequences of Limitation in Regulation of STs

Motor deficits and abnormal movement synergies after stroke are traditionally thought to be expressions of excessive reflex activity because of the loss of descending modulatory control (Burke 1988). However, these physiological mechanisms by themselves do not explain how movement deficits arise. The concept of ST regulation allows us to describe how excessive reflex activity may lead to the appearance of abnormal movement synergies and motor compensations. In other words, it provides a means to describe how the deficits can be expressed in a spatial frame of reference, or within the context of movements made by the body. Figure 14.6 is a schematic diagram of a model of disordered motor control giving rise to abnormal synergy patterns. Each joint range, shown by horizontal bands, is characterized by spatial ranges in which active control is possible and where spasticity is present in either

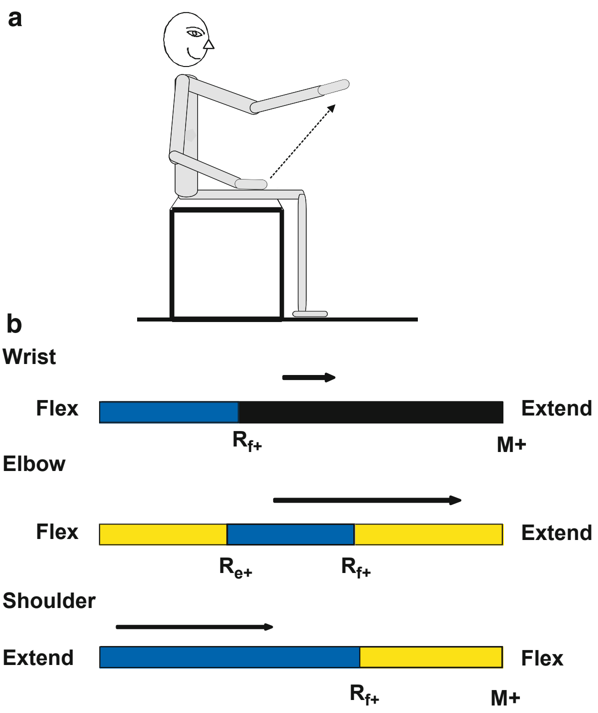

Fig. 14.6 Hypothetical model of how disordered control of spatial thresholds (*STs*) may give rise to abnormal muscle synergies. When a patient attempts to make a reaching movement **a**, the ability to activate muscles depends on the location of the *ST* within the joint range of each degree of freedom involved in the movement **b**. *STs* are indicated in each joint range as R_{f+} for flexor muscles and R_{e+} for extensor muscles and mark the angles at which spasticity begins. Ranges of movement required at each joint are indicated by horizontal arrows. For the movement shown in **a**, shoulder flexor activation is normal throughout the movement (first horizontal band—*black* range), while elbow extensors are unopposed initially (second horizontal band, *blue* zone) but coactivation of flexors occurs when R_{f+} is reached (second horizontal band—right *yellow* zone) and wrist muscles are coactivated throughout the movement (third horizontal band, *blue* zone). Abnormal interjoint couplings and restricted ranges of regulation of *STs* may explain limitations in the kinematic redundancy of the affected limbs

agonist or antagonist muscles. Active control zones are limited in each of the joints so that when movements are attempted that require one or several joints to move into spasticity zones, abnormal couplings between joints or abnormal synergies may arise. These abnormal interjoint couplings and restricted ranges of regulation of STs may explain limitations in the kinematic redundancy of the affected limbs. An example is shown in Fig. 14.5 by overlapping spasticity zones in elbow–shoulder joint space (Musampa et al. 2007). Thus, individuals who have deficits in multiple ST regulation have a limited number of possible joint combinations with which to produce different actions. If one extends this concept to more than two joints in the seven degree of freedom upper limb, then one would have multiple areas within the

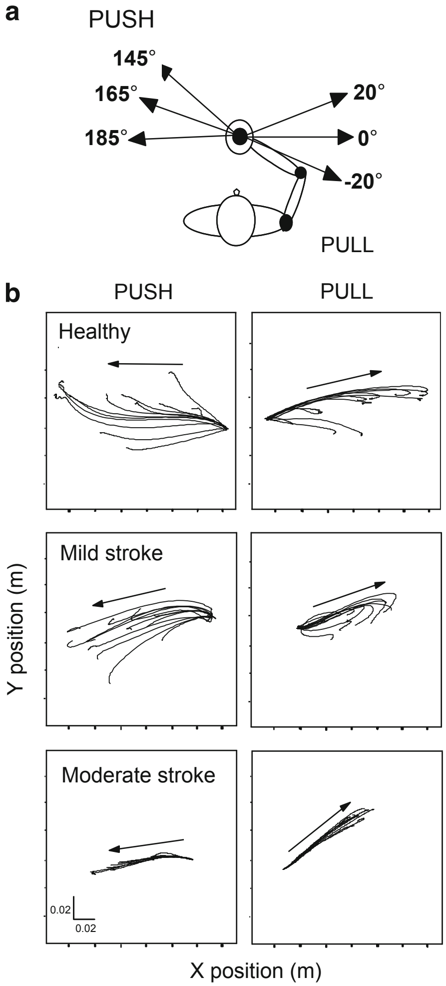

Fig. 14.7 Example of limited redundancy in upper limb movements in patients with stroke. **a** Subjects isometrically pushed or pulled a handle against a load in three different directions. The initial load of 30 % MVC was fully or partially removed in six steps for each load direction. **b** Hand trajectories after unloading for one healthy subject (*top panels*) and for two patients with stroke (*middle, lower panels*). Spatial dispersions of hand trajectories were smaller and more restricted in stroke compared to healthy subjects. (Adapted with permission from Mihaltchev et al. 2005)

3D arm workspace in which there would be restrictions in the number of available combinations of joint movements.

Another example of limited redundancy in stroke is shown for an upper limb pushing/pulling task. The subject was asked to resist a load while either pushing (Fig. 14.7, left panels) or pulling (Fig. 14.7, right panels) against it in three different directions (see Mihaltchev et al. 2005 for full details). The initial load of 30 % of their maximal voluntary contraction (MVC) was fully or partially removed in six steps for each load direction. Figure 14.7 also shows the hand trajectories after unloading for one healthy subject (Fig. 14.7b, top panels) and for two patients with stroke (Fig. 14.7b, middle and bottom panels). Compared to the healthy subject, the spatial dispersions of the hand trajectories were smaller and more restricted in terms of their variability in most participants with stroke. In this example and others (Reisman and

Scholz 2003; van Kordelaar et al. 2012), arm movements made by subjects with stroke are characterized by limitations in the variability of joint rotations, leading to stereotypical endpoint trajectories, as seen here, which are more marked in people with more severe sensorimotor impairment.

The presence of stereotypical movement patterns is related to the severity of the hemiparesis. Brunnstrom (1970) described five stages of recovery from stroke in which severe pathology is characterized by the presence of hyperactive segmental reflexes, spasticity and, when present, movement of the limbs only within defined flexor and/or extensor synergistic patterns, called “abnormal synergy patterns.” In the upper limb, the abnormal flexor synergy consists of shoulder retraction, upper arm flexion, abduction and external rotation coupled with elbow flexion, forearm supination and finger flexion. The extensor synergy includes shoulder extension, adduction, and internal rotation coupled with elbow extension, forearm pronation and finger extension. Patients at various levels of recovery demonstrate all or some of the elements of abnormal synergies when they attempt to make voluntary movements. Movements are often also characterized by compensatory movement patterns such as excessive shoulder elevation and/or shoulder protraction when attempting to flex the upper arm (Merdler et al. 2013; Niessen et al., 2008) and excessive trunk displacement when attempting to move the hand away from the body (Cirstea and Levin 2000; Levin et al. 2002). Thus, there is evidence for both limited redundancy in the joints affected by reduced ST regulation leading to a restricted range of movement with limited variability and a preserved redundancy in joints not affected by such limitations leading to the appearance of motor compensations.

Indeed, recovery of upper limb movement is often evidenced by the ability of system to express more appropriate redundancy: The appearance of fractionated movements and movements out of pathological synergies due to a decrease in synergistic coupling between joints and/or by the use of fewer compensatory motor strategies (Lang and Schieber 2004; Michaelsen et al. 2006).

14.3 Summary

Despite detailed knowledge of the anatomo-physiological changes in descending, ascending, and spinal pathways after stroke, the relationship between spasticity and disordered motor control remains elusive. Part of the problem is that these have been considered to be separate phenomena. However, the role of the corticospinal tract in regulating STs provides a mechanism by which these motor impairments can be considered together. An important consideration is that motor deficits are present when subjects with stroke move or intend to move paretic limbs while most physiological examinations of spasticity are conducted at rest. In addition, previous studies have not considered the spatial nature of the impairments when measuring corticospinal output.

The extent to which the corticospinal tract is involved in ST regulation merits further investigation. By analyzing motor deficits within the experimentally based context of ST control, it is possible to go beyond the usual characterization of motor impairments after CNS injury as separate phenomena. Consideration of the motor impairment in spasticity as being derived from a common deficit in the descending regulation of STs at which neuromuscular elements, including reflexes, begin to act, provides a way to understand the relationships between them and possibly provide an explanation for the reduced kinematic redundancy in the motor system typically seen in patients after CNS lesions. Identification of spasticity zones can also be used to monitor improvements in patient status due to pharmacological, medical, and physical treatment interventions.

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Chapter 15
Enhancing Postural Stability and Adaptability in Multiple Sclerosis

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15.1 Introduction

Multiple sclerosis (MS) is a chronic demyelinating disease of the central nervous system and is the most common neurological disease in 20 to 50 year-old individuals. People living with MS consistently rate balance and walking impairments as having the greatest negative impacts on their quality of life, yet our understanding of the cause of instability in these individuals remains limited (Ford et al. 2001; Hemmett et al. 2004). A growing body of research aims to understand the sensorimotor contributions to balance dysfunction and difficulty with walking in people with MS. Our own research on MS aims to investigate how fatigue, muscle weakness, and sensory loss interact to limit physical function and mobility (see Fig. 15.1). In this chapter, we relate aspects of somatosensory loss and symptomatic fatigue to balance function, and provide new insights into the mechanisms of balance and gait dysfunction in MS, through the use of novel analytical methods and experimental paradigms. We first review existing methods and paradigms to assess postural and gait stability in research on MS. Next, we introduce novel measures to assess the stability and adaptability of posture and gait in people with MS that are based on nonlinear and complex systems methods. These novel methods include (1) boundary-relevant measures of postural stability and control (postural "time to contact") and (2) entropy measures for assessing postural and gait adaptability that emphasize the functional role of variability in motor control. We also discuss how these methods and paradigms may help to develop innovative treatments for balance and gait dysfunction in people with MS.

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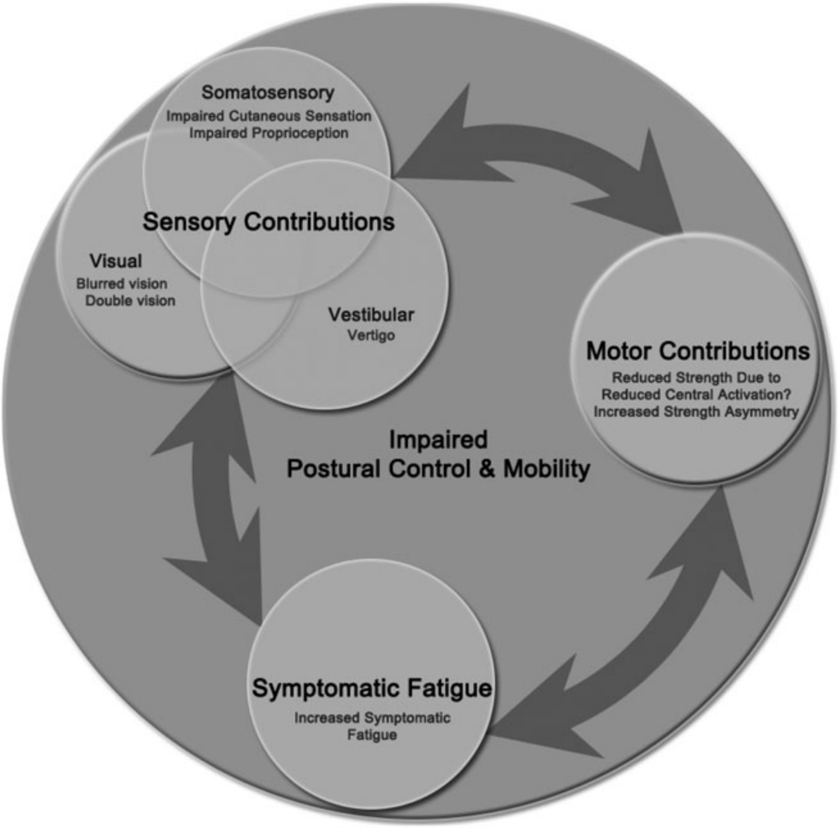

Fig. 15.1 Contribution of different subsystems to postural instability and mobility problems in multiple sclerosis (*MS*)

15.2 Changes in the Control of Posture and Locomotion in MS

Among the most devastating effects of MS is impairment of balance and mobility. Reports of balance dysfunction in individuals with MS have reached 90 % by some estimates, and roughly three-quarters of people with MS report balance impairments as having a moderate-to-severe impact on their daily functions (Ford et al. 2001; Hemmett et al. 2004). The pervasive effects of demyelination in MS can lead to complex and multifactorial impacts on balance function involving all aspects of sensorimotor function (see Fig. 15.1). Understanding the relative contributions and interactions between these systems will provide vital information with which to identify targets and modalities for interventions to slow or stall the progress of the disease-related impairments.

15.2.1 Balance Impairment in MS

The majority of individuals with MS report balance and/or mobility impairments that often worsen as the disease progresses. It has been reported that 50 % of individuals with MS will require ambulatory assistance within 15 years of their initial diagnosis (Weinshenker et al. 1989), providing a significant social and economic burden (Pike et al. 2012). Roughly half of those with MS reported falls within a 3 to 6 month period (Finlayson et al. 2006; Nilsagard et al. 2009), and despite having no increased prevalence of falls among those using ambulatory aids (Coote et al. 2013), use of these aids has been identified as a significant risk factor for falls (Cattaneo et al. 2002; Nilsagard et al. 2009). Contributors to fall risk are considered multifactorial, as fall risk has also been linked to fatigue (Coote et al. 2013), increased fear of falling (Finlayson et al. 2006), spasticity (Nilsagard et al. 2009), and impaired proprioception (Nilsagard et al. 2009). However, equivocal results on clinical balance and gait tests have been reported (Cattaneo et al. 2002; Coote et al. 2013; Nilsagard et al. 2009) that may reflect the significant heterogeneity of the MS population. In addition, it is plausible that many of the clinical tests used to assess balance and mobility in this population may not be sensitive enough to quantify the decrements that can be assessed using sophisticated, laboratory-based measures (Findling et al. 2011; Martin et al. 2006). Balance decrements, as indicated by increasing postural sway, have been shown to worsen with increased disability and progressive MS subtypes (Boes et al. 2012; Corporaal et al. 2013; Fjeldstad et al. 2011; Gutierrez et al. 2005; Soyuer et al. 2006), lending further support to heterogeneity as the source of the equivocal findings regarding balance and gait impairments. This heterogeneity may relate to the multifactorial etiology of balance dysfunction in individuals with MS that can result from a combination of underlying impairments of sensory and motor functioning.

Laboratory-based balance assessments have shown that people with MS demonstrate diminished performance on timed balance tasks (Frzovic et al. 2000; Soyuer et al. 2006), increased center of pressure (CoP) velocity (Boes et al. 2012; Porosinska et al. 2010), and increased CoP or trunk sway during quiet standing and reaching/leaning tasks (Boes et al. 2012; Corporaal et al. 2013; Findling et al. 2011; Porosinska et al. 2010; Spain et al. 2012; Van Emmerik et al. 2010). Balance in MS has also been shown to worsen with increasing difficulty of the task, either through base of support restrictions (Frzovic et al. 2000), reaching and leaning (Frzovic et al. 2000; Karst et al. 2005; Van Emmerik et al. 2010), dual tasks (Negahban et al. 2011), or altered sensory conditions (Cattaneo and Jonsdottir 2009; Fjeldstad et al. 2009; Porosinska et al. 2010; Spain et al. 2012).

Individuals with MS, particularly those with vestibular or proprioceptive impairment, demonstrate increased reliance on the visual system during balance tasks (Soyuer et al. 2006; Van Emmerik et al. 2010), since removal of vision has one of the most profound effects on balance performance during standing postural tasks. This compensation may be necessary, given the high prevalence of somatosensory impairments demonstrated by individuals with MS (Citaker et al. 2011; Kelleher et al. 2010; Soyuer et al. 2006; Van Emmerik et al. 2010). Indeed, balance responses demonstrated by those with MS show alterations consistent with an etiology of somatosensory impairment (Cameron et al. 2008; Corporaal et al. 2013). Postural responses to unexpected balance disruption are significantly delayed, resulting in hypermetric responses to successfully maintain balance (Cameron et al. 2008). These delays correlate with delays in spinal transmission of somatosensory-evoked potentials, suggesting that individuals with MS may have impaired transmission, and/or processing of somatosensory information. In addition, strong relationships between impaired somatosensation and balance ability in people with MS have been reported (Citaker et al. 2011; Corporaal et al. 2013).

15.2.2 Motor Impairments, Strength, and Balance in MS

Deficits in somatosensory function may require greater control from higher brain centers in those with MS. Enhanced predictive scaling of postural response magnitudes, to unexpected perturbations when the perturbation amplitude is known *a priori* (Cameron et al. 2008), has been demonstrated among individuals with MS, which may be indicative of increased reliance on the cerebellum and cortical structures. Feedforward control of posture is also disrupted in those with MS, possibly reflecting the impact of MS on balance mediated by higher brain centers (Krishnan et al. 2012b). Delayed onset of anticipatory postural adjustments (APAs) (Jacobs and Kasser 2012a; Krishnan et al. 2012a), as well as reduced magnitude of the APA and ability to move the center of mass (CoM) to its stability limits (Krishnan et al. 2012a), have been identified in those with MS. These delays are exacerbated under dual task conditions (Jacobs and Kasser 2012b), further supporting a greater involvement of the higher brain centers in control of APAs in those with MS.

Despite these severely delayed postural responses, the magnitude of postural adjustments is not reduced in MS, suggesting little impairment in the efferent pathways that compose balance responses (Cameron et al. 2008). This is puzzling, given evidence that individuals with MS demonstrate strength reductions (De Haan et al. 2000; Newsome et al. 2011; Rice et al. 1992) that can be traced to both peripheral and central deficits (Newsome et al. 2011; Ng et al. 2004). Most studies demonstrate impaired strength in those with MS, although this may be more evident in dynamic rather than isometric paradigms (Chung et al. 2008). It has been suggested that these strength differences, particularly those that correlate with walking or balance impairments, may be related to central impairments in motor drive (Chung et al. 2008; De Haan et al. 2000; Ng et al. 1997, 2004) as demonstrated by reduced central activation ratio and reduced ability to perform rapid foot taps. Although peripheral motor impairments in the form of reduced relaxation time (Ng et al. 2004), slower contraction speed (Ng et al. 2004), and perhaps lower oxidative capacity (Kent-Braun et al. 1994) and atrophy (Kent-Braun et al. 1997) have been identified in those with MS, these may be secondary to reduced central activation leading to decreased motor neuron discharge (Kent-Braun et al. 1997; Ng et al. 2004). Importantly, there appears to be a link between motor impairments and balance performance, given that a greater knee joint power asymmetry was related to reduced balance performance during quiet standing (Chung et al. 2008).

15.2.3 Relationship Between Fatigue and Balance and Mobility in MS

The above-described motor impairments may be exacerbated by both central and peripheral fatigue. Fatigue experienced by those with MS, termed “symptomatic fatigue,” differs from what is experienced by healthy adults and has been defined as “reversible motor and cognitive impairment with reduced motivation and desire to rest, either appearing spontaneously or brought on by mental or physical activity, humidity, acute infections, and food ingestion. It is relieved by daytime sleep or rest without sleep. It can occur at any time, but is usually worse in the afternoon” (Mills and Young 2008). Fatigue has not been shown to correlate with measures of central activation or other measures of muscle function (Ng et al. 2004).

Symptomatic fatigue in those with MS has been correlated with perceived walking impairment and balance confidence (Noguiera et al. 2013), and with a decline in walking speed during the 6- and 12-min walk tests (Burschka et al. 2012). These declines occurred at a greater rate in those with moderate MS compared to healthy controls. Symptomatic fatigue has also been negatively correlated to performance on standing balance assessments. Both acute (Visual Analog Fatigue Scale) and chronic (Fatigue Severity Scale) measures of symptomatic fatigue correlate modestly with increased postural sway during quiet standing in those with MS (Chung et al. 2008). However, symptomatic fatigue appears to have a stronger relationship with balance as postural challenge increases. Specifically, the Modified Fatigue Impact Scale has strong negative correlations for both the physical and cognitive subscales with balance as assessed by the sensory organization test (posturography) (Hebert and Corboy 2013), particularly during tasks in which somatosensory feedback was nullified and vision manipulated. Indeed, 62 % of the variance in balance scores was explained by symptomatic fatigue, pointing to a significant relationship between fatigue and balance. Standing balance assessment, following a fatiguing protocol, supports a greater effect on balance in those with MS as task difficulty increases (Van Emmerik et al. 2010). Individuals with MS demonstrate reduced forward lean performance and decreased postural stability in backward leans, but no effect on quiet standing following fatiguing protocols (Van Emmerik et al. 2010). These findings suggest that symptomatic fatigue has the potential to greatly impact balance in those with MS and may require functional adaptations to operate safely within the environment, particularly as fatigue heightens throughout the day and following physical exertion.

15.2.4 Altered Walking Patterns in MS

To combat reduced balance ability that is exacerbated by fatigue, individuals with MS may rely on proactive behavior during voluntary movements to compensate for peripheral sensory and motor impairments. Individuals with MS walk in a more cautious way, typified by slowed walking velocity, shorter stride lengths, increased stride width, and a prolonged double-support phase (Benedetti et al. 1999; Gianfrancesco et al. 2011; Remelius et al. 2012; Sosnoff et al. 2012). These stride changes are accompanied by decreased ankle, knee, hip, and trunk ranges of motion (Corporaal et al. 2013; Huisinga et al. 2013; Martin et al. 2006) in the sagittal plane and increased trunk range of motion in the frontal and transverse planes, with the frontal plane being the most discriminative between individuals with and without MS (Spain et al. 2012). Kinetic alterations also provide evidence of a more cautious walking pattern with reduced frequencies of vertical forces (indicating a reduced vertical oscillation and perhaps a less dynamic walking pattern) (Wurdeman et al. 2011) and reduced torques at the lower limbs, particularly when torque would contribute to propelling the body forward (e.g., reduced dorsiflexor torque during early stance and plantar flexor torque during late stance) (Huisinga et al. 2013). Increased co-contraction of ankle musculature through the stance phase, accomplished through early onset of gastrocnemius and late relaxation of the tibialis anterior muscles, has also been observed and may act to stiffen the ankle joint during the stance phase (Benedetti et al. 1999).

While these gait alterations are widely reported, the majority of these research studies have made comparisons between individuals with and without MS in which the groups differed in their walking speeds. Thus, the altered gait parameters reported could represent speed-related group differences as opposed to alterations that were related to MS. Recent studies have supported that at least some of these parameters appear to be different between MS and non-MS independent of walking speed; specifically, increased stride width and prolonged double-support phase have been identified even when MS and control cohorts walk at matched speeds (Remelius et al. 2012). Kinematics, kinetics, and muscle activation have yet to be studied between those with and without MS at matched speeds. However, when using walking speed as a covariate, reduced joint ranges of motion and torque appear to be MS-related gait characteristics (Huisinga et al. 2013).

Gait modifications that are characteristic of a protective strategy may reflect an attempt to increase stability. Wider strides enable the walker to maintain a larger base of support, and increased double support time could be an attempt to prolong foot contact with the ground, both of which could reflect an attempt to increase walking stability. Prolonged foot contact would also allow for increased peripheral sensory feedback from the foot-surface interface, which may be of vital importance in those with MS who have reduced cutaneous sensitivity. Individuals with MS also alter their body position by leading with their trunk and head, as opposed to their swing foot, particularly at higher walking speeds, which may represent an attempt to gain further sensory information by enhancing visualization of step placement (Remelius et al. 2012). Although these strategies may be an attempt to enhance stability of the movement, they may precipitate detrimental consequences that could instead increase the likelihood of balance loss. Prolonging double support time requires a shortened swing time if walking speed is to be maintained; however, hastening swing time may prove destabilizing, potentially increasing the likelihood of balance loss during the single support phase of walking (Remelius et al. 2012). In addition, attempting to gain more visual information during walking may necessitate the more forward directed head/trunk position demonstrated by individuals with MS (Remelius et al. 2012). However, this body position could prove to be less stable, given that the body CoM is closer to the forward stability boundary, providing less time to respond to unexpected balance perturbations.

15.3 Boundary-Relevant Measures of Posture and Gait: Time to contact

We now turn to a discussion of boundary-relevant measures of postural stability and control (postural "time to contact") that have emerged from complex and nonlinear systems approaches. A central element in assessing stability and adaptability is the relation between essential movement variables such as body CoM and stability boundaries formed by the base of support at the ground. It is anticipated that this approach will offer novel insights into MS-related changes in static and dynamic postural control and help determine whether these changes represent a functional adaptation to maintain stability or reflect MS-related limitations.

15.3.1 Stability Boundaries and Postural Fluctuations

Postural instability in MS during upright standing is often associated with increased CoP standard deviation, sway area, or average velocity (Chung et al. 2008; Fjeldstad et al. 2011; Van Emmerik et al. 2010). However, as we and others have argued, postural fluctuations can provide functional information regarding (1) geometry of support surface, (2) state of disequilibrium, and (3) approach to boundaries (Riccio 1993). From this perspective, postural fluctuations can be an expression of both exploratory and performatory aspects of postural sway (Riley et al. 1997; Slobounov et al. 1997; Van Emmerik and Van Wegen 2002).

Standing balance is maintained when the CoM of the body remains within the boundaries of the base of support at the foot–ground interface (Fig. 15.2a). While in standing balance this base of support is fixed, under dynamic conditions, such as locomotion, these boundaries continually shift (Fig. 15.2b). Fluctuations in the foot CoP during upright stance control the CoM and stabilize the body under different postural conditions (Winter 1995). To quantify dynamic balance with respect to these boundaries, the time to contact the stability boundary can be obtained by

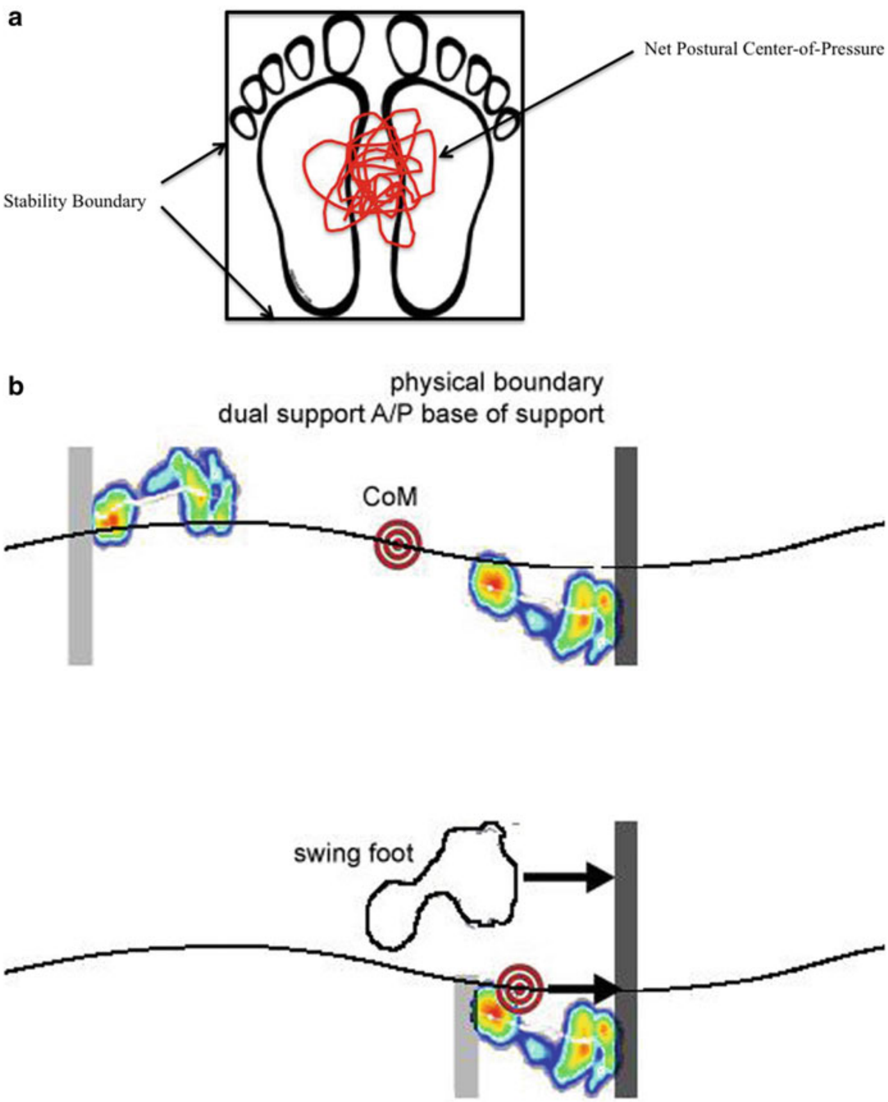

Fig. 15.2 Static (**a**) and dynamic (**b**) base of support

assessing the instantaneous distance, velocity, and/or acceleration of the CoP or CoM (Hasson et al. 2008, 2009; Remelius et al. 2008; Van Wegen et al. 2001, 2002). Research on CoP and CoM control, relative to these stability boundaries, has provided novel insights regarding the role of postural fluctuations. For example, postural control research in Parkinson's disease has shown that the time-to-contact variability of the CoP to the stability boundary at the feet is lower in people with Parkinson's disease compared to controls (Van Wegen et al. 2001; Van Emmerik et al. 2013). In contrast, CoP displacement variability was larger in the Parkinson group, a result consistent with previous findings in the literature. These postural fluctuations in relation to the stability boundary, as measured by time to contact, may facilitate the pickup of perceptual information regarding boundaries between stable and unstable postures and therefore enhance postural stability and adaptations in response to changing conditions. Time to contact the postural support boundaries may therefore be a sensitive measure in assessing postural stability.

The original time-to-contact concept emerged from vision research that sought to characterize the visual perception of a distance closure (gap closure) as a directly perceivable temporal variable called *tau* (τ) (Lee and Lishman 1977; Lee 2009). Lee's general tau theory states that: (1) all purposeful (prospective) movements entail controlling the closure of action gaps (between effectors and goals), (2) the time to closure of the action-gap (at current rate), *tau*, is what is sensed and controlled and directly perceivable in any sensory modality, and (3) the principal method of movement guidance is coupling and coordinating *tau*'s of different action gaps. In the remainder of this section, we will address all three aspects of Lee's General Tau theory by examining time to contact in the postural and locomotor control domains. This was originally developed by Riccio (1993) and formalized by Slobounov et al. (1997).

15.3.2 Boundary-Relevant Analysis of Postural Control

Research assessing spatial limits with respect to the base of support has been in existence for some time (e.g., McCollum and Leen 1989), and work by Said et al. (2008) assessed the spatial separation of the CoM and CoP in relation to the stance foot–heel boundary during walking over obstacles. Pai and Patton (1997) and Espy et al. (2010) used a phase space (position–velocity) representation as a "dynamic" boundary to identify regions of initiation for forward and backward falls during upright stance and walking. Spatiotemporal proximity to the stability boundary based on Lee's (2009) visual *tau* and Riccio's (1993) expansion to the postural domain has recently inspired a rapidly developing line of research on postural time to contact, with applications to aging (Forth et al. 2007; Slobounov et al. 1998; Van Wegen et al. 2002), neurological disorders (Van Wegen et al. 2001; Remelius et al. 2008; Van Emmerik and Van Wegen 2002; Van Emmerik et al. 2010), orthopedic injuries (Hertel and Olmsted-Kramer 2007), as well as conceptual/methodological developments (Haddad et al. 2006; Hof et al. 2005; Slobounov et al. 1997).

In research on people with MS, studies have found reduced postural time to contact in upright standing tasks with sensory manipulations (Van Emmerik et al. 2010; Cattaneo 2012). Van Emmerik et al. (2010) observed decreased time to contact of the CoM to the support boundaries under a variety of postural tasks, including reaching and leaning in different directions. Cattaneo (2012) found time to contact to be a sensitive and valid method to assess balance changes in MS under static balance conditions (comparing sold and compliant surfaces) and sensory manipulations (eyes open and closed). The static time to contact, however, was not found to be a predictor of falls in the MS group in this study (Cattaneo 2012). These results suggest that time to contact may be a more sensitive measure when used under dynamic conditions, such as in balance perturbations or locomotion.

15.3.3 Time to Contact and the Initiation of Stepping

The majority of studies to date using postural time to contact have assessed differences between populations. During gait initiation, Remelius et al. (2008) observed reduced gait initiation speed, a wider stance base, longer time to contact, and reduced anticipatory postural reactions during the initiation of gait in MS. These results indicate functional adaptations in people with MS that reduce proximity to stability boundaries prior to stepping. Whether or not these adaptations are possible and observed during gait initiation at different speeds is not known.

Little research exists addressing Lee's (2009) claim that time to contact is sensed and controlled in any modality. Slobounov et al. (2009) asked participants to stand on one leg as long as possible and assessed the transition to stepping back on two legs. They found that minimum time to contact (and variability) increased during the transition to instability. Time to contact may also function as a control parameter in the transition from a stationary base of support to taking a step (Hasson et al. 2008, 2009). In earlier research, we investigated the postural responses elicited by balance perturbations of increasing magnitude applied to the upper body in younger and older adults (Hasson et al. 2008, 2009). A key variable in the analysis of postural responses was the time to contact the anterior stability boundary. We found that minimum time to contact predicts the perturbation level that elicits a stepping response that acts to create a larger base of support and maintains postural stability. Healthy older adults (without a history of falls) stepped at lower perturbation levels than younger adults, but this response was functional as they experienced greater CoM accelerations. In both age groups similar time to contact and muscular response patterns to increasing perturbation magnitude were observed, suggesting that time to contact may be used as an informational variable to regulate muscle activity in maintaining postural stability (Hasson et al. 2009).

15.3.4 Dynamic Time to Contact: Changing Boundaries During Locomotion

Gait research has found that people with MS walk with a slower preferred speed, shorter stride length, altered limb kinematics, and longer dual-support times (Benedetti et al. 1999; Martin et al. 2006; Kelleher et al. 2010; Remelius et al. 2012). Many of the altered gait parameters that have been observed during walking could be due to different gait speeds between MS and control groups. Remelius et al. (2012) controlled for gait speed and found that the increased dual-support time at preferred speed is also present when speed is controlled for. At slow (0.6 m/s), medium (1.0 m/s), and fast speeds (1.4 m/s), the MS group showed increased dual support times compared to age-matched controls. This increased dual support time may be seen as a protective gait strategy in which people with MS adapt their gait to optimize dual support to enhance stability. However, Remelius et al. (2012) also

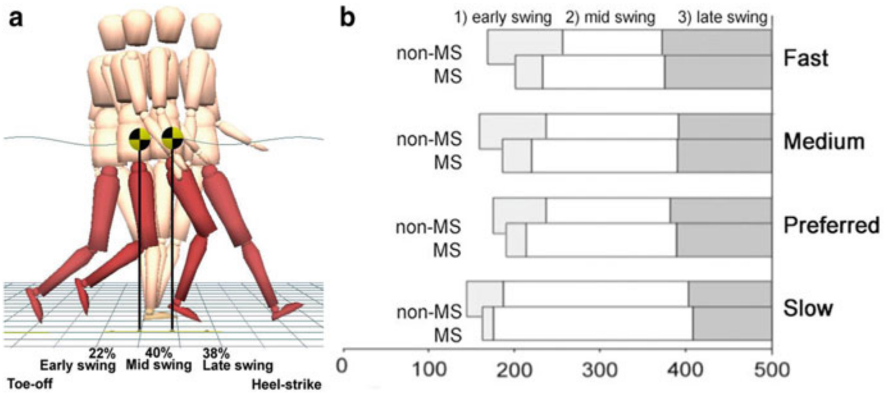

Fig. 15.3 **a** Partitioning of swing into phases relative to the boundaries of the base of support. *Early swing*: from toe-off to center of mass (*CoM*) reaching heel boundary. *Mid swing*: CoM moves from heel-to-toe boundary. Late swing: from CoM passing the toe boundary to next heel contact. **b** Differences in timing (ms) of phases of swing between an individual with MS compared to age- and gender-matched control

found that at slower and faster imposed speeds the MS group altered the kinematics of swing to accommodate these dual-support adaptations. These alterations in swing could provide different challenges to postural stability, as discussed below.

Phases of swing are usually defined on the basis of lower extremity kinematics, such as maximal knee joint angle (Winter 1983). However, the phases of swing can also be defined by the position and movement of the CoM relative to the stability boundary formed by the base of support at the foot–ground interface. In this approach, two events serve to partition swing: the point in swing when the CoM moves in front of the posterior limit of the stance foot (heel), and when it moves beyond the anterior limit of the stance foot (toe) in the sagittal plane. Thus, the phases of swing can be defined as: early swing (CoM of body behind the stance foot), mid swing (CoM of body between heel and toe of the stance foot), and late swing (CoM in front of the stance foot) (see Fig. 15.3a). Our proposed description of swing thus defines the phases of swing in organism–environment relevant terms, here represented by the movement of the CoM in relation to the limits of the base of support at the body–ground interface. Figure 15.3b shows the changes in these three phases of swing when comparing walking in a person with MS to a healthy age-matched control. In the person with MS, there is a decrease in early swing time and an increase in mid swing, with the late swing timing left relatively intact compared to the healthy control participant. These changes are representative of group differences observed by Remelius et al. (2012) and highlight the increased importance of the mid-swing part of gait when the CoM is positioned over the single base of support of the stance leg.

As indicated earlier, increased dual-support times during walking in people with MS may be adaptive and increase stability during gait, but Remelius et al. (2012)

suggested that these adaptations may also require potentially destabilizing modifications to the swing-phase dynamics of walking. In the Remelius et al. (2012) study, we found that individuals with MS positioned their head and body CoM closer to the anterior support boundary compared to non-MS controls when entering the unstable equilibrium of the swing phase (the point at which the swing foot passes the anterior boundary of the base of support). At faster velocities, the head even tended to lead the swing foot into the unstable equilibrium for individuals with MS (see Fig. 15.4a). This altered sequence in the approach to the unstable equilibrium may indicate an attempt to better visualize step placement, as we have also found that people with MS maintain a head orientation (and presumably point of gaze) closer to the body compared to age-matched controls (Fig. 15.4b). This increased reliance on visual control of foot placement and swing formation likely results from decreased somatosensory function. However, these adaptations could have serious implications for stability during this phase because the swing foot may be in a less optimal position to reestablish the base of support, should balance be perturbed (Remelius et al. 2012). Further study is needed to determine whether the functional adaptation to lengthen dual-support time is related to increased risk of falls for individuals with MS.

The CoM time to contact (TtC_{CoM}) of the approach towards the stability boundaries can be computed by dividing the first derivative of CoM position (velocity, Eq. 15.1) by the distance between the current position of the CoM and the physical boundary (B_{p}: the stance foot toe) or the anticipated boundary (B_{a}: heel of the next foot contact):

$$TtC_{\mathrm{CoM}}(s) = \frac{B_{\mathrm{p,a}} - CoM(m)}{velocity_{\mathrm{CoM}}(m/s)} \tag{15.1}$$

where $B_{\mathrm{p,a}}$ can either be the physical (B_{p}) or anticipated (B_{a}) boundary. The swing foot time to contact ($TtC_{\mathrm{swing\ foot}}$) is computed similarly. The B_{p} and B_{a} locations are obtained from kinematic records post-hoc. Examples of the time-to-contact approach to the physical boundary for a participant with MS and an age-matched control are presented in Fig. 15.5. To investigate Lee's (2009) third aspect of his general tau theory, that movement guidance emerges from coupling different tau's, coupling ratios can be computed to describe the relationship between temporal closures and coordination of the CoM and swing foot with the physical boundary (B_{p}) or the anticipated boundary (next step landing area; B_{a}):

$$\frac{TtC_{\mathrm{swing\ foot}}}{TtC_{\mathrm{CoM}}} = K_{\mathrm{p,a}} \tag{15.2}$$

where $K_{\mathrm{p,a}}$ can either be the coupling ratio for the approach to the physical (K_{p}) or anticipated (K_{a}) boundary. The point in swing when the coupling ratio (K_{p}) becomes less than 1.0 indicates when the $TtC_{\mathrm{swing\ foot}}$ has dropped below TtC_{CoM} in the approach to the B_{p}, signifying that the swing foot will arrive before the CoM enters the unstable equilibrium, and the swing foot will lead the body in the approach to the next anticipated boundary. A $K_{\mathrm{p}} = 1$ that occurs later in the swing phase may

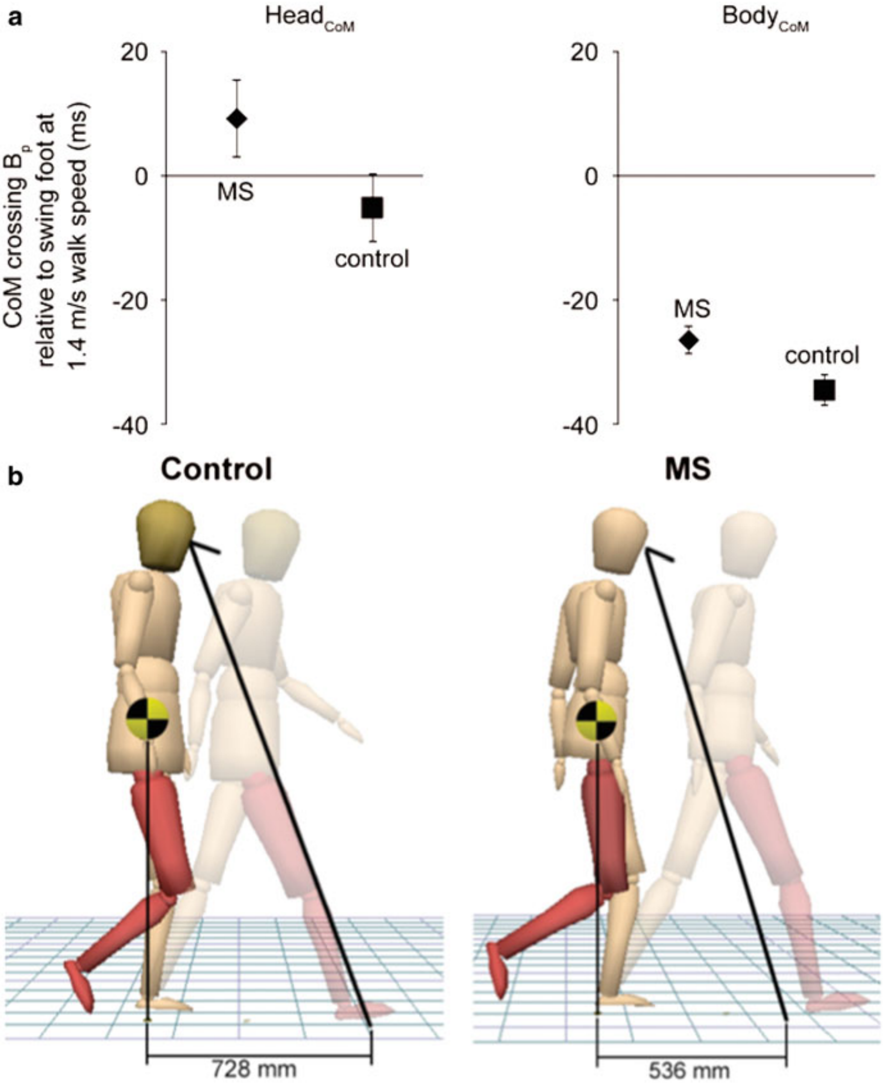

Fig. 15.4 **a** Timing of center of mass (*head and body*) and swing foot relative to crossing the anterior stability boundary (B_p) while walking at 1.4 m/s. Negative values: CoM crossing after swing foot; positive values: CoM crossing before swing foot (adapted from Remelius et al. (2012). **b** Projection of head orientation on the surface of support in the direction of locomotion. Distances indicated are from the intersection of the head vector on the ground to the body (the vertical projection of the CoM)

indicate a less stable final part of swing and less controlled foot placement. This can be observed in the time-to-contact time series and coupling ratio in the case of a person with MS (see Fig. 15.5); the $K_p = 1$ occurs later in the swing phase compared to the age-matched control (24 % versus 9 % of swing).

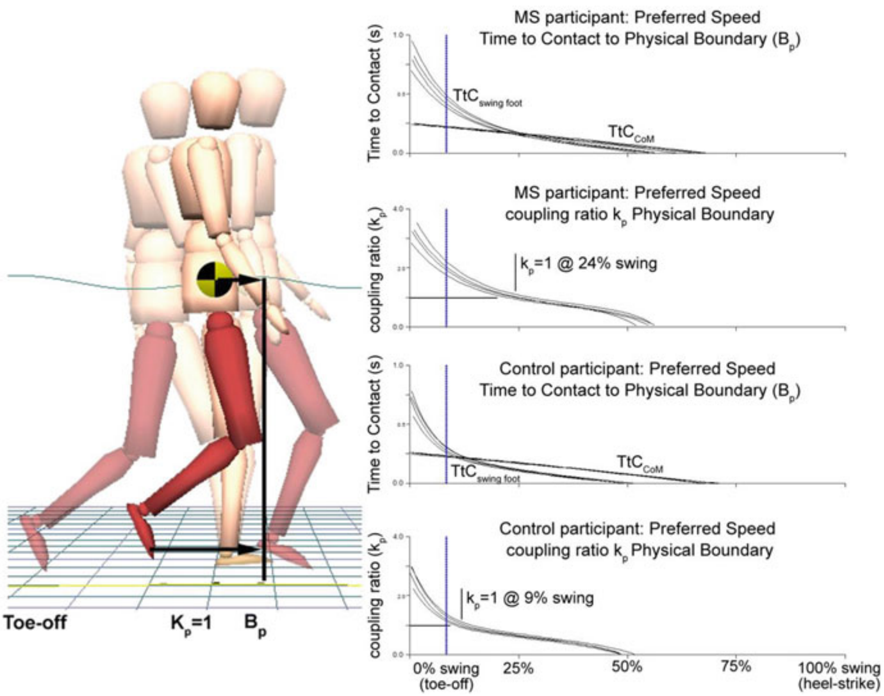

Fig. 15.5 Time to contact the physical (B_p) boundary for swing leg and body CoM and their coupling ratio for a control and MS participant

The coupling ratio K_a (Eq. 15.2) reflects the approach to the anticipated boundary and quantifies the difference in contact estimates of the swing foot and the CoM. A high K_a ratio indicates the CoM arriving shortly after the swing foot, whereas a low K_a ratio indicates a longer estimated time between swing foot arrival at the B_a and the eventual CoM arrival. Espy et al. (2010) provided evidence that a higher CoM velocity (associated with greater overground gait speeds) increases stability and reduces falls when exposed to a slip upon foot contact. As a higher CoM velocity is likely linked to a reduced time to contact, this would mean that a higher K_a ratio results in a safer step-landing pattern, reducing the probability of balance loss during a slip. However, a ratio approaching 1 would indicate simultaneous arrival of the CoM and swing foot and less of a controlled fall during late swing with little time for proper foot placement before full weight acceptance. The relation between this ratio and gait stability may therefore be U-shaped with optimal stability between 0 and 1. People with mild-to-moderate impairment due to MS were found to have similar K_a ratios compared to age-matched controls, suggesting that the approach to the step-landing area is preserved during walking (Remelius 2012). This may be the result of different body and head orientations during walking that enable greater visual input of foot placement and the step-landing area (Remelius 2012). This ratio may be affected in those with greater disability and balance disturbances due to their MS.

In summary, the boundary-relevant measures of postural and gait control presented here, together with the time-to-contact analysis, have provided novel insights into the formation of swing during walking in people with MS. These findings indicate systematic changes in the approach to the unstable equilibrium (the “controlled fall” phase of gait) that may reflect instability and potentially greater vulnerability to postural perturbations. In contrast, the analysis also showed that the approach to the step-landing area is preserved in people with mild-to-moderate MS, possibly due to greater use of vision of the immediate area under the feet.

The approach presented here assesses postural stability in relation to the stability boundaries and has significant potential in furthering our understanding of changes in postural stability due to aging and various pathologies. Another promising approach is the assessment of fluctuations in movement variables such as the CoP or the CoM on the basis of entropy analysis that can quantify the complexity and adaptability of the movement dynamics.

15.4 Nonlinear Entropy Analysis of Posture and Gait: Assessing Movement Adaptability in MS

Current research in the biological and physical sciences stresses the beneficial and adaptive aspects of variability that emerge from the interaction of the many degrees of freedom in a complex system (Glass 2001; Lipsitz 2002; Van Emmerik and Van Wegen 2002). These developments question the previously dominant perspective in which decreased variability is universally associated with increased competence, skill, and health. Instead, the path to frailty or disease is identified by a loss of variability in fundamental variables reflecting biological function, as well as reduced “complexity” related to the interactions between the multiple degrees of freedom (Glass 2001; Lipsitz 2002). Over time, reductions in effective degrees of freedom as well as loss of interactivity between them may become associated with a loss of variability. When these reductions in degrees of freedom and variability reach a critical threshold, injury or disease may emerge. Various nonlinear analysis tools have been developed to assess these changes in system complexity or adaptability, including Lyapunov analysis, detrended fluctuation analysis, and various assessments of entropy (Glass 2001; Lipsitz 2002). In the next sections, we discuss developments related to entropy measures, and how these have been used to assess changes in the nature of movement control in people with MS.

15.4.1 Introduction to Entropy Analysis for Posture and Gait

The movement science literature has seen a recent emergence of various entropy analysis techniques to assess the complexity and adaptability of human motion by quantifying fluctuations in physiological time series data. Currently, there are three different entropy measures used in the analysis of postural and gait control: Approximate entropy (ApEn; Pincus 1991), sample entropy (SampEn; Richman and Moorman 2000), and multiscale entropy (MSE; Costa et al. 2002), all of which are estimates of Kolmogorov entropy. While each measure operates with slightly different computational mechanics, all are nonlinear techniques intended to assess time series fluctuations. Richman and Moorman (2000) outlined limitations of the ApEn method and provided an alternative measure, SampEn, for the estimation of the complexity of biological time series. A major issue with ApEn is that entropy measures can be inflated due to self-matching bias (i.e., comparing a single data point to itself) when assessing similarity between points in the time series. The power of SampEn has been expanded by the work of Costa and colleagues (Costa et al. 2002, 2005, 2007) into MSE, which determines SampEn over many time scales, and then calculates the integral of the resulting curve to compute the complexity index (C_i), a measure that is informative of how complexity changes over the time scales in question. A meaningful way to evaluate the outcomes of entropy calculations is through the "loss of complexity hypothesis" (Lipsitz and Goldberger 1992), which views loss of system complexity as a pathway to disability or injury. Analysis of postural and locomotor fluctuations based on entropy analysis has the potential to augment our understanding of how different diseases, such as MS, constrain the movement output and limit adaptability of the system.

15.4.2 Loss of Complexity

Lipsitz and Goldberger (1992) introduced the loss of complexity hypothesis in the early 1990s, and have provided evidence for the framework in light of some challenges to its premises (Vaillancourt and Newell 2002). The insight conferred by studies using MSE analysis provides a robust way of evaluating the complexity of physiological systems, where reduced complexity can lead to maladaptive outcomes, such as loss of balance and falls. Various studies examining aging and frailty have demonstrated loss of complexity in postural control using entropy measures (Costa et al. 2002, 2005, 2007; Kang et al. 2009; Manor et al. 2010). The inclusion of multiple time scales in the MSE analysis, rather than a single time scale approach, allows for a more complete view of the dynamics of the relevant physiological processes that impact postural control in individuals with MS (Goldberger et al. 2002). Single time-scale approaches are limited, as the observed differences or similarity in entropy at a particular time scale may not be representative for other relevant time scales that impact system dynamics.

The strength of entropy-based methods compared to other measures of time series variability is that point-to-point fluctuations in noncyclical tasks can be analyzed, such as those observed in postural control of the CoP. Entropy analysis of the CoP allows assessment of postural fluctuations through estimates of the amount of Shannon Information (Shannon and Weaver 1949) within the signal. Signals with higher entropy values, regardless of method used, contain greater information and are thereby deemed more complex. The particular advantage of the MSE entropy method is that it provides the most comprehensive insight into how the complexity varies over the multiple time scales that are of physiological relevance to a particular biological signal.

15.4.3 Complexity Changes due to MS

As mentioned earlier, balance and gait impairments in people with MS are common and can have major impact on quality of life and daily activities. Increased understanding of adaptability through entropy analysis during static and dynamic movements may provide insights into how the disease impacts a person's ability to suitably adapt responses to postural challenges. ApEn has been used to evaluate changes in postural control in people with MS (Huisinga et al. 2012), and shown that people with MS exhibit reduced ApEn values during quiet standing in the mediolateral CoP time series (with both eyes open and eyes closed). These changes in the point-to-point fluctuations as measured by ApEn may be indicative of a reduced ability to manage unexpected perturbations, especially in the mediolateral direction. These changes in postural control fit well with the conclusion from Maki et al. (1994) that impaired mediolateral control of posture may place subjects at increased fall risk. The lack of differences observed in anterior–posterior CoP fluctuations may arise from previously noted issues with the ApEn measure (Richman and Moorman 2000).

Kaipust et al. (2012) examined spatial aspects of the walking-gait cycle at a self-selected speed, and found reductions in ApEn in those with MS compared to controls. There was, however, no ability to differentiate those with mild from moderate impairment due to MS, indicating that ApEn may lack the sensitivity to distinguish between MS subpopulations. MSE has shown to be effective in distinguishing between clinical subgroups in those with adolescent idiopathic scoliosis (Gruber et al. 2011) as well as identifying systematic differences between older individuals with and without a history of falls (Costa et al. 2007), frailty (Kang et al. 2009), and sensory impairments (Manor et al. 2010). The outcomes of these postural studies indicate that MSE analysis may have the ability to discriminate between those with and without MS and/or different MS subtypes.

15.4.4 Multiscale Entropy: An Example

Here, we will present a comparison of the mediolateral CoP time series during quiet upright standing for a person with mild MS and an age- and gender-matched person without MS. The purpose of this comparison is to demonstrate how MS impacts CoP fluctuations. The MSE analysis represents data across ten time scales of interest, ranging from 0.11–0.2 s. This analysis uses an $r = 0.15$ of the standard deviation

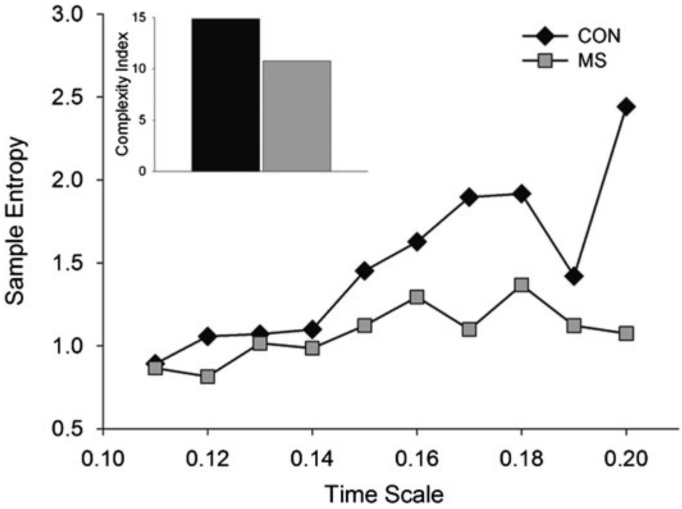

Fig. 15.6 Example of multiscale entropy (*MSE*) of the medial–lateral foot center of pressure (*CoP*) for one MS and one control participant.Time scale in (s). *Inset*: Complexity index across all time scales

across the entire time series and $m = 2$, where r is the tolerance for accepting matches and m is the length of the sequence to be compared. From Fig. 15.6, it is apparent that the person with MS exhibits reduced SampEn across the time scales of interest, resulting in a reduced MSE complexity index compared to the person without MS. The observed lower entropy is consistent with other findings from the literature (Costa et al. 2007; Manor et al. 2010) that demonstrate a reduction in functional degrees of freedom controlling the system, resulting in less adaptable movements.

These preliminary results using entropy analysis suggest that even in those with minimal physical symptoms due to their MS, systematic changes in the nature and adaptability of their postural control can be revealed. Epidemiological evidence indicates that those with MS are at increased risk for falls (Cattaneo et al. 2002), demonstrating a strong need for sensitive tests to assess disease progression that may also inform rehabilitative strategies. The MSE analysis technique presented here has the potential to perform such assessments by measuring subtle changes in the complexity and adaptability of postural control in MS.

In summary, entropy techniques are beginning to provide sensitive analyses of the postural control changes in people with MS. The different entropy analysis techniques are all rooted in similar theoretical principles (Richman and Moorman 2000), though SampEn and MSE algorithms are more valid as they avoid self-matching bias. The MSE analysis also allows assessment of many time scales of a particular time series, which could provide insights into how posture is regulated using input from the somatosensory, visual, or vestibular systems with different temporal dynamics. It is therefore important to consider a variety of time scales when evaluating the impact of a disorder on the postural control system, as postural instability and loss of balance result from the deterioration and loss of interaction of many subsystems.

15.5 Novel Treatments for Balance and Gait in MS: Tai Chi

Methods that aim to improve the overall complexity or adaptability of all of the subsystems (e.g., somatosensation, muscle strength, flexibility) that affect postural control may prove to be a more robust way of improving balance compared to interventions that aim to improve single subsystems. We now turn our focus to interventions aimed at improving balance and mobility in people with MS, and in particular the effects of using Tai Chi as an intervention that integrates coordination, strength, and sensory function to enhance adaptive postural control.

15.5.1 Current Intervention Research in MS

Several different rehabilitation and training protocols have been used in the MS population to reduce symptom severity. The most common exercise interventions have included aerobic, resistance, and balance training, alone or in combination. Aerobic training interventions have demonstrated improvements in mobility, level of fatigue, and perceived balance (Learmonth et al. 2013; Dettmers et al. 2009). Similarly, resistance training interventions have shown improvements in balance and locomotion, as well as reductions in fatigue (Cakt et al. 2010; Gutierrez et al. 2005). Balance training interventions have reported improvements in fatigue, standing balance, and quality of life (Hebert et al. 2011; Tarakci et al. 2013). An 8-week intervention that used a combination of aerobic, resistance, and balance training to reduce symptom severity reported improved 25-ft walk times, functional ambulatory scores, and Timed Up and Go times (Motl et al. 2012), indicating improved mobility following the 8-week intervention.

After a review of 11 different exercise interventions for MS (studies were divided into four categories: aerobic, flexibility, strengthening/resistance training, or yoga), Asano et al. (2009) concluded that while each program has its own benefits, an exercise intervention that integrates aerobic capacity, flexibility or coordination, strength, and balance training may prove to be the most effective treatment. Tai Chi is an exercise form that combines all these aspects and has the potential to enhance both static and dynamic balance in individuals with MS.

15.5.2 Tai Chi as a Comprehensive Intervention

Tai Chi is an ancient Chinese martial art that consists of gentle flowing movements that have made it an adaptable and efficient exercise for a wide range of people. Tai Chi has been used as an intervention to reduce symptom severity and increase quality of life in older individuals and in diabetic, stroke, and Parkinson's populations. In healthy older adults Tai Chi practice has been reported to reduce fear of falling and improve joint proprioception, reaction time, and static balance

(Fong and Ng 2006; Sattin et al. 2005; Tsang and Hui-Chan 2004). Individuals with diabetes have demonstrated increased peripheral nerve conduction and improvements in balance and plantar sensation following a 6-month Tai Chi intervention (Hung et al. 2009; Li and Manor 2010; Richerson and Rosendale 2007). Participants with mild-to-moderate Parkinson's disease showed improved performance on clinical measures such as the 6-minute walk, Timed Up and Go test, and backward walking (Hackney and Earhart 2008) following a 3-month Tai Chi training program. Chronic stroke patients who participated in a 12-week Tai Chi program showed improved static and dynamic balance compared to non-Tai Chi stroke controls (Au-Yeung and Hui-Chan 2009).

15.5.3 Tai Chi as a Balance Intervention in MS

Husted et al. (1999) found improvements in 25-ft walking speed, hamstring flexibility, and psychosocial well-being after an 8-week Tai Chi intervention in individuals with MS, while Mills et al. (2000) found positive effects on balance and reductions in depression following a 2-month Tai Chi intervention. We recently completed a 3-week Tai Chi pilot intervention study to assess changes in functional status and static balance in individuals with mild-to-moderate MS (Averill 2013). The Tai Chi intervention consisted of 9 h of Tai Chi standing meditation and Tai Chi slow walking training practiced in a group setting. Following the intervention, participants with MS increased neural drive (rapid foot tapping), leg strength (repeated sit-to-stand movements), and improved their standing balance (Fig. 15.7). For static balance, an increase in the CoP time to contact during tandem stance (a task that was not practiced during the intervention) was observed following the intervention, indicating increased temporal margins to the stability boundary. For dynamic balance during Tai Chi standing meditation with arm movements, participants were more likely to challenge their stability boundaries as shown by a decreased time to contact during this condition (see Fig. 15.7).

The significance of Tai Chi as an intervention is its generalizability in treating a wide variety of impairments experienced by those with MS. Larger and more comprehensive intervention studies evaluating Tai Chi and other interventions are needed to assess the most effective way to enhance balance control and somatosensory function in people with MS. Once treated, improvements in balance control and mobility may help to increase physical activity levels, reduce fatigue, and optimize quality of life, allowing people with MS to retain their independence for as long as possible.

15.6 Summary and Conclusions

Understanding the nature and mechanisms of balance impairments in MS is essential because of the major impact that reduced mobility has on quality of life, combined with the fact that MS affects people at relative early stages in their lives. A growing

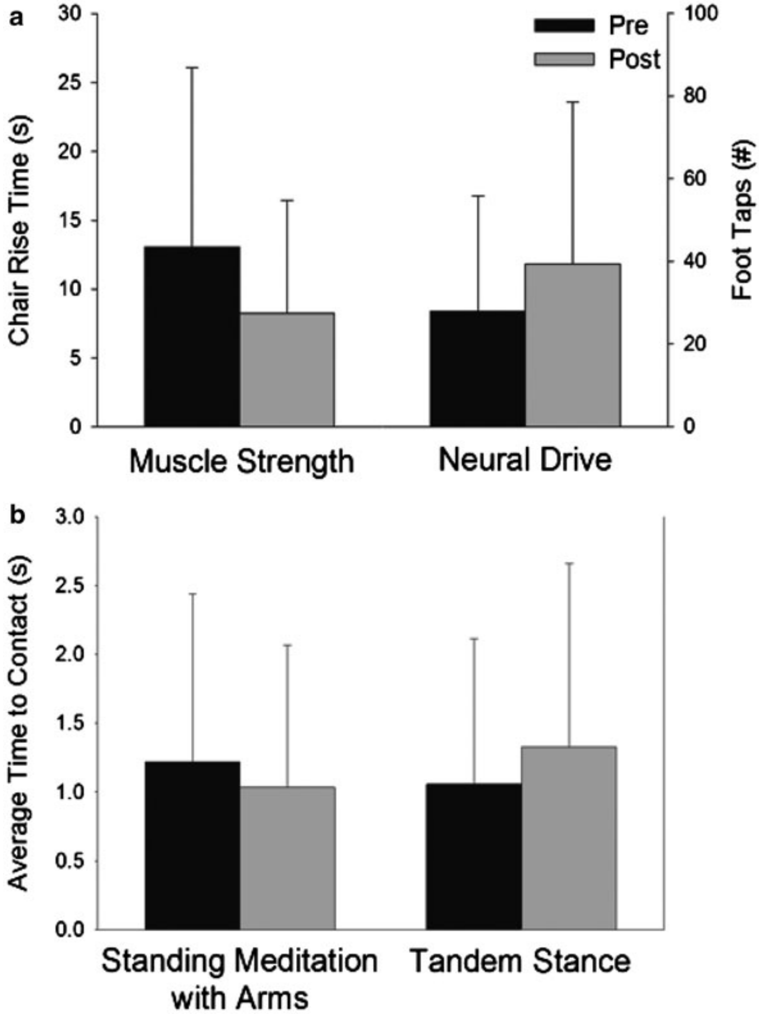

Fig. 15.7 **a** Changes in muscular strength (time to complete five-chair rises) and neural drive (number of foot taps completed in 15 s) following a 3-week Tai Chi intervention for three participants with MS. Data represent means and standard deviations. **b** Changes in time to contact (s) of the instantaneous center of foot pressure (*CoP*) to the base of support following a 3-week Tai Chi intervention for three participants with MS during standing meditation with arm movement and tandem stance. Data represent means and standard deviations

body of literature is emerging that addresses the nature of these postural and locomotor impairments in MS. Here, we reviewed the major changes in postural and gait control in MS and showed how strength, fatigue and somatosensory loss impact balance function. We also provided new insights into conditions under which postural instability emerges through the application of novel analytical methods and experimental paradigms based on nonlinear and complex systems methods. These novel methods included (1) boundary-relevant measures of postural stability and control (postural "time to contact") and (2) entropy measures for assessing postural and gait adaptability. The promise of these novel methods is that they allow us to differentiate between postural and gait variability caused by dysfunction and variability that provides adaptability to respond to postural challenges. Finally, we discussed how these methods and paradigms may help to develop innovative treatments for balance and gait dysfunction in people with MS. In particular, we showed that using a Tai Chi intervention, which integrates aspects of aerobic exercise, coordination and flexibility training, somatosensory function, as well as strength and balance, is a promising exercise intervention that may improve balance and mobility and therefore have a major impact on quality of life in people living with MS.

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