

Chapter 7

Why Is Neuromechanical Modeling of Balance and Locomotion So Hard?

Jessica L. Allen and Lena H. Ting

Abstract A goal and challenge in neuromechanical modeling is to develop validated simulations to predict the effects of neuromotor deficits and therapies on movements. This has been particularly challenging in balance and locomotion because they are inherently unstable, making it difficult to explore model parameters in a way that still coordinates the body in a functional way. Integrating realistic and validated musculoskeletal models with neural control mechanisms is critical to our ability to predict how human robustly move in the environment. Here we briefly review both human locomotion models, which generally focus on modeling the physical dynamics of movement with simplified models of neural control, as well as balance models, which model sensorimotor dynamics and processing with simplified biomechanical models. Combining complex neural and musculoskeletal models increases the redundancy in a model and allows us to study how motor variability and robustness are exploited to produce movements in both healthy and impaired individuals. To advance, the integration of neuromechanical modeling and experimental approaches will be critical in testing specific hypotheses concerning how and why neuromechanical flexibility is both exploited and constrained under various movement contexts. We give a few examples of how the close interplay between models and experiments can reveal neuromechanical principles of movement.

Keywords Balance control · Biomechanics · Musculoskeletal modeling · Neuromechanics · Locomotion · Postural control · Muscle synergies · Sensorimotor control · Sensorimotor integration · Sensorimotor feedback

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197

7.1 Introduction

Our ability to use models to simulate and predict motor behaviors in humans based on principles of neural control and biomechanics remains elusive. This is particularly true for whole-body behaviors that are inherently unstable and involve significant balance control, including locomotor behaviors such as walking and running. Balance and locomotor functions are impaired by a wide range of neurological and musculoskeletal disorders, negatively affecting quality of life (CDC 2008). Validated and predictive neuromechanical models have the potential to help diagnose, accurately characterize, and optimize treatments for a broad range of movement deficits. These models could allow researchers and clinicians to play “*what if*” by changing the neural control and biomechanical parameters of the model and observing the motor behaviors that emerge. Thus, a grand challenge in neuromechanical modeling is to develop predictive models that can be used to understand effects of neuromuscular deficits, predict outcomes of rehabilitation interventions, and develop individualized interventions and therapies optimized to the abilities of each participant.

There are a number of barriers to the development of validated neuromechanical models in balance and locomotion that we discuss in this chapter. In the first part of this chapter we review the current state of the art in human locomotion and balance models. Although walking and balance are integrated motor behaviors, there is a disciplinary divide in the investigation of balance control and locomotion, both experimentally and computationally. Neuromechanical models of human locomotion and balance thus reflect this divide and are not well integrated. Whereas the goal in locomotion is to move the body from one place to another resulting in large, measurable external movements amenable to biomechanical analysis, in standing balance the goal is to maintain a stable posture resulting in very small motions that belie the complex underlying sensorimotor processing. To date, much of the focus of locomotion modeling has been on reproducing the mechanics of the movement whereas balance modeling has typically focused on understanding the underlying neural control mechanisms, with very minimal overlap between the two modeling endeavors.

To advance, it will be necessary to develop integrated experiments and neuromechanical models to test fundamental sensorimotor principles for integration of balance and locomotion. A primary challenge is in validating both the neural and biomechanical elements of a neuromechanical model. Neuromechanical models may be a necessary tool to decompose and interpret the multifaceted ways in which balance and locomotor function can be achieved in different individuals and impairments. Experimental observations are difficult to interpret from a mechanistic level because internal signals such as muscle force and neural activity cannot be directly measured. Moreover, there is a great deal of redundancy in biomechanical and neural contributions to locomotion and balance, which may be a major contributor to the high level of variability observed in muscle and neural activity compared to measures of motor function. Using neuromechanical models tailored to a particular hypothesis and experimental paradigm will thus be critical for drawing conclusions

about how balance and locomotion are jointly achieved. In the second part of the chapter we will give some examples from our work of how experimental and computational approaches can be combined to reveal fundamental principles of human balance and locomotion that could form a foundation for the development of predictive neuromechanical models.

7.2 Current Neuromechanical Models of Locomotion and Balance

7.2.1 Locomotion Models are Mechanics-Focused

Neuromechanical models of locomotion, from the very simple to the very complex, typically focus on reproducing the mechanics of gait without emphasis on underlying neural control mechanisms. The simplest models demonstrate that locomotor-like motion can be generated almost entirely by passive. More complex models typically focus on identifying the necessary joint torques or muscle forces that replicate experimentally observed locomotor patterns, but without regard to how they are generated from a neural or sensorimotor perspective. Such models have generated a large body of literature regarding the mechanics of walking and how muscles can be coordinated to achieve the necessary biomechanical subtasks of locomotion. Both simple and complex models are essential for understanding the physical constraints and principles governing locomotion, defining the biomechanical tasks and functions critical for a successful neural controller to achieve. In some cases they can identify aspects of the movement that are governed by the properties of the musculoskeletal system as well as performance criteria governing kinematic and muscular patterns. However, to date, human locomotion models generally do not address specific neural control mechanisms that contribute to the generation of locomotor motor patterns and movement strategies.

7.2.2 Simple Locomotion Models Describe Body Mechanics

Point mass models of locomotion are important because they may describe the targets of neural control (e.g., neural control variables) and demonstrate the reconfigurability and versatility of the body when subject to neural control. The simplest locomotion models are typically energetics based, motivated by experimental evidence of the different mechanisms for exchange of kinetic and potential energy during walking and running (Cavagna et al. 1964, 1977; Dickinson et al. 2000). These energetic exchanges resemble the patterns that occur in common mechanical elements subject to gravity, such as pendulums and springs. Simple locomotion models based on such elements require minimal control and instead rely on initial conditions and

gravity to produce motion. They are thought to reflect energetically efficient modes of locomotion that result from the optimal tuning and interactions between complex neural and musculoskeletal systems (Srinivasan and Ruina 2006) and the overall movement goals of neuromechanical control (Full and Koditschek 1999).

Multisegmental models can reveal features of locomotion that are dominated by the mechanical properties of the body versus those that require more active neural regulation. Such models have facilitated the development of more energy efficient robots and revealed mechanisms of human gait. For example, walking motions can be achieved with minimal actuation by harnessing the passive dynamics of pendulum-like limbs. Machines built on such mechanisms can walk down a gentle slope without any active control of the joints (McGeer 1990a, b) and require only minimal actuation when walking on level ground (e.g., Collins et al. 2001, 2005; Collins and Ruina 2005). These passive walking models reveal that the swing phase of walking can be driven entirely by passive mechanics of the swinging limb resulting from gravity, which has been corroborated through comparison to experimental data (Mochon and McMahon 1980; Hoy and Zernicke 1986). Although muscle activity is often present during swing (Sutherland 1984; Perry 1992) the fact that passive dynamics can generate realistic swing kinematics suggests that neural control may be less critical within this region of the gait cycle. In contrast, appropriately timed hip or ankle torque in late stance can propel the center-of-mass (CoM) forward and is sufficient to generate steady state walking on level ground (Collins et al. 2005; Collins and Ruina 2005; Wisse et al. 2007). The need for actuation for propulsion provides evidence that neural mechanisms are necessary to produce the bio-mechanical function of forward propulsion. Running dynamics can be reproduced by passive spring-mass systems (Blickhan 1989; McMahon and Cheng 1990) and the addition of springs to pendulum-based models further improves the realism of gait features such as the characteristic M-shaped curve of the vertical ground reaction force in walking (Geyer et al. 2006). This suggests that the characteristics of the mechanical system are equally important to the neural controller in generating realistic movements. Different gaits can be achieved by modulating the leg stiffness or compliance, which could be achieved biologically through the active regulation of neural commands to muscles. However, neural control mechanisms cannot be explicitly examined in such models and require the addition of actively controlled muscle models with appropriate mechanical properties.

7.2.3 Complex Locomotion Models Describe Musculoskeletal Mechanics

Neuromechanical models that incorporate muscles are necessary in order to examine the detailed neural excitation signals to multiple muscles necessary to drive locomotion. A primary focus of musculoskeletal modeling studies of locomotion has been to find the appropriate muscle excitation patterns to reproduce a particular gait that was measured experimentally. These studies have provided important information about

the biomechanical functions of muscles during walking and how muscles can be coordinated to produce the necessary biomechanical subtasks of walking. However, because of the redundancy in the musculoskeletal system in production of actions, there are many feasible solutions to a particular motor task (Collins 1995; Martelli et al. 2013; Sohn et al. 2013; Simpson et al. 2015) and so optimization techniques are used to identify a single pattern of muscle activation that are sufficient to replicate experimentally observed kinematics and/or kinetics (e.g., Neptune et al. 2001; McLean et al. 2003; Liu et al. 2008). The criteria for optimization are typically based on minimizing muscle stress, which has been assumed to be a goal of the neural control system (Crowinshield and Brand 1981; Collins 1995; Erdemir et al. 2007). The choice of the cost function can have large effects on the selected optimal solution of muscle activations and thus realistic optimality criteria are essential for predictive, optimal control models that can be used to examine the effects of surgical interventions, rehabilitation, etc (Ackermann and van den Bogert 2010). However, even if realistic optimality criteria are chosen, the patterns of muscle activation are found without specific consideration of various neural mechanisms that may impose other constraints or features (Ting et al. 2012). Therefore, while the physics of the motion may be accurate in such models, the neural origin on muscle activity (e.g. feedforward motor pattern vs. feedback response to error) cannot be identified.

Another common focus of studies using detailed musculoskeletal models is to understand how altered muscle coordination in clinical populations (e.g., in cerebral palsy, stroke, amputation, etc.) affects walking performance (Higginson et al. 2006; Hall et al. 2011; Peterson et al. 2011; Silverman and Neptune 2012; Steele et al. 2012, 2013). Towards this goal, a variety of studies have examined how the contributions of specific muscles to important biomechanical subtasks of walking are altered. However, such models cannot provide information about *why* muscle coordination is changed because muscle coordination is usually determined only by reproducing experimentally observed data. Therefore, dissociation between the effect of an initial impairment versus compensation for that impairment is difficult and yet gait deficiencies resulting from impairment versus compensation may benefit from different rehabilitation strategies. It is also difficult to make predictions using the results of models that were found by tracking experimental measures and do not contain explicit representations of neural mechanisms that can be altered. Even if it were possible, the number of parameters in the model make it difficult to “emerge” new strategies based on various performance criteria and constraints compared to simpler models (e.g., Srinivasan and Ruina 2006).

7.2.4 Locomotion Models Designed to Incorporate Neural Control Are Unvalidated

There are several examples of locomotion models that can produce stable human-like locomotion using biologically-inspired control mechanisms yet none have been rigorously tested as a predictive model of real human walking. Most neurally-driven

models are based upon the hypothesis that spinal central pattern generators (CPGs) produce feedforward muscle excitation patterns that are modulated by sensory feedback. But, how the CPG is modeled, which types of sensory feedback are utilized and how sensory information is integrated differs widely across models. For example, there are CPG models based on the half-center hypothesis (Brown 1914) in which alternating flexor and extensor activity produces the basic muscle activity underlying gait (Taga 1995a, b; Ogiwara and Yamazaki 2001; Paul et al. 2005), while others are based on a more complex two-layer CPG network composed of a rhythm generator that provides the basic locomotor rhythm and a pattern formation network that distributes this activity to the appropriate set of muscles (Jo and Matsuquai 2007; Aoi et al. 2010; Aoi 2015). Similarly, these models also use different methods of modifying the CPG and its outputs based on sensory feedback. Despite these differences, however, all of these models reproduce locomotion that is qualitatively similar to experimentally observed gait patterns. Although some validation of each control scheme has been performed, none of the models have been rigorously tested against experimental data, particularly data designed specifically to test the validity of specific components of the model. This is particularly important as these models typically incorporate a large number of parameters in both neural and biomechanical components, increasing the sources of redundancy. Thus, while current neuromechanical models of locomotion do provide some insight into the role of different neural mechanisms in locomotion, to date they represent more of a proof of concept such that their utility for addressing questions about the neural mechanisms contributing to locomotion and to predict the effect of lesions is currently limited.

7.2.5 Balance Models Are Focused on Understanding Neural Control

An obvious difference in standing balance compared to locomotion is that there is much less movement involved while standing still, and even when responding to perturbations that occur while standing. This may make balance tasks seem boring or trivial from a mechanics perspective and yet there are no feedforward models of balance that can stand independently without eventually going unstable. Thus, from a neural perspective balance is an interesting problem of neural sensorimotor control. The focus of a majority of studies on standing balance control have therefore been on understanding this underlying sensorimotor control system rather than the more detailed mechanics of the musculoskeletal system. A commonly assumed goal of standing balance control is to keep the CoM within the base of support. However, this can be achieved by a number of joint and muscle level strategies. As it is unclear how the sensorimotor system controls the specific patterns associated with different postural strategies, most studies of standing balance control have focused on the control of relatively simple mechanical variables such as body orientation or CoM dynamics without regard for the control of multi-muscle patterns that generate different biomechanical strategies.

7.2.6 *Simple Models of Balance Reveal Principles of Sensorimotor Control*

Torque-actuated, inverted pendulum models are commonly used to investigate the sensorimotor control of standing balance. Typically, torque at the base of the pendulum is representative of muscle actions at the ankle. Models usually include a physiologically-relevant time delay, are inherently unstable, and therefore require some form of neural control scheme to remain upright. There has been considerable debate about the role of feedforward versus feedback control in standing balance control, as well as which variables or error signals are necessary to reliably return the body to equilibrium given a perturbation. Further, which sensory signals are used to generate a feedback signal is unclear, as well as how this information is transformed into motor actions in response to perturbations.

Simple inverted pendulum postural models have been used on both sides of the debate of whether movement during quiet standing is generated from feedforward or feedback neural mechanisms. Even in the absence of external perturbations the body is in constant motion. This motion, typically referred to as postural or body sway, is a low-frequency movement that can easily be quantified using measures of center of pressure (CoP) displacement. It has been suggested the intrinsic stiffness of active muscles about the ankle is sufficient to stabilize the body during quiet stance (Winter et al. 1998). However, torque-actuated inverted pendulum models demonstrate that the necessary ankle stiffness is higher than any experimental estimates of ankle stiffness during standing (Morasso and Schieppati 1999; Peterka 2002), providing evidence that some active control is necessary. Experimental studies of CoP displacement suggest that both feedforward and feedback mechanisms are at play. Competing concepts describe this as either a slow feedforward motion of the desired CoP location with faster feedback oscillations about that trajectory (Zatsiorsky and Duarte 1999), or alternately a feedforward mechanism that acts on short timescale with a slower feedback mechanism acting on longer timescales (Collins and De Luca 1993). Simple models of postural control on both sides of this debate can generate spontaneous body sway and reproduce experimentally observed patterns of CoP deviations. For example, a simple inverted pendulum model controlled using delayed position and velocity feedback on error that simulates sensory noise can reproduce a wide variety of common time and frequency domain CoP measures (Peterka 2000; Maurer and Peterka 2005). In contrast, sway-like motion has also been demonstrated using a predictive feedforward mechanism (Loram et al. 2005; Gawthrop et al. 2009). Because these models have only been used to reproduce observations, they only show that it is possible for either mechanism to control quiet stance. In order to provide strong evidence regarding the role of either mechanism in postural control, experiments must be carefully designed to dissociate the feedforward from feedback components. However, there are limitations in system identification techniques in conditions where sensory noise is dominant over external perturbations as in quiet stance where movement is minimal (van der Kooij et al. 2005).

In response to perturbations during standing balance, simple, torque-actuated inverted pendulum models have provided clear evidence that feedback involving the flexible integration of different sensory systems (e.g., proprioceptive, vestibular and visual information) is necessary for balance control. Modifiable multisensory integration mechanisms are important for providing accurate estimates of body orientation with respect to vertical in a range of biomechanical contexts. Conflicting sensory information can be generated experimentally through perturbations to either the visual system (rotating a visual surround) or the proprioceptive system (rotating the support surface). The reliance on different sensory modalities can be dissociated by fitting experimental sway data to a simple inverted pendulum model with variable weightings on different sensory channels. Whereas healthy subjects tend to rely on proprioceptive information and align themselves with small support-surface rotation amplitude and frequencies, they must increase their reliance on vestibular information to align with the vertical (Peterka 2002, and see Chap. 9 in this volume) for faster and larger components of perturbations. This simple model predicts that stability can no longer be maintained for larger perturbations in the absence of both visual and vestibular information, consistent with responses observed in individuals with bilateral vestibular loss. That the model can correctly predict how balance fails under sensory loss provides support for the proposed control scheme and demonstrates how computational models, when used to interpret carefully designed experiments, can provide evidence regarding underlying neural control and provide a mechanism for examining the cause and effect of neural impairments.

Evidence supporting the role of task-level feedback governing balance control has also come from inverted pendulum models incorporating muscles to produce the torque about the ankle. Examining muscle activity in response to perturbations has provided evidence that the transformation from sensory information to motor action is based on the estimation of the CoM, a task-level variable estimated through multisensory integration, rather than local joint-level variables. Whereas the initial burst of muscle activity was previously proposed to be due to feed-forward processes, reflecting a stereotypical response to a perturbation (Diener et al. 1988), more recent studies demonstrate that the magnitude and timing of this initial burst is scaled according to the CoM acceleration signal at the onset of the perturbation prior to the observed muscle response (Lockhart and Ting 2007; Welch and Ting 2008, 2009). Moreover, the entire time course of muscle activity can be reproduced and used to stabilize a simple inverted pendulum model with delayed feedback on CoM acceleration, velocity, and displacement. Note that this model assumes that the CoM is accurately estimated by multisensory integration mechanisms (Peterka 2002, 2015). In combination with experiments in which accelerations were varied, the model demonstrated that acceleration information is necessary to accurately reproduce the measured muscle activity responses across a wide range of perturbation (Lockhart and Ting 2007; Welch and Ting 2009; Savavynia and Ting 2013a). The model also demonstrates how the delayed feedback on acceleration information generates peak muscle activity that occurs earlier than and appears to “predict” future peak CoM displacement (Welch and Ting 2009;

Inspurger et al. 2013). Together, these models suggest that delayed acceleration feedback due to sensory noise could account for the appearance of a feedforward component in both perturbed and quiet standing, although as mentioned previously, challenges exist in system identification where sensory noise is dominant (van der Kooij et al. 2005).

Even when multisegmental movements are not well-described by inverted pendulum models, the response to perturbations can still be predicted based on task-level CoM kinematics, reflecting sensorimotor rather than biomechanical processes. For example, the sensorimotor integration model of Peterka (Peterka 2002, 2015) holds true even when hip movement occurs (personal communication). Muscle activity in response to perturbations can also be predicted based on measured CoM kinematic error even during a response predominated by hip motion (Welch and Ting 2008, 2009). This suggests that the delayed feedback sensorimotor transformation for reactive balance uses neutrally-computed CoM information to drive the excitation of multiple muscles independent of joint-level motions. This is further supported by evidence that CoM kinematics are a better predictor of muscle activity than joint level kinematics (Safavynia and Ting 2013a), and may drive the coordinated recruitment of multiple muscles throughout the body (Safavynia and Ting 2013b). Although a simplification of body dynamics appears inherent in the excitation of multiple muscles, more complex musculoskeletal models are necessary to demonstrate that such control signals are sufficient to provide postural stability in multisegmental models of balance.

7.2.7 *Multisegmental Models of Balance*

Multisegmental models typically incorporate sagittal-plane ankle, hip, and sometimes knee joints to examine how multisensory information is integrated to control the multiple joints of the body. These models are able to include proprioception at joints other than the ankle, demonstrating more complicated integration of sensory information in controlling the body (e.g. information from hip proprioceptors may be important for controlling the ankle and vice-versa). Multisegmental models have also provided evidence that humans likely utilize some internal model to overcome noisy or conflicting signals, and have facilitated study of multi-joint coordination strategies that is not possible with simple single-inverted pendulum models.

Multisegmental biomechanical models reveal that biomechanical as well as neural influences govern the choice of multi-joint movement strategy in balance control. Different multi-joint coordination strategies can be used to achieve the same higher task-level outcome due to redundancy in joint-space. Typically, small perturbations to standing balance elicit motions predominantly about the ankle (“ankle” strategy) whereas larger perturbations that tend to place the CoM near the edge of the base of support, evoke flexion or extension at the hips (“hip” strategy) (Diener et al. 1988). Kuo and Zajac (1993) demonstrate the ankle strategy is insufficient to keep the feet on the ground for larger perturbations, necessitating a hip strategy

response. Similarly, Alexandrov and colleagues (2005) also found that the hip strategy is more efficient at restoring the body at larger perturbations by comparing three eigenmovements that were primarily dominated by motion at one joint (e.g., ankle, knee and hip eigenmovements). However, in both cases there was no biomechanical reason for the selection of an ankle strategy over the hip strategy, thus there likely exist other reasons (such as minimizing motion head or increasing trunk stability) that lead to the preferred selection of the ankle strategy for small perturbations.

Models incorporating sensory dynamics further demonstrate that movement strategies may also depend on the ability of the nervous system to obtain reliable sensory information. Multisegmental models have shown that the healthy nervous system is very good at accounting for sensory noise and errors (van der Kooij et al. 1999, e.g., Kuo 2005). In combination with a feedback scheme to keep the body upright, such models also incorporate a state estimator to minimize the error associated with imperfect sensors and to represent an internal model of the body and sensor dynamics. Modifying the parameters of the model to simulate removing a sensor or increasing sensory noise can reproduce changes in postural responses strategies used in healthy individuals under altered sensory conditions using both two-link (hip and ankle, Kuo 2005) and three-link inverted pendulum models (hip, knee, and ankle, van der Kooij et al. 1999). They can also produce similar responses to those found experimentally in older adults and vestibular loss patients. Together, the ability of these models to fail in a similar way to the human system suggests that an internal model of sensorimotor dynamics is critical in controlling balance.

Optimal control theory applied to multisegmental models of standing balance provide insight into the modulation and variation of response strategies by the nervous system. Several models simulate postural response strategies based on local feedback at each joint where the torque produced is based on joint kinematics. However, a single set of feedback gains cannot generate the appropriate postural response across biomechanical contexts given biomechanical limitations, including differences in maximum muscle torque about each joint, different postural configurations, and different perturbation levels. Therefore the nervous system must use knowledge of the current biomechanical state to plan future responses. For example, Park and colleagues (Park et al. 2004) used a two degree-of-freedom model (hip and ankle) to demonstrate that feedback control gains are continuously scaled as perturbation levels increase. As the postural challenge increased, the gains at the hip increased while ankle gains decreased, consistent with increased hip strategy for larger perturbation. In this case, the optimal feedback gains were found by replicating experimentally-recorded data, rather than testing a specific neural hypothesis. However similar results were found in a data-free model by optimizing the criteria of minimizing CoM excursion while maintaining upright stance (Kuo 1995). Although promising, these types of studies can only provide evidence that it is *possible* that the nervous system selects strategies based on particular task-level goals, but do not rule out the possibility that controlling other variables may also produce similar results. A further challenge remains in identifying which neural systems produce such behaviors and how these idealized commands are translated into muscle recruitment and coordination signals.

7.2.8 *Complex Models of Balance with Muscles*

In order to examine how the different neural control strategies identified in simple models translate to multi-muscle coordination, detailed musculoskeletal models that incorporate realistic musculotendon elements are necessary. Such models face increased challenges for validation associated with neuromechanical redundancy in sensory systems, different joint-level strategies, and the control of multiple muscles crossing the joints. To date, there have been a few attempts at modeling standing balance control in the sagittal plane using detailed musculoskeletal models. For example, Jo and Massaquoi (2004) developed a planar muscle-driven model that was designed to demonstrate the possible cerebrocerebellar influence on postural control. Reinbolt and colleagues (Clark et al. 2011; Mansouri et al. 2012) developed a three-dimensional muscle-driven model that responds to perturbations to balance using local stretch-reflex mechanisms, and Nataraj and colleagues (Nataraj et al. 2010; 2012a, b) incorporated both local joint feedback and whole body center of mass feedback in a three-dimensional musculoskeletal model. Each of these models are capable of remaining upright in response to perturbations and reproduce a kinematic response that looks qualitatively like the experimentally-observed response. Similar to the neurally-driven models of walking discussed above, there are variety of different control mechanisms that can be used to achieve similar results, and thorough validation efforts must be performed to test any given neural control scheme. However, it is not clear that we have sufficient information about the neural control of balance to perform these validations.

7.3 **Challenges in Developing Validated Neuromechanical Models**

Substantial challenges remain in the development of neuromechanical models of locomotion and balance that can be used to understand and predict mechanisms of motor dysfunction and rehabilitation. Combining complex musculoskeletal and neural control models exponentially compounds the redundancy “problem” facing neuromechanical modelers. Yet it is exactly this redundancy—or flexibility—between mechanical and neural contributions to movement that we need to understand in order to identify how compensatory mechanisms may facilitate movement in neuromotor deficits, and how different people could find different solutions for performing the same task. Ultimately, predictive neuromechanical models would incorporate both the musculoskeletal complexity used in many biomechanical walking simulations as well as the robust feedforward and feedback control systems found in balance models and other complexities including multisensory integration models and parallel feedback mechanisms with different time delays and tunable passive mechanics (Ting et al. 2009).

The integration of neuromechanical modeling and experimental approaches will be critical in testing specific hypotheses concerning how and why neuromechanical flexibility is both exploited and constrained under various movement contexts. As neuromechanical redundancy increases as more elements are included, the more critical it will be to go beyond simply reproducing a single measured behavior. While optimization is an important tool for predicting movement and in resolving redundancy, evidence suggests that humans do not always use optimal solutions (Muller and Sternad 2004; Welch and Ting 2008; de Rugy et al. 2012; Loeb 2012). Further, optimal solutions are highly dependent on the structure of the model as well as the constraints and the costs specified in the problem formulation. Thus, identifying neural constraints are critical for identifying relevant optimal solutions (Ting et al. 2012). To support the principled addition of model complexity, studies demonstrating where extant models fail to reproduce experimental data will be important (McKay et al. 2007, e.g., McKay and Ting 2008, McKay and Ting 2012) as well as robustly reproducing multiple experimental conditions. Even better, specific experiments should be designed to support or refute explicit hypotheses about how redundancy is exploited or constrained. In fact, neuromechanical models may be *necessary* to help interpret data by dissociating the effect of various underlying mechanisms of movement. Identifying neural constraints on muscle activity will likely be a more effective and physiologically-relevant way to resolve redundancy than through optimization alone. Below, we give some examples of how such constraints and limits can be identified through investigations combining both experimental and computational analyses and how they aid in the advancement of neuromechanical models for balance and walking and can define a range of possible motor patterns for the same movement as well as variations in movement observed across individuals.

7.3.1 Neuromechanical Models Dissociate Neural Versus Mechanical Contributions to Movement

Any given movement results from interactions between neural and mechanical dynamics, including the passive mechanics of the body and muscles, changes in muscle properties with excitation level and muscle state, as well as parallel neural pathways with different delays and different information content (Ting et al. 2009; Roth et al. 2014). As passive mechanical models have the capability of exhibiting movements similar to those observed during behavior, it is important to dissociate the contributions that are due to neural control signals versus mechanical dynamics. Under various conditions and especially in impaired populations, the dependence upon neural versus mechanical elements could vary substantially. Neuromechanical models may be necessary to identify both the possible range of variability in neural signals as well as the degree of neural versus mechanical control for a given measured behavior.

One example of how a simple neuromechanical model can be used to define the necessary contributions and possible variations in neural control signals to balance control is a frontal plane model of balance control driven by delayed feedback (Scrivens et al. 2006; Bingham et al. 2011; Bingham and Ting 2013). We sought to understand why the dynamics of the CoM after a postural perturbation are similar when subjects stand at different stance widths even though the magnitude of muscle activity differs dramatically (Henry et al. 2001; Torres-Oviedo and Ting 2010). This suggests a variation in the neural and mechanical contributions to standing stability within an individual across biomechanical contexts. To understand and quantify these neuromechanical interactions, we developed a model of lateral balance control using a four-bar linkage model where the distance between the feet can be altered. A delayed feedback signal based on hip angle position and velocity drive the torque about that joint. This is reasonable as the acceleration signal in the muscle activation pattern is essentially low-passed filtered by muscle activation contraction dynamics in the production of force. When altering the stance width, we found that the same feedback gain values could no longer be used to stabilize the system and that similar variations in postural stability could be generated in the model based on changing only feedback gains or stance width, demonstrating neuromechanical redundancy in postural control (Scrivens et al. 2006). Indeed, large differences in torques are necessary to produce the same CoM motion when standing at wide vs. narrow stance such that the set of possible delayed feedback gains varies dramatically with stance width (Fig. 7.1) (Bingham and Ting 2013). An analysis of stability in our model further revealed substantial variability in the magnitudes of the feedback gains that can be used within each stance, which is corroborated with the variations in feedback gains that we observe across individuals (Bingham et al. 2011).

While we can use the model to investigate the effects of non-delayed passive stiffness and damping due to tonic muscle activity prior to the perturbations, we were not able to accurately identify the passive versus active contributions to kinematics even in simulated data where those components were known. While there is a delay between the effects of passive versus active torque generation at the beginning of the perturbation, there was simply not enough information in the kinematic signals in the perturbations that we used to reliably dissociate their effects (Bingham et al. 2011). In healthy individuals the passive contributions are typically about 10% of the overall torque generating in perturbed balance control, but this value could increase substantially in individuals with neuromotor impairments (Dietz and Sinkjaer 2007). To allow the effects to be more apparent in the kinematics data, we further designed specific experiments that modified the effects of passive versus active dynamics by altering subject mass, passive joint stiffness, and delayed feedback gains and extended the duration of perturbation (Bingham 2013). Similar variations in the model were implemented to examine how feedback gains are altered. Across stance widths, we also found that the level of stability could vary across individuals, and that these differences were preserved across stance widths, suggesting a higher level goal driving the selection of redundant neuromechanical strategies that could differ across individuals and movement contexts.

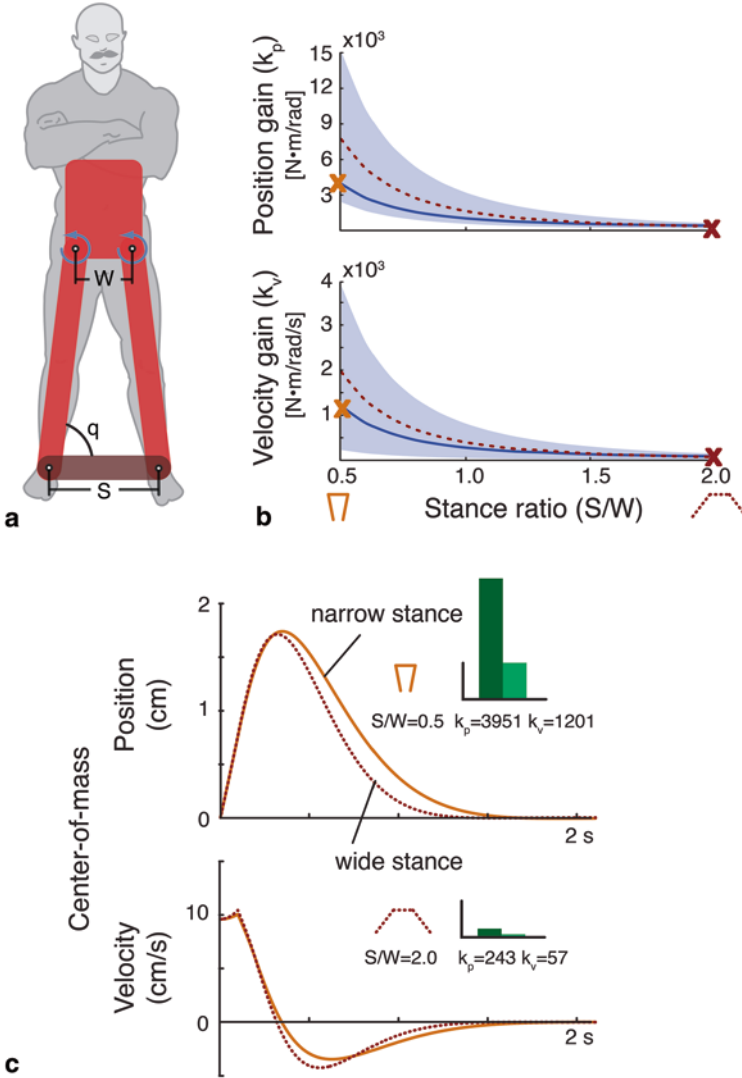


Fig. 7.1 Frontal plane model of human mediolateral balance control. **a** Frontal plane motion of the body is modeled as a four-bar linkage. Two bars represent the legs, the third bar is the torso, and the fourth bar is the ground. Perturbations are applied as ground translations. Important parameters of the model are the hip width (W), stance width (S), hip torque (T_H) and ankle angle (q_A). **b** Stable feedback gains vary across stance widths. The dotted line indicates the feedback gain pairs that produced maximum stability across stance widths. The solid line indicates the feedback gain values that produced identical stability characteristics across stance widths. **c** Simulated CoM position across stance widths that have similar stability characteristics. Narrow (*top*) and wide (*bottom*) stance responses correspond to feedback gains from orange and red X's in **b**, respectively. Although feedback gain values differed substantially across stance widths, the resulting CoM motion produced in response to a change in the initial state of the system was similar in narrow (*solid*) and wide (*dotted*) stance widths when feedback gains with the same stability characteristics were used. (Reprinted with permission from Bingham and Ting 2013)

7.3.2 *EMG Provides Better Information for Validating Neuromechanical Models*

Using kinematic measures to validate model outputs is an obvious and necessary step, but may be a very blunt instrument for validating neuromechanical systems. Indeed, Bernstein's original formulation of the redundancy problem arose from the very idea that the internal forces that generated a given kinematic trajectory could not be uniquely identified (Bernstein 1967). This redundancy is due to the fact that forces are integrated twice to produce movements, computations that are also dependent upon the position, velocity, and inertial properties of the limb. Adding ground-reaction forces is helpful, but still leaves intersegmental dynamics at the level of kinematics. An example of this problem can be seen in the use of modern digital control in controlling motors; it is well known that a smooth trajectory can be generated either from a constant torque or a series of pulses as long as the area under the curves are equivalent. The differences in the resulting trajectories are too small to be discerned and cannot be used to back out the forces going in. Therefore, using kinematics alone is insufficient to distinguish different neural control strategies that result from different forces or patterns of muscle activation, potentially indicating different mechanisms of sensorimotor control.

Muscle activity as recorded through electromyography (EMG) can provide important information as it represents amplified motor neuron pool activity and is also related to muscle force (Milner-Brown and Stein 1975; Basmajian and De Luca 1985; Winter 2009). Not only can EMGs help validate neuromechanical models, but models may also be necessary to understand EMG activity. Although EMG provides only partial information about the outputs of the nervous system, the full information contained in such signals has yet to be fully exploited in the development and validation of neuromechanical models. While using EMG to drive models has been attempted e.g., (Lloyd and Besier 2003; Buchanan et al. 2004; Shao et al. 2009; Sartori et al. 2012), there are issues in appropriately converting EMG to muscle force and in many cases only the general on and off and mean amplitude of muscle activation patterns are used to validate optimal model excitations (Zajac et al. 2002; Thelen et al. 2003; Damsgaard et al. 2006). One reason could be that EMG patterns are highly variable compared to biomechanical measures making them difficult to analyze and interpret using statistical tests. Yet the relative consistency of motor outputs compared to the flexible neural strategies we use to generate them are at the crux of the questions that neuromechanical models can and should answer. The variability observed both within and across subjects can be used to identify the task-level goals that are controlled by the nervous system (Scholz and Schoner 1999; Todorov and Jordan 2003) and the underlying structure of the signals can be used to identify constraints on the organization of motor activity (Torres-Oviedo and Ting 2007; Welch and Ting 2008, 2009; Torres-Oviedo and Ting 2010; Safavynia and Ting 2013b), some of which could improve optimization and simulation of walking and balance (McKay and Ting 2012; Borzelli et al. 2013; Walter et al. 2014). Neuromechanical models become essential to understanding the

impact of variations in muscle activity on biomechanical performance (e.g., Kutch and Valero-Cuevas 2011; Sohn et al. 2013; Simpson et al. 2015). While it may be considered ideal to access neural signals directly, there are substantial limitations in current invasive and noninvasive techniques and advances in understanding variability in muscle activity will provide insights for incorporating more complex neural models

As an example of how a simple neuromechanical model used to predict muscle activity can reveal fundamental neural mechanisms of balance, our sensorimotor feedback model demonstrated the importance of acceleration feedback in reactive balance responses. A simple delayed feedback loop using COM acceleration, velocity, and displacement can reproduce the entire time course of muscle activity during postural perturbations to standing balance in both humans and other animals (Fig. 7.2) (Lockhart and Ting 2007; Welch and Ting 2008). We found that the steep initial rise of muscle activity occurring at a long latency (~ 40 ms in cats, ~ 100 ms in humans) after a perturbation follows the initial acceleration induced by the perturbation. Feedback on the acceleration signal can account for what can appear to be a predictive, or feedforward, burst of muscle activity (Diener et al. 1988) where the peak in muscle activity precedes the peak in CoM displacement induced by the perturbation. Removing acceleration feedback from the model only reduced the goodness of fit to recorded data by about 2%, yet the initial burst was eliminated, altering the qualitative shape of the response (Lockhart and Ting 2007); adding jerk to the model did not improve fits. Using current quantitative metrics of similarity it would thus be possible to simulate muscle activation patterns that quantitatively account for the variance in the data, but which generate qualitatively different response patterns. Further, clues to the physiological basis of the acceleration information were obtained by demonstrating that the initial burst is lost after large-fiber peripheral neuropathy (Fig. 7.2) (Lockhart and Ting 2007). In this condition, the large diameter muscle spindle, Golgi tendon organ, and cutaneous afferents were damaged (Stapley et al. 2002). The selection of feedback gains could be predicted by the same optimization criteria with a further constraint on removing acceleration feedback, suggesting there was a common motor goal driving the selection of the motor pattern both before and after neuropathy. While qualitative changes in the muscle activity were found, the kinematics of the CoM were quite similar before and after neuropathy, differing only in magnitude (Fig. 7.3). This highlights the relative insensitivity of the kinematic signals to changes in the underlying neural control system.

Since qualitative differences may not be easily identified using typical quantitative statistical analyses, better exploratory statistical tools are necessary to facilitate better neuromechanical models that can identify subtle but potentially important differences between and across conditions as well as to compare simulated and experimental kinematic and muscle activity data. High variability across trials and subjects often hinder our ability to rigorously test the fidelity of neuromechanical models, leaving many to be validated “by eye”. Often models are considered valid if they roughly lie within the broad 95% confidence limits of the data, which allow for

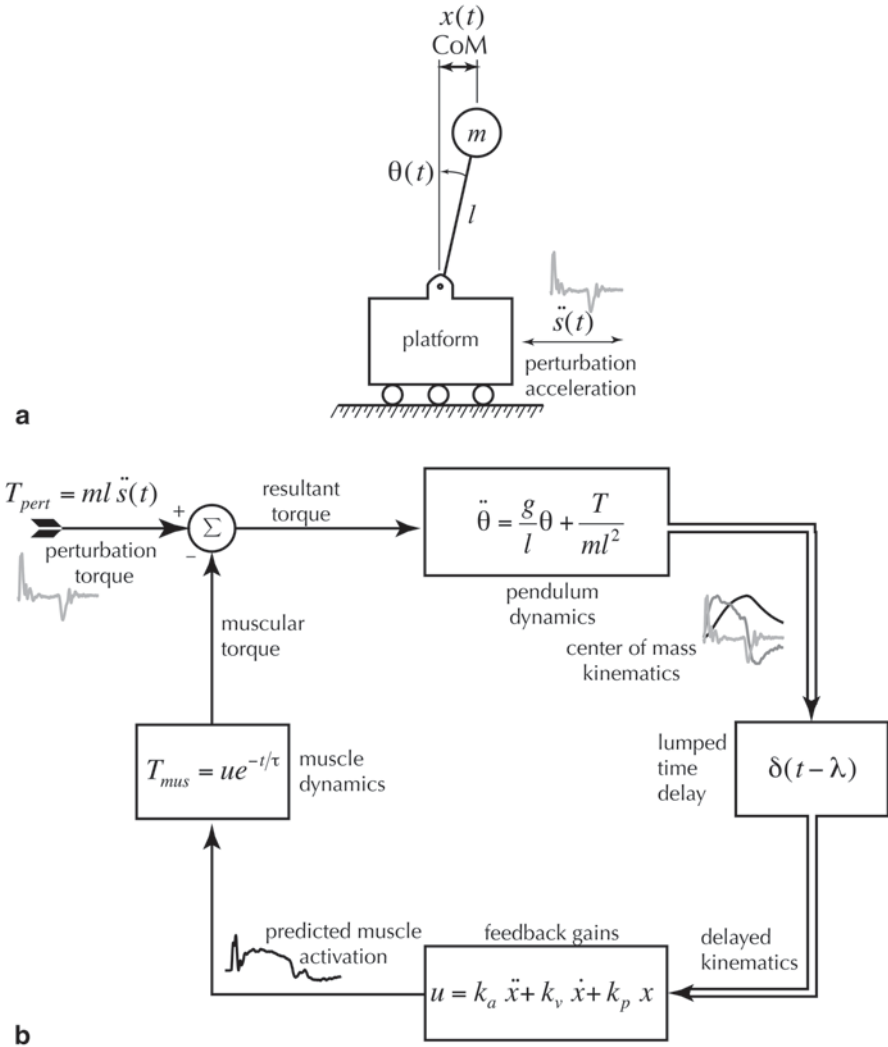


Fig. 7.2 Simple feedback model of postural control used to predict muscle activity during reactive balance responses. **a** The mechanics of the body during balance is approximated as an inverted pendulum on a moving cart. Experimentally measured accelerations of the platform were applied to the cart so that realistic acceleration, velocity and displacement trajectories of the platform were modeled. **b** The perturbation acceleration generates a disturbance torque at the base of the pendulum. Delayed kinematics of the horizontal CoM were used in a simple feedback law to generate model muscle-activation patterns, which were compared with those measured experimentally. The modeled muscle activation then generated a stabilizing torque about the representative joint. (Reprinted with permission from Lockhart and Ting 2007)

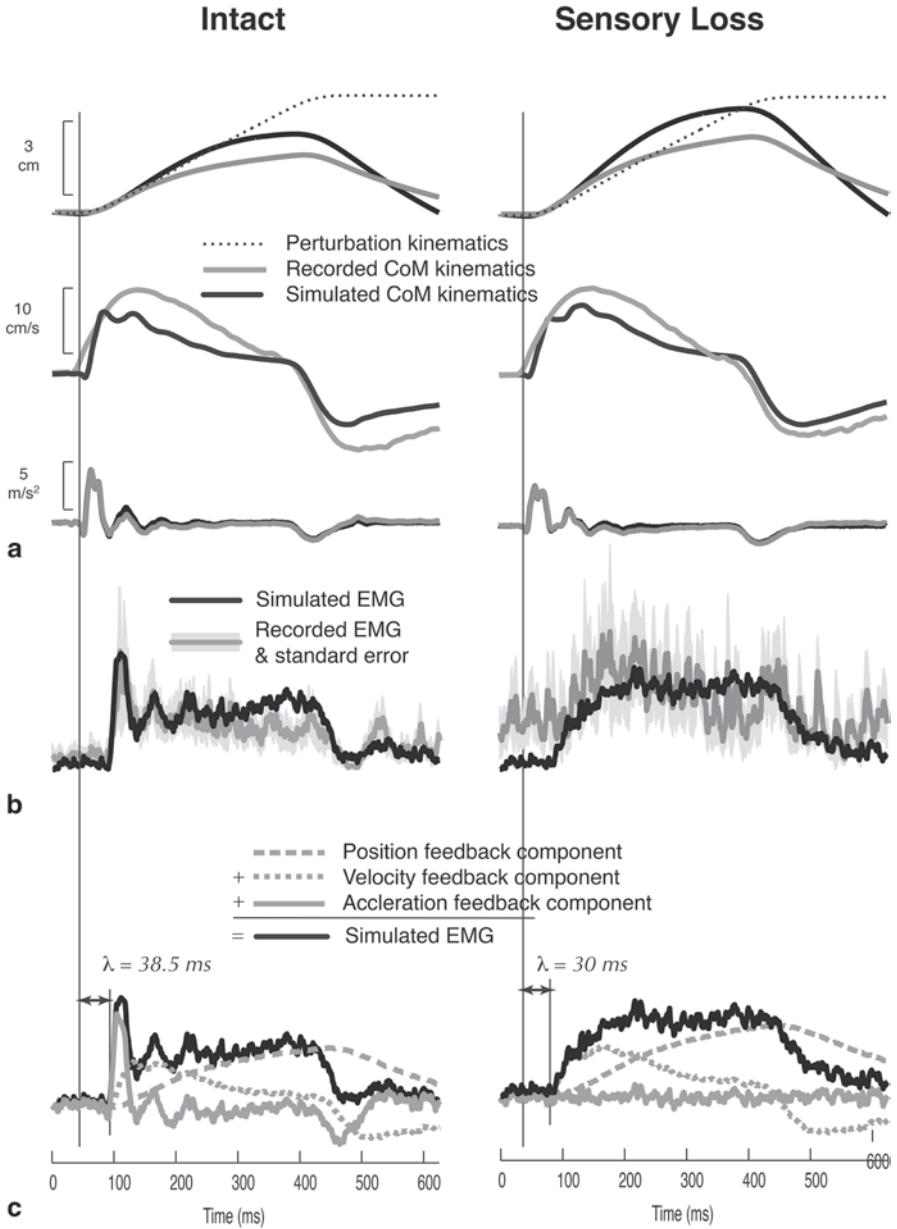


Fig. 7.3 Comparison of recorded and simulated muscle activation and CoM kinematics before and after large-fiber peripheral neuropathy. **a** Recorded (gray lines) and simulated (black lines) CoM displacement, velocity and acceleration. **b** Recorded (gray line) muscle activity and simulated (black line) muscle activity from the best-match model parameters. **c** Decomposition of simulated muscle activity (black line) into components arising from CoM position feedback (gray dashed line), CoM velocity feedback (gray dotted line), and CoM acceleration feedback (gray solid line). Note that the initial burst in the intact condition (left panel) is due primarily to acceleration feedback and the absence of the initial burst and acceleration feedback in the sensory loss condition (right panel). (Reprinted with permission from Lockhart and Ting 2007)

qualitative differences in the traces, or only certain features such as peak amplitude and timing are used in statistical analysis. Toward the development of better tools to compare curves, we recently proposed a new method for functional analysis of variance (fANOVA) based on the wavelet representations of EMG signals (McKay et al. 2013). The statistically significant differences identified within the wavelet domain are then transformed back into the time domain rendering clearly interpretable difference curves between conditions. These analyses have the potential to reveal critical features that are typically hard to quantify such as inflection points and small bursts of activity and could be expanded to demonstrate differences between model outputs and experimental data with more power and better temporal resolution than traditional methods, ultimately enhancing our ability to develop and validate neuromechanical models.

7.3.3 Neuromechanical Constraints on Musculoskeletal Redundancy

Developing validated neuromechanical models using muscles has the further challenge of dealing with musculoskeletal redundancy in a physiologically-relevant way as adding neural complexity only furthers the “problem” of redundancy and model validation (Prinz et al. 2004). It is well known that many different coordination patterns across multiple muscles can be used to generate a given set of joint torques at an instant in time. Some evidence suggests that the activity of multiple muscles during movements can be predicted based on optimality criteria typically minimizing muscle stress or force (Crowninshield and Brand 1981; Thelen et al. 2003; Kurtzer et al. 2006; Erdemir et al. 2007). However, these produce only a single solution for a given task, whereas great variability within and across subjects is often observed. Our work using a musculoskeletal model demonstrates that substantial variations in the amplitude of activity in a given muscle are possible to achieve a given biomechanical task (Sohn et al. 2013; Simpson et al. 2015). How thus do we interpret and quantify these deviations in muscle coordination? And to what degree do these need to be accounted for in neuromechanical models?

In order to develop a new framework for understanding, quantifying, and predicting muscle activation patterns we have performed a number of experimental studies to investigate constraint of the spatial activation of muscles and their relationship to biomechanical functions. Our work in combination with studies from upper extremity movements suggest that muscles are not activated independently, as assumed by optimization models, but are constrained to be active in modular units specifying fixed spatial patterns of muscle activity (d’Avella et al. 2003; Bizzi et al. 2008; Ting and Chvatal 2010). These motor modules, also referred to as muscle synergies, coordinate muscles across multiple joints and can produce consistent biomechanical outputs necessary to achieve a task (Ting and Macpherson 2005; Chvatal et al. 2011). Within this framework, movements are constructed by combining and varying the recruitment of motor modules to achieve a task (Fig. 7.4). Thus, motor

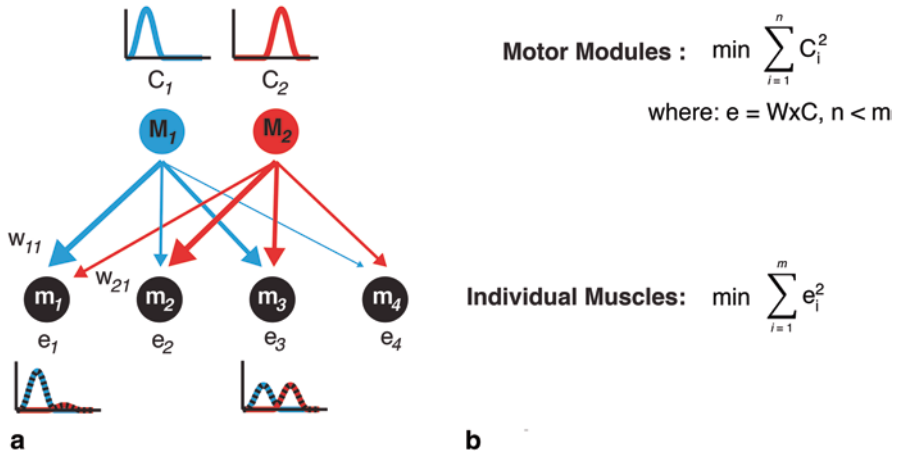


Fig. 7.4 Motor module concept. **a** Each motor module (M_i) contributes to the activation (e_j) of a single muscle (m_j) with a fixed weight (w_{ij} , where $i=1$ to number of motor module and $j=1$ to number of muscles) with an activation profile that can vary over time (C_i). In this example, the weight of the connection between each motor module and muscle is depicted by the width of the arrow. For example, the activity of muscle 1 (e_1) has a large contribution from module 1 (*blue*) and a much smaller contribution from module 2 (*red*). In contrast, the activity of muscle 3 (e_3) has approximately equal contributions from both modules. **b** This allows the search space of neural control inputs to satisfy the objective function be constrained to a smaller number

modules provide a framework for understanding variability observed both within and across subjects. For example, trial-by-trial variations in reactive balance and cycle-by-cycle variations in walking can be explained by different levels of recruitment of motor modules rather than muscles (Clark et al. 2010; Torres-Oviedo and Ting 2010). Further, we observe different number and structure of motor modules across individuals (Torres-Oviedo and Ting 2007). Moreover, these are preserved across different biomechanical contexts consistent with the idea that motor modules are neural constraints (Torres-Oviedo and Ting 2010; Chvatal et al. 2011) that could represent preferred motor patterns (de Ruyg et al. 2012). The same motor modules are even shared across walking and balance tasks (Chvatal and Ting 2012; 2013). Finally, in the upper extremity, performance of novel force generation tasks that can be achieved using existing motor modules are much easier for subjects to learn than those that require muscle activation patterns that are not compatible with existing muscle synergies (Berger et al. 2013).

Incorporating motor modules into neuromechanical models is necessary to effectively understand motor function; in return they may also improve the predictive capabilities of model performance. Several studies have demonstrated that similar motor performance can be achieved through optimal control of individual muscle versus recruitment of muscle groups (Raasch and Zajac 1999; McKay and Ting 2012). In reactive balance responses, we demonstrated that minimizing mo-

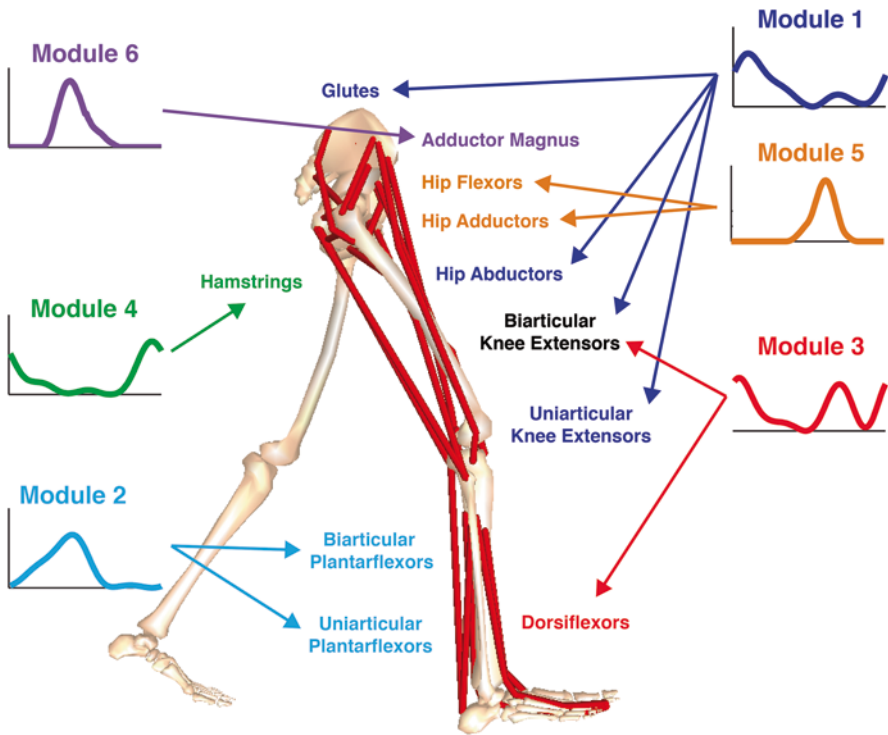


Fig. 7.5 Detailed musculoskeletal models with motor modules instead of individual muscles as the control inputs can be used to successfully reproduce well-coordinated walking patterns. Allen and Neptune 2012 demonstrated that the six motor modules shown here are sufficient to satisfy the biomechanical demands present during walking. Each motor module coordinates multiple muscles with a common temporal recruitment pattern

tor module recruitment better matched the force evoked during reactive balance responses compared to minimizing individual muscle activation (McKay and Ting 2012). While the total level of muscle activation was increased slightly compared to the minimum possible activity, the computation time required to find an optimal solution was improved. The feasibility of using motor modules in simulations of human walking has also been demonstrated (Neptune et al. 2009; Allen and Neptune 2012; Sartori et al. 2013) (Fig. 7.5), as well as the detrimental consequences of altered motor modules to walking function observed in stroke (Allen et al. 2013). Further, the internal joint loading force predictions are improved in a torque-based model of walking when motor module constraints are considered (Walter et al. 2014). Therefore, using motor modules constraints may be an important step to both validating motor modules as a mechanism for motor control as well as improving the predictive power of model on an individual basis.

7.4 Conclusion

In conclusion, neuromechanical models are becoming increasingly important in elucidating principles of movement in balance and locomotion. Advancing the integration of neuromechanical modeling and experimental approaches will require researchers to have a training in a diverse set of disciplines spanning neural and musculoskeletal systems, experimental design, as well as computational modeling techniques. As computational tools for analyzing and simulating both musculoskeletal models and their control improve (Cofer et al. 2010; Bunderson et al. 2012; Bunderson and Bingham 2015; Markin et al. 2015) our ability to develop models that can not only describe but also predict movement strategies and control will also improve. Focus on a principled increase in complexity of models, with explicit tests to demonstrate the contributions of each component will help to justify the necessity of each component to explain the robustness of human locomotor and balance behaviors.

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