

Chapter 4

Sensorimotor control of standing balance

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Abstract

For most individuals, balancing upright is a simple task that requires little effort. The inherent difficulties associated with standing balance are not revealed until a pathology or injury impairs its control. Fundamentally, standing upright requires us to balance our unstable whole-body load within a small base of support. Small movements of the upright body are detected by various sensory receptors, all encoding these movements through their own coordinate system with specific dynamics. The balance controller filters, processes, and integrates sensory cues of body motion to produce an error signal between predicted and actual sensory consequences of balance-related movements. Compensatory motor commands are generated in response to this error to maintain upright standing. In the present review, we first briefly describe the biomechanics and sensor dynamics of standing balance. We further review sensorimotor and perceptual approaches revealing operational principles of the balance system, along with computational approaches that explore control processes underlying upright stance. Finally, we present robotic tools that virtualize the sensory consequences, biomechanics, and/or environmental factors inherent to the standing balance task. Throughout, we emphasize works that combine sensorimotor, computational, and/or robotics approaches to highlight the task dependency, multisensory cue combinations, cortical-subcortical contributions, and internal representations underpinning balance control.

INTRODUCTION

As we stand, our balance controller regulates the musculature involved in maintaining upright orientation. This ability has puzzled researchers for centuries (von Vierordt, 1862). Early observations of standing balance revealed that the body center of mass is constantly moving and not static as it appears to be. Over the years, a wealth of information has emerged describing standing balance behavior, how it responds to altered sensory conditions (e.g., eyes open vs. eyes closed), or how it generates reactive postural responses to unexpected perturbations (see reviews by Horak and Macpherson, 1996; Horak et al., 1997; Balasubramaniam and Wing, 2002; Bolton, 2015; Mergner, 2010). We have begun to understand how standing balance is controlled and this

has led to the emergence of several computational models and robotic simulations of the balance system.

This review first considers the contribution of the body's mechanics and sensory systems to the control of standing balance focusing specifically on how this information pertains to computational modeling and robotic simulations of the balance system. Building on that, we review methods that researchers have used to probe and understand the operating principles of the balance controller. We also present conceptual and computational models of standing balance, describing how these efforts help us understand the balance controller. To conclude this review, we will discuss new robotic approaches combining mechanics, sensors, and models of standing balance to address the physiological principles underlying balance control. These theoretical

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and technical advancements enable researchers to address fundamental questions about the balance controller (e.g., by targeting the motor output and/or the sensory inputs) that cannot be answered simply by observing balance behavior.

BIOMECHANICS OF STANDING BALANCE

Standing balance requires the regulation of the body center of mass within a base of support defined by the lateral, anterior, and posterior edges of the feet. The body center of mass, located approximately at the height of the sacral vertebrae when standing upright, is typically positioned in front of the ankles during standing (Cotton, 1931; Smith, 1957). This upright posture is inherently unstable due to gravity's downward pull and continual disturbances caused by breathing, heart beat, and intrinsic noise in sensory and motor systems. Because the standing body cannot be stabilized solely by passive tissue structures (Woodhull et al., 1985), standing balance requires continuous muscle activity despite being often described as almost effortless. Biomechanical models of standing can help reveal how the central nervous system can maintain upright stance. These models capture the interlimb coupling and muscle forces required to keep the body upright, and are thus essential for computational and robotic simulations of balance control considered further in this review. Therefore, we will devote this section to key aspects of standing balance biomechanics related to both anteroposterior and mediolateral directions.

Anteroposterior standing balance

Standing balance in the anteroposterior direction is commonly modeled using a single-link inverted pendulum. This model assumes whole-body sway occurs only at the ankle joints, and is suitable for modeling anteroposterior sway observed during unperturbed standing (Smith, 1957; Nashner, 1976; Fitzpatrick et al., 1992; Gage et al., 2004). A more complex double-link inverted-pendulum model, however, is required to account for ankle and hip movements arising from perturbations (Horak and Nashner, 1986; Runge et al., 1999). With the center of mass normally in front of the ankles, an ankle plantarflexor torque generated by the triceps surae muscles is required to overcome the toppling torque due to gravity and prevent the body from falling. If the ankle plantarflexor torque is equal and opposite to the gravity-induced torque, the body will remain in a quasistatic posture. Any added plantarflexor torque accelerates the whole body backwards while the opposite occurs if it decreases.

The relationship between ankle torque and ankle angle when a person stands is described by the differential equation shown in Figure 4.1A (Fitzpatrick et al., 1992; Winter et al., 1997; Loram et al., 2001; Luu et al., 2011). When standing quasistatically, this relationship can be simplified to describe whole-body load stiffness ($\frac{T}{\theta} = -mgL$) and relates the minimal ankle torque required to prevent the body from falling at a given body angle (Smith, 1957). These equations also explain how body inertia (and intrinsic muscle properties) mechanically low-pass filters forces generated by high-frequency motor unit firing (6–8 Hz; Mochizuki et al., 2006; Dalton et al., 2009; Héroux et al., 2014) into lower-limb moments (< 3–5 Hz; Olney and Winter, 1985; Fitzpatrick et al., 1996; Dakin et al., 2010) and whole-body sway (< 1 Hz; Benseal and Dzendolet, 1968; Soames and Atha, 1982; Latt et al., 2003; Dakin et al., 2010) during standing.

Two general sources of ankle torque contribute to standing balance: an active torque based on the modulation of the neural drive to muscles and a passive torque generated by tissue deformation and tonic muscle stiffness (Peterka, 2002). Based on the assumption that the ankle joint can be made stiff enough to support the load of the body, Winter et al. (1998) proposed that balance could be maintained via a spring stiffness model wherein corrective torque is generated instantaneously via tonic muscle activity. The spring stiffness model was challenged based on the argument that intrinsic ankle stiffness alone is insufficient to maintain quiet standing due to the compliance of the Achilles tendon (Morasso and Schieppati, 1999; Loram and Lakie, 2002; Morasso and Sanguineti, 2002; Casadio et al., 2005). Furthermore, because ankle stiffness is movement-dependent, more active control of plantar- and dorsiflexors is required when postural sway increases (Sakanaka et al., 2016).

Instead, to maintain balance, others have proposed that plantarflexor muscles rapidly and intermittently shorten to add tension to the Achilles tendon (Bottaro et al., 2005; Loram et al., 2006, 2011; Asai et al., 2009). This active pulsatile behavior (~2–3 Hz) has been observed in triceps surae muscles and provides sufficient restorative ankle plantarflexor torque to maintain the whole body upright along the sagittal plane (Loram et al., 2005). Mechanically, paradoxical plantarflexor muscle shortening is also observed during forward sway while the whole muscle–tendon unit lengthens (Loram et al., 2004, 2009). However, not all muscles of the lower limb behave this way. The tibialis anterior muscle fibers (or at least its deep fibers) exhibit changes in length that follow that of the whole muscle–tendon unit (Di Giulio et al., 2009; Day et al., 2013).

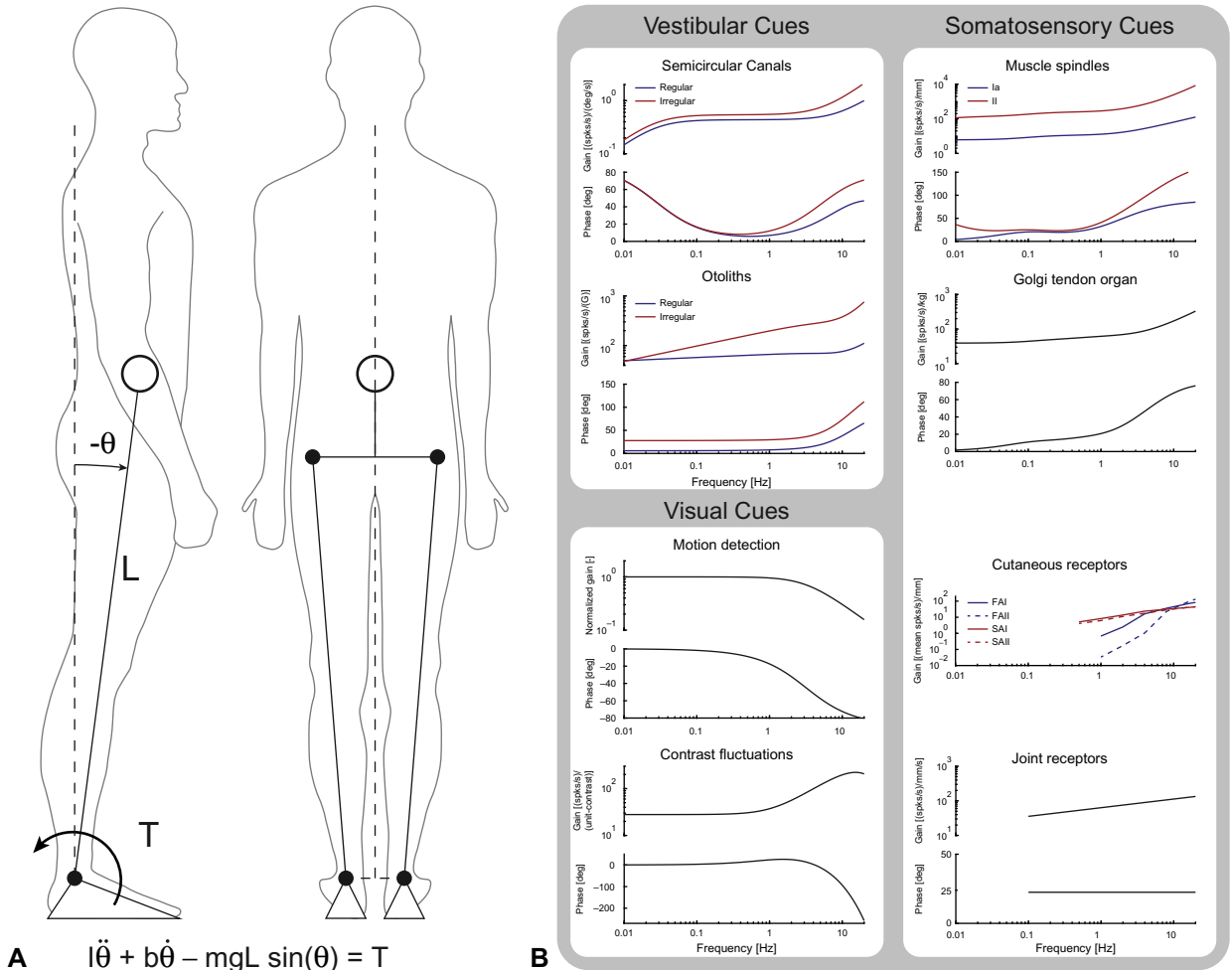


Fig. 4.1. Biomechanics and sensory dynamics of standing balance. **(A)** Anteroposterior and mediolateral model of standing balance as represented using an inverted pendulum. The differential equation describes the dynamics of standing balance with the following parameters: L , height from ankle to center of mass (white circle), θ , angular displacement of center of mass from idealized upright alignment (dashed lines); T , torque with black arrow signifying direction; I , mass moment of inertia; m , whole-body mass; g , gravitational acceleration; b , viscous ankle damping. **(B)** Sensor frequency response characteristics (gain and phase) for vestibular, visual, and somatosensory cues. Vestibular responses for regular and irregular afferents are estimated by transfer functions replicating nonhuman primate vestibular afferent data (Schneider et al., 2015). Visual contrast fluctuation responses are described by a transfer function depicting mean values from on and off cells in nonhuman primates (Benardete and Kaplan, 1999). Motion detection responses are described by a first-order low-pass filter with a 50 ms time constant based upon similarities between the insect motion detector model described by Egelhaaf and Reichardt (1987) and human psychophysical studies. Muscle spindle and Golgi tendon organ responses are described by transfer functions replicating data from cats (Poppele and Bowman, 1970; Anderson, 1974). Cutaneous responses are described by the mean firing rate per cycle of input displacement for slow- (SA) and fast-adapting (FA) type I and II cells obtained from human microneurography data (Johansson et al., 1982). Joint receptor responses are described by a transfer function matched to cat data (McCall et al., 1974); however, because there is uncertainty regarding the response properties of joint receptors, they have been grayed out. Auditory responses were not included due to a lack of available data.

Mediolateral standing balance

Our understanding of balance in the frontal plane is less complete than in the sagittal plane. This is due to the added complexity of various degrees of freedom from the lower body (hips and ankles) and upper body (torso)

as well as the variability in feet position on the ground (stance width). An accepted biomechanical model of mediolateral standing balance also uses an inverted pendulum but with dual links (i.e., both limbs; Day et al., 1993; Winter, 1995; Winter et al., 1998) (Fig. 4.1A). This model assumes negligible knee movement, with the two

limbs and pelvis forming a quadrilateral defined by the hip and ankle joints. Any deviation in the center-of-mass position from an idealized upright alignment requires a corrective cumulative torque defined by the sum of all torques acting on the hip and ankle joints. Subsequently, during quasistatic standing, the load–stiffness relationship can be represented using the same equation as anteroposterior standing, where the torque (T) is the sum of all joints and the angle (θ) is the orientation of the center of mass relative to a point halfway between the ankles. When the center of mass is exactly halfway between the ankles, the sum of the four torques equals zero.

Mediolateral control of postural sway is thought to involve a load/unload mechanism by the hip abductors and adductors (Day et al., 1993; Winter, 1995; Winter et al., 1996). Increased right hip abductor activity will load the right leg, resulting in a simultaneous and proportional unloading of the left leg (Winter et al., 1996). However, muscles around the ankle joint also contribute to mediolateral standing. For example, plantarflexor muscle activity from the soleus and medial gastrocnemius is correlated to mediolateral torque production during quiet stance (Héroux et al., 2014). Similarly, ankle invertors and evertors increase activity and contribute to balance at narrower stances (Day et al., 1993; Winter et al., 1996; Gatev et al., 1999).

Changes in stance width have a significant impact on the biomechanics of standing balance in the frontal plane. Under normal standing, the preferred natural stance width (~ 17 cm) is with the feet in line with the hips (McIlroy and Maki, 1997; Kim et al., 2014). In unstable conditions, such as riding on a bus, people often stand with their feet further apart. A wider stance width increases the base of support and allows for larger excursions of the body center of mass. It also increases coupling between ankle and hip joints during lateral sway, thereby increasing passive stiffness (Day et al., 1993), and makes the corrective torques at the hip joints more effective at accelerating the pelvis laterally (Scrivens et al., 2008; Bingham et al., 2011; Goodworth and Peterka, 2012). In addition, because muscles and tendons around joints change in length with stance width (Day et al., 1993), intrinsic stiffness and damping as well as proprioceptive information from muscles and tendons also change.

Indeed, these biomechanical effects of stance width are linked to alterations in sway (Day et al., 1993; Goodworth and Peterka, 2010) and muscle activity (Gatev et al., 1999; Lemos et al., 2015), both of which decrease with increased stance width during quiet standing. These results (and our intuition) suggest that a wider stance increases stability; however, recent modeling and experimental studies have indicated that

such increase in stability is only possible when accompanied with appropriate changes in neural feedback (Bingham et al., 2011; Goodworth et al., 2014; Mian and Day, 2014).

CHARACTERISTICS OF SENSORY CUES CONTRIBUTING TO STANDING BALANCE

Low-frequency whole-body oscillations and higher-frequency accelerations, as well as muscle movements and forces related to standing balance, must be encoded by our various sensory systems to enable the active control necessary to stand. Sensors are commonly modeled as low- or high-pass filters, which encode signals with frequencies either lower or higher than a given cutoff frequency, respectively, and attenuate signals with frequencies either higher or lower than the cutoff frequency. The present section discusses briefly the frequency response dynamics (i.e., transfer functions) encoded by sensory afferents innervating sensory receptors from the vestibular, somatosensory, visual, and auditory systems, emphasizing how they may encode low-frequency postural sway (for detailed physiological reviews regarding these sensors, see Robinson, 1981; Hunt, 1990; Jami, 1992; Johnson, 2001; Goldberg et al., 2012; Pickles, 2015).

Vestibular cues

The peripheral vestibular system encodes motion of the head in three translational and three rotational dimensions using two distinct sensors: the otoliths, which detect linear motion (Lowenstein and Saunders, 1975), and the semicircular canals, which detect rotational motion (Lowenstein and Sand, 1940). Each end organ is innervated by regular and irregular afferents as classified by the variability of their resting discharge (see reviews by Goldberg, 2000; Cullen, 2012). Otolith primary afferents respond to linear accelerations in all directions, including static head tilts relative to gravity (Fernández and Goldberg, 1976; Jamali et al., 2013). This makes them well suited to transmit static and low-frequency changes in head orientation associated with postural oscillations, i.e., below 0.5 Hz (Dichgans and Brandt, 1978; Borger et al., 1999), and to contribute to our sense of postural verticality (i.e., being upright; see Chapter 3). Semicircular canal afferents encode primarily head angular velocity in space (Fernández and Goldberg, 1971; Ramachandran and Lisberger, 2006; Sadeghi et al., 2007). Their low gain for angular velocities below 0.1 Hz (Goldberg et al., 1982) suggests they transmit limited information regarding slow oscillations characteristic of unperturbed standing balance (Fig. 4.1B). At higher frequencies, both otolith (above

0.5 Hz) and semicircular canal (above 0.5–1 Hz) afferents encode with a higher gain head linear accelerations (Fernández and Goldberg, 1976; Angelaki and Dickman, 2000; Jamali et al., 2013) and head angular velocity (Ramachandran and Lisberger, 2006; Sadeghi et al., 2007), respectively (Fig. 4.1B). This may be useful for detecting transient impulses to the head but would be of limited use for the control of unperturbed standing balance.

Visual cues

Visual signals of self-motion arise from motion of brightness/contrast changes detected by photoreceptors spanning the retina (optic flow), which are relayed to the primary visual cortex, middle temporal area, and dorsal region of the medial superior temporal areas via transient retinal ganglion cells and the magnocellular lateral geniculate nucleus. Primate retinal ganglion cells coding for motion have large receptive fields and exhibit neuronal dynamics to contrast fluctuations peaking at ~10 Hz (Fig. 4.1B) (Benardete and Kaplan, 1999; Kaplan and Benardete, 2001). Retinal ganglion cells frequency responses to electrical stimuli (in rats) also exhibit characteristics of low-pass or band-pass filters with low-pass cutoffs ranging from 8 to >56 Hz (Hadjinicolaou et al., 2016). Direction-sensitive retinal ganglion cells provide information that can be decomposed by the brain as translational or rotational self-motion signals when combining information coded by ganglion cells from both eyes (Sabbah et al., 2017). Neural encoding specific to these two motion directions is further observed in cells in the dorsal middle temporal superior areas (Duffy and Wurtz, 1995; Beardsley and Vaina, 1997; Britten and van Wezel, 1998; Gu et al., 2006; Takahashi et al., 2007), implying that translational and rotational visual field information related to standing balance (i.e., translational visual scene motion vs. rotational motion during natural sway) may be extracted from visual cues.

A model has been proposed to describe motion detection in insects; it fits human psychophysical data well when using a movement detection time constant ranging from 13 to 80 ms (Fig. 4.1B) (Egelhaaf and Reichardt, 1987; Borst and Egelhaaf, 1989). However, when considering both spatial and temporal features of motion, the detection functions can be estimated either by low- or band-pass filters depending on the spatial or temporal frequencies associated with the motion (Burr et al., 1986). Based on these observations and because visual cues contribute to our sense of verticality – through multisensory processes adapted to expectations of more frequent vertical and horizontal

contours in the visual surround (see Chapter 3) – an important role of visual signals for standing balance can be assumed.

Somatosensory cues

Receptors found in muscles, joints, and skin provide sensation of our limb position and movement. In general, somatosensors exhibit transfer functions that can be described as high-pass filters of the input(s) they respond to. Receptors in the muscles, termed muscle spindles, are fusiform-shaped organs consisting of several intrafusal fibers embedded within muscles (Sherrington, 1894; Ruffini, 1898). Primary (Ia) and secondary (II) afferents innervating muscle spindles encode both muscle length and velocity, showing flat gain from 0.1 to 1 Hz and steadily increasing gain from 1 to 20 Hz (but steeper in Ia afferents, Fig. 4.1B; Matthews and Stein, 1969; Poppele and Bowman, 1970; Poppele and Kennedy, 1974; Chen and Poppele, 1978; Houk et al., 1981; Prochazka and Gorassini, 1998). Consequently, muscle spindles are mostly sensitive to transient inputs while balancing upright but their flat gain at low frequencies may encode the low-frequency ankle movements associated with postural sway (Day et al., 2017; Peters et al., 2017).

Because the paradoxical behavior of the plantarflexors during standing balance could obscure muscle spindle encoding of body sway, Loram et al. (2009) postulated that Golgi tendon organs may provide important balance-related proprioceptive information. Golgi tendon organs are capsular mechanoreceptors at the musculotendinous junction that encode active muscle force production (Stephens et al., 1975) but are relatively insensitive to passive muscle stretching (Gregory et al., 2002). Their low-frequency sensitivity (0.1–1 Hz) may encode the low-frequency muscle tension exerted to maintain upright balance, but their improved sensitivity for higher-frequency signals (1–30 Hz) suggests they preferentially encode transient inputs (Fig. 4.1B) (Anderson, 1974).

Cutaneous afferents supplying receptors in glabrous skin are classified as one of four subtypes based on their receptive field size (type I, small; type II, large) and adaptation to sustained skin indentation (SA, slow-adapting; FA, fast-adapting). Skin receptors are located at the interface of the body with the external world and may be important for the balance controller to detect a slip, a change in load distribution under the foot sole, or skin strains associated with joint angle changes. SAI (innervating Merkel cells) and SAII (innervating Ruffini endings) afferents encode skin indentation and static skin stretch, respectively. SA afferents exhibit slow adapta-

tion (e.g., sustained coding of prolonged stimuli), preferred sensitivity to low-frequency stimuli, and may encode passive joint movements (Iggo and Muir, 1969; Johansson et al., 1982; Looft, 1996; Edin, 2001). These properties may confer SA afferents an important role in encoding pressure under the feet and skin stretch across joints (i.e., joint angles) while standing. FAI (innervating Meissner corpuscles) and FAII (innervating Pacinian corpuscles) afferents respond to dynamic skin deformation and vibration of the skin, respectively (Loewenstein and Skalak, 1966; Iggo and Muir, 1969; Iggo, 1977; Roudaut et al., 2012). They exhibit a gain increase across frequencies that is more pronounced for FAII (Fig. 4.1B) (Johansson et al., 1982; Ribot-Ciscar et al., 1989; Looft, 1996). These properties may confer a role for FA afferents in coding transient balance-related movements (Kennedy and Inglis, 2002; Fallon et al., 2005). Note that loading of the feet while maintaining upright balance may increase the threshold of the foot sole afferents (Mildren et al., 2016), emphasizing that recordings from cutaneous afferents in a standing posture are critically needed to understand their role in balance.

Afferents innervating joint receptors involved in somatosensation include low-threshold SA type I (Ruffini endings), low-threshold FA type II (Pacinian corpuscle), and high-threshold SA type III (Golgi-like-receptors). Joint receptors can detect deformations in the joint capsule but their afferents encode joint movements ambiguously (firing bi-directionally and along multiple – and nonphysiological – axes of motion) and are preferentially active at the limits of joint motion (Burgess and Clark, 1969; Burke et al., 1988; Macefield, 2005). SA afferents exhibit adaptation to maintained joint angles and a gain increase from 0.1 to 7 Hz (McCall et al., 1974), hence behaving as a high-pass filter (Fig. 4.1B). From these limited data, it appears joint receptors may provide inconsistent code regarding static or dynamic oscillations associated with standing balance.

Auditory cues

Located in the inner ear, the cochlea encodes sounds via deformation of its basilar membrane which bends embedded hair cells, mechanoelectrically transducing pressure waves into electrical signals. Auditory cues can induce illusion of self-motion (Urbantschitsch, 1897) and audiokinetic nystagmus (Dodge, 1923), similar (but weaker) to visual cues (Marne-Karelse and Bles, 1977; Tanahashi et al., 2015; for review, see Völjamäe, 2009 and Campos et al., 2018). For example, psychophysical testing of visual and auditory localization demonstrates a 0.0014° threshold during visual (Vernier) acuity tests and 1° threshold during minimum

audible angle tests (Mills, 1958; Westheimer and McKee, 1977; Boucher et al., 2004). Sound intensity, interaural time, and interaural level differences, as well as Doppler effects, potentially all contribute to our sense of auditory motion (for review on auditory motion perception, see Carlile and Leung, 2016). Interaural time and level difference cues are predominant at low and high frequencies of human hearing, respectively (Strutt, 1907; Wightman and Kistler, 1999), and likely also contribute to our auditory sense of motion when standing. In contrast, because Doppler effects become prominent at object velocities larger than 10 m/s (Lutfi and Wang, 1999), they likely have little impact on the lower average sway velocity (~ 0.01 m/s; Winter et al., 1998) observed during standing balance. Interindividual factors (i.e., head shadow, torso, and pinna effects) induce location-dependent filtering (Chung et al., 2000) that also contributes to our perception of auditory motion (Miller and Matin, 2011). Although the frequency response of signals underpinning auditory self-motion is not well known, the contribution of auditory cues to the control of standing balance can be assumed based on our ability to localize static objects and the effects of auditory cues on whole-body sway (Easton et al., 1998; Hofman and Van Opstal, 2002; Völjamäe, 2009; for review, see Campos et al. 2018).

PROBING THE BALANCE CONTROLLER

The relative contribution of sensory cues to standing balance control can be examined using mechanical and sensory perturbations. A common approach is to sway reference visual and/or somatosensory information in varying combinations (Nashner and Berthoz, 1978; Nashner et al., 1982) to estimate the sensory organization of standing balance. This approach has had a large impact in the clinic (Nashner and Peters, 1990), where patients with balance impairments are assessed in their ability to make effective use of different sensory information.

An alternative approach is to characterize whole-body and muscle reactions to discrete linear or rotational perturbations applied to the feet or body (Nashner, 1971; Allum, 1983; Diener et al., 1984; Horak and Nashner, 1986; Carpenter et al., 1999; McIlroy and Maki, 1999; Robinovitch et al., 2002; Torres-Oviedo et al., 2006). The transient nature of this approach, however, evokes equally transient motor responses, which may not be related to the ongoing sensorimotor control of standing. Recognizing this limitation, other researchers (Maki et al., 1987; Johansson et al., 1988; Oie et al., 2002; Peterka, 2002; Peterka and Loughlin, 2004) have designed prolonged oscillatory perturbations to observe the steady-state regulation of standing and estimating transfer functions between the input

perturbations and output balance responses. Such prolonged perturbations enable the identification and modeling of important parameters related to reactive balance responses (e.g., stiffness, damping, time delay).

Compensatory responses evoked by external perturbations undoubtedly contribute to the maintenance of our vertical posture but may not involve the mechanisms or processes underlying unperturbed balance control (see Nielsen (2002) for locomotor analogy). This is particularly true for perturbations that evoke stretch reflexes or responses evoked by brain stimuli (e.g., transcranial magnetic stimuli), which induce muscle activity irrespective of a muscle's involvement in balance. On the contrary, certain vestibular and visual disturbances evoke balance responses only when these sensory signals are relevant to the balance task, thus providing a unique window into the balance controller. Admittedly, we recognize that these sensory stimuli may also evoke responses unrelated to unperturbed stance but may be mitigated by carefully designing experiments adhering to the natural roles our sensors play during standing balance. Building on this notion, this section will examine vestibular, visual, and perceptual approaches specifically probing human standing that have proven critical in revealing the neural principles of balance control.

Vestibular control of standing balance

The vestibular control of balance can be assessed using electrical stimulation of the vestibular apparatus (electrical vestibular stimulation: EVS). EVS represents a powerful tool to reveal the neural integration and central processing required to encode, decode, and transduce balance-related vestibular signals into motor commands. Current applied to the mastoid processes delivers an isolated craniocentric (Nashner and Wolfson, 1974; Lund and Broberg, 1983; Iles and Pisini, 1992; Britton et al., 1993; Dakin et al., 2007) vestibular error signal that, with the exception of local cutaneous cues, is absent of other sensory input (Fitzpatrick and Day, 2004). When delivered in a binaural-bipolar configuration, the stimulus generates primarily a sensation of head roll velocity (Day and Fitzpatrick, 2005; Peters et al., 2015), which has been estimated based on vestibular afferent populations and the assumption that the current activates all afferents bilaterally (otoliths and semicircular canals) (Fitzpatrick and Day, 2004; Day et al., 2010; Mian et al., 2010). While balancing upright, EVS evokes compensatory muscle and whole-body responses with latencies of ~60–120 and ~110–290 ms, respectively, that contribute to standing balance control (Nashner and Wolfson, 1974; Iles and Pisini, 1992; Britton et al., 1993; Day et al., 1997; Wardman et al., 2003a, b; Dakin et al., 2007, 2010; Son et al., 2008). The timing

of these EVS-evoked muscle responses, however, occurs 30 ms later than those obtained with motor cortex stimulation (Britton et al., 1993; Dakin et al., 2016). Because cortical and vestibular inputs travel to spinal motoneurons via pathways with similar conduction velocities, it has been argued that additional central processing of vestibular signals is required for balance stability.

Part of this additional central processing may be associated with the task dependence of vestibular-evoked responses. For example, lower-limb responses are absent when standing subjects are either fixed to a rigid back-board and contract lower-limb muscles or stabilize a body-equivalent inverted pendulum with their ankle muscles (Fitzpatrick et al., 1994). Because the body is stationary in both conditions, this indicates that responses are only evoked when vestibular information is relevant and required to balance. Recent work has further refined this concept, showing that responses also depend on the alignment between the induced vestibular error and the balance directions (Forbes et al., 2016). As these two directions rotate orthogonally to one another, vestibular-evoked responses are progressively suppressed even though subjects are engaged in balance. This suggests that the vestibular contribution to balance muscle activity is the result of an organized response that differs from simple vestibulospinal reflexes (Forbes et al., 2016). It further explains why the direction of the balance response becomes biased towards directions of reduced stability, e.g., when the body is more stable mediolaterally with larger stance width (Day et al., 1997; Mian and Day, 2014).

The processing of vestibular information is also sufficiently dynamic to account for changes in the direction of the vestibular error signal induced by active and passive head movements, partially explaining why the head can be moved actively and passively without disturbing upright balance (Dakin, 2012; Osler and Reynolds, 2012). Further principles regarding the vestibular control of standing are presented in the robotics section, below.

Visual control of standing balance

Vision provides self-motion information for stabilizing standing balance. Visual signals, however, can be ambiguous: arising from motion of one's body, the environment, or both. The brain must resolve this ambiguity before appropriate balance responses can be generated. For example, when standing in a room whose walls move, subjects experience illusions of self-motion that are accompanied by corrective balance responses (Lishman and Lee, 1973; Brandt et al., 1974; Lee and Lishman, 1975; Bronstein and Buckwell, 1997),

implying partial attribution of visual motion (i.e., the wall) to body movement. The visual motion-to-body motion relationship is not linear. As the amplitude of the visual scene motion increases, the relative magnitude of the compensatory sway decreases (Peterka and Benolken, 1995; Mergner et al., 2005), indicating flexibility in how the brain attributes the cause of visual flow to one's self or the environment. This effect may be related to perceptual thresholds of available nonvisual sensory inputs contributing to balance control (Mergner et al., 2005). Under normal balance conditions, sway reaches a peak (i.e., saturated) of 0.1° and $0.1^\circ/\text{s}$, but when ankle motion is sway referenced, sway reaches a peak of 1° and $1^\circ/\text{s}$. Noting the similarities between these sway characteristics and the upright somatosensory (0.1° and $0.1^\circ/\text{s}$) and vestibular (1° and $1^\circ/\text{s}$) perceptual thresholds (Fitzpatrick and McCloskey, 1994), Mergner et al. (2005) argued that nonvisual sensory cues limit visually-evoked body excursions when sway exceeds their thresholds.

Dokka et al. (2010) instead proposed that the non-linear visually-evoked sway responses are driven by the low probability of experiencing rapid visual signals of whole-body self-motion during standing. In other words, slower visual representations of self-motion are expected and deemed more likely by the nervous system. Compared to alternative models, including threshold effects, this expectation hypothesis described better the balance responses evoked by sinusoidal visual translations. Using discrete, unidirectional visual rotations, Day et al. (2016) revealed two consecutive, yet separate, balance components: an early response (~ 0.19 seconds) that minimizes apparent self-motion evoked by the stimulus and a later response (> 0.7 seconds) that aligns the body with the brain's erroneous estimate of gravity. The early (self-motion-related) response decreased with faster visual motion, but was achieved through changes in timing of corrective balance responses, occurring earlier with faster visual motion. Early response attenuation at higher velocities could be explained assuming Dokka and colleagues' (2010) suggested prior expectation for slower visual motion. The latter response, in contrast, increased with visual motion and is thought to be related to a biasing of the brain's estimate of gravity by prolonged visual motion. This previously unknown feature of the balance controller points to a gravity-dependent response.

Perceptual aspects of standing balance

Standing balance, like breathing, involves subcortical processes, yet we are partially aware of its actions and can volitionally control it when desired. Models of balance control should take into account the shared

contribution of cortical and subcortical processes. However, conscious perception of balance control mechanisms is limited, perhaps reflecting a narrow cortical role in the process. Despite our limited perception of these mechanisms, important information can be gleaned from the identification of the processes that are, or are not, accessible to conscious perception.

Fitzpatrick and McCloskey (1994) designed an inverted equivalent-body pendulum modeling the sway dynamics of the human body to evaluate isolated (and combined – see next section) sensory perceptions of sway. They found that lower-limb somatosensory information is the most sensitive sensory system for detecting whole-body sway (somatosensory: 0.1° , $0.1^\circ/\text{s}$; visual: 0.3° , $0.1\text{--}0.3^\circ/\text{s}$; vestibular: 1° , $1^\circ/\text{s}$). Subsequently, Luu (2010) evaluated how humans perceive ankle plantarflexor moments generated by the balance controller. After accounting for passive force contributions to standing balance, subjects reproduced (hence perceived) only one-third of the torque necessary to maintain standing balance when they were asked to match it during braced upright standing. Subjects could, however, actively replicate the ankle torque required to balance a body-equivalent inverted pendulum (balancing only with their ankles, without whole-body movement).

When we consider our limited perception of the balance drive with the balance-dependent vestibular control of standing (Fitzpatrick et al., 1994) and the reduction (two-thirds) in corticomuscular coherence during upright balance compared to a volitionally generated ankle moment (Luu, 2010), it appears the dominant portion of the balance drive is subcortical, with an accessory cortical contribution. Further indirect evidence suggesting minimal cortical drive during standing balance comes from the regulation of blood pressure. When subjects generate isometric ankle plantarflexor torques, there is an associated increase in blood pressure termed the central pressor response (Liang et al., 2011). This central pressor response is also observed when subjects balance a body-equivalent inverted pendulum while braced upright but not when they are free to balance upright (Luu, 2010).

Combination of sensory cues related to standing balance

The relative importance of each sensory cue or their integration in the balance controller still remains uncertain. At the perceptual level, the detection threshold of combined sensory cues is equivalent to the lowest threshold from the isolated sensory cues (Fitzpatrick and McCloskey, 1994). This suggests that the nervous system relies only on the sensory modality with the greatest acuity to detect whole-body sway, in contrast to the

expectation that multiple sensory sources undergo optimal cue combinations weighted by the accuracy and precision (i.e., inverse variance) of each cue (Ernst and Banks, 2002).

On the other hand, studies probing balance responses with sensory stimuli suggest the importance of multisensory cue combination for maintaining upright stance (Britton et al., 1993; Marsden et al., 2002; Peterka, 2002). For example, Day and Cole (2002) argued that the gain of the vestibular channel is set by the balance controller based on the information available from all sensory cues, though likely all sensory channels are affected. In support of this, early vestibular-evoked responses vary when prestimulus visual information differs (i.e., light or dark), even when poststimulus visual environments are equivalent (Day and Guerraz, 2007). Nevertheless, feedback effects from the poststimulus environment are also observed and affect the later parts of the response ($> \sim 400$ ms). This setting of the vestibular channel's gain can explain how vestibular responses evoked in healthy controls change with the amount of available visual (Smetanin et al., 1990; Britton et al., 1993; Fitzpatrick and McCloskey, 1994; Day and Guerraz, 2007) or somatosensory (Britton et al., 1993; Fitzpatrick and McCloskey, 1994; Marsden et al., 2003; Muise et al., 2012; Mian and Day, 2014) cues of self-motion.

Despite these testable predictions, one critical caveat to these multisensory balance responses must be acknowledged. Typically, modifications of the acuity of specific sensory information (e.g., vision vs. sway-referenced vision) or its absence (e.g., eyes closed) are accompanied by changes in whole-body postural sway (Nashner and Berthoz, 1978; Nashner et al., 1982; Black et al., 1988). The increased postural sway will lead to larger whole-body motion which may be associated with an increase in the amplitude of the vestibular-evoked balance responses (see example in robotics section, below). Consequently, well-controlled experiments are required to disentangle the relative contribution of sensory vs. mechanical factors on the multisensory control of standing.

CONCEPTUAL AND COMPUTATIONAL APPROACHES TO STANDING BALANCE

As similarly expressed by Robinson (1981) when describing oculomotor control, the use of conceptual and computational models of standing balance, in combination with experimental data, indicates the progression from observing balance to understanding it. Indeed, neuroscientists have relied on modeling approaches to extract working principles and develop our understanding of biological systems. A widely

accepted view of motor control is that the brain relies on internal models of the sensory consequences of one's actions to overcome sensorimotor delays, acquire new skills, and adapt to changing environments (Schmidt, 1975; Wolpert et al., 1998; Scott, 2004; Shadmehr et al., 2010; Krakauer and Mazzoni, 2011; Brooks et al., 2015). These models allow the nervous system to compute a sensory prediction error, i.e., the difference between actual sensory feedback and the models' sensory expectation of intended motor behaviors.

Sensory prediction errors are commonly considered in relation to motor adaptations when exposed to changes in the effector (i.e., body) or world, and when sensory stimulation is externally imposed (exafference) rather than self-generated (reafference). In this section, we review three key aspects of standing balance control that have benefited from the insight provided by conceptual and computational models, including: (1) internal representation of the body for standing balance; (2) controller computations for upright stance; and (3) multisensory integration models for balance.

Internal representation of the body for standing balance

As with other aspects of sensorimotor control, internal models are thought to have a role in standing balance. This possibility was explored by Nashner et al. (1982); however, it was dismissed in favor of an alternative theory: that the vestibular system is used as an internal reference about which adaptive changes in visual and somatosensory inputs are made. The authors argued that the rapid reorganization of sensory inputs for posture, in contrast to longer-term vestibulo-ocular and vestibular-perceptual adaptations, is the product of a fixed hierarchical organization of sensory inputs controlled by higher-level processes (Nashner and McCollum, 1985). Despite this being met with heavy criticism (see commentary in Nashner and McCollum, 1985), it has led to a large body of research exploring the central programming (i.e., "central set") of balance behaviors in both healthy and clinical populations (see Horak and Nashner (1986) and review by Jacobs and Horak (2007)). The extensive connectivity of the vestibular system throughout the nervous system (Goldberg et al., 2012), however, suggests flexibility in its organization. Moreover, different research groups have shown rapid adaptation of the vestibular system for the control of standing balance, locomotion, and head-neck control (Day and Guerraz, 2007; Luu et al., 2012; Mian and Day, 2014; Brooks et al., 2015; Héroux et al., 2015; Forbes et al., 2016, 2017; Tisserand et al., 2018).

Gurfinkel and colleagues postulated that standing balance is governed by a representation of self, referred to as

a body schema (Gurfinkel and Levik, 1979). Their hypothesis states that sensory and motor signals are utilized by the nervous system to form a single internal representation of the body's current configuration (e.g., postural orientation) which is responsible for both the conscious perception of orientation and the transformation of sensory signals for balance control (Popov et al., 1986; Gurfinkel et al., 1988; Gurfinkel and Levick, 1991; Massion, 1994). For instance, during head-on-feet perceptual illusions elicited through muscle vibration or prolonged head-turned postures, the transformation of vestibular-evoked balance responses follows the perceived instead of the actual body orientation (Popov et al., 1986; Gurfinkel et al., 1989).

Although Gurfinkel and colleagues did not postulate on the brain areas responsible for this internal representation, their hypothesis would suggest cortical and subcortical regions have equal access to this central representation. Gurfinkel's theory, however, has been recently challenged: an alternative model stipulates that, although sensory and motor cues are available to the balance controller and conscious perception, each process differs in its use of the available cues leading to separate internal representations of body orientation (Fig. 4.2) (Dalton et al., 2017). When replicating the head rotation illusions elicited through prolonged passively-held head-turned postures, Dalton et al. (2017) also found that the transformation of vestibular-evoked balance responses followed the perceived instead of the actual body orientation. When subjects opened their eyes, however, the availability of static visual cues updated the perceptual estimate of head postures but not the (re-)orientation of the vestibular-evoked balance responses induced by the prolonged head turn. The visual update (from static

cues) of only the perceptual estimate of head posture highlights the presence of distinct internal representations (perceptual vs. balance) of body orientation in the brain.

These results suggest that the balance controller does not combine static visual cues with other sensory and motor cues to estimate head-on-body orientation. This separate balance estimate may be advantageous by requiring less processing by the brain while providing a good estimate of head-on-feet orientation for most daily situations.

Controller computations for upright stance

A fundamental question when modeling standing balance is how the brain controls upright stance, and whether this is maintained through feedback or feedforward control. Theoretically, a feedback control model generates muscle activity in response to deviations of whole-body sway from a desired setpoint. The most common feedback model for human stance is based on a control engineering framework whereby deviations from a setpoint are multiplied by proportional, integral, and/or derivative terms (i.e., a PID controller) to generate corrective muscle activity or torque responses. The control parameters (or gains) can be estimated by fitting the model to postural responses to changing mechanical perturbations under a variety of sensory conditions (Peterka, 2000; Maurer and Peterka, 2005; van der Kooij and de Vlugt, 2007). The relative simplicity of this model makes it potentially useful for clinical implementations (Meskers et al., 2015; Pasma et al., 2016).

The disadvantage of a PID (or PD) controller is that it lacks any knowledge of the ongoing control process.

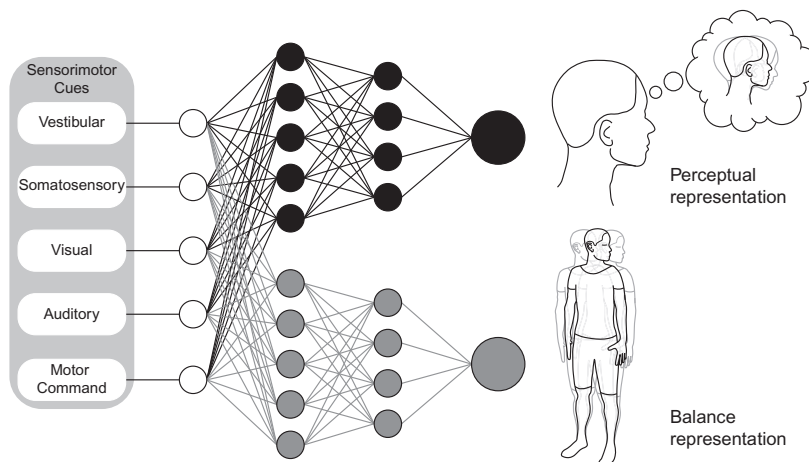


Fig. 4.2. Schematic representing the theoretical framework of separate sensorimotor integration processes related to the internal body representation for perception and balance control. Sensory and motor cues are fed to a network of sensorimotor neurons (circles) that form two distinct internal representations of body orientation for conscious perception (black circles) and the vestibular control of balance (gray circles).

Optimal control theory addresses this issue by estimating optimal feedback gains using a cost function that penalizes control signals (i.e., muscle activity or torque) or state variables (i.e., whole-body sway) (Kuo, 1995, 2005; van der Kooij et al., 1999; Todorov and Jordan, 2002; Todorov, 2004). This approach avoids having to explicitly fit the model to data and instead reveals the validity of hypothesized cost functions through the model's ability to replicate the data. For example, Kiemel et al. (2011) used optimal control theory to compare experimentally identified feedback to optimal feedback for a range of cost functions, and found that standing balance could be best approximated by minimizing muscle activity rather than sway.

Feedforward models of human standing have been proposed to be necessary for balance because of low-feedback loop gains (Fitzpatrick et al., 1996), which are insufficient to maintain upright stance, as well as the observation that electromyogram leads whole-body motion (Gatev et al., 1999). Others have argued, however, that a truly feedforward system can never ensure stabilization because the control variable (muscle activity or torque) is independent of the output variable (body sway) (van der Kooij and de Vlugt, 2007). Instead, van der Kooij and de Vlugt stated that the feedforward model proposed by Fitzpatrick et al. (1996) was actually an adaptive feedback controller and shares similarities with the internal model structure that uses sensory prediction errors to drive the controller (see next section). Furthermore, the electromyogram leading whole-body motion reported by Gatev et al. (1999) can be replicated using a simple feedback model with position and velocity terms (van der Kooij and de Vlugt, 2007) or a biologically-inspired neuromusculoskeletal model of somatosensory spinal circuits that is absent of any feedforward mechanisms (Elias et al., 2014).

Feedback and adaptive feedback models maintain continuous control of the corrective ankle torque. Intermittent, ballistic-like control of lower-limb muscles has been proposed (Bottaro et al., 2005; Loram et al., 2006, 2011; Asai et al., 2009). This control scheme is thought to involve intrinsic predictive mechanisms used by the nervous system that may be driven by low-frequency updates (Loram et al., 2006) or when sensory thresholds are exceeded (Bottaro et al., 2008). Researchers have shown that medial gastrocnemius motor units discharge intermittently (Vieira et al., 2012; Héroux et al., 2014), which some have argued is due to an intermittent control signal generated by the brain (Vieira et al., 2012). However, the biologically-inspired spinal circuit model by Elias et al. (2014) demonstrated that intermittent recruitment of medial gastrocnemius can be obtained without the predictive central mechanisms proposed by Loram and colleagues.

Based on their model, Elias et al. (2014) proposed that spinal mechanisms may provide a combination of intermittent and continuous control of human standing, mediated via the medial gastrocnemius and soleus muscles respectively. Because the soleus muscle is more homogeneous with a higher number of low-threshold motor units, it can maintain near continuous muscle activity that counters the gravitational toppling torque (Joseph and Nightingale, 1952; Mori, 1973; Mochizuki et al., 2006; Elias et al., 2014; Héroux et al., 2014).

Multisensory integration models for balance

In humans, each sensor may encode whole-body sway within its own coordinate system. Consequently, the nervous system must transform and combine sensory information through multisensory integration. For example, the vestibular system detects head motion relative to inertial space, visual signals detect head motion relative to the visual environment, and somatosensory signals detect limb motion relative to the support surface or another limb.

Peterka (2002) proposed a direct integration model, where separate sensory cues are combined linearly and the corrective torque is generated using a weighted sum of the separate error signals. This direct form of integration, however, fails to account for sensory dynamics, which differ for each sensor (e.g., low- vs high-pass filter-like properties; Fig. 4.1B) and result in frequency-dependent contributions to balance control. Models including neural integration, Bayesian, Kalman, and particle filters address this drawback by processing or filtering the different sensory cues to produce an internal estimate of body state (i.e., a balance representation) as output (Fig. 4.3A) (Kuo, 1995, 2005; van der Kooij et al., 1999, 2001; Kiemel et al., 2002; Haggerty et al., 2017). These models differ in their application to either discrete/static (Bayesian filter) or dynamic/continuous (integration, Kalman, and particle filters) situations and their ability to consider non-Gaussian noise distributions and nonlinear system dynamics (integration and particle filter only) (see review by MacNeilage et al. (2008)). With the exception of the integration filter, all of these approaches rely on statistical inferences related to the noise or probability distributions associated with sensory or motor signals, and pre-existing knowledge or experience.

The Kalman filter is the most commonly used model to study standing balance (Kuo, 1995, 2005; van der Kooij et al., 1999), and generates a sensory prediction error by calculating the difference between estimated and measured sensory information (Fig. 4.3). The sensory prediction error is then multiplied by a Kalman gain

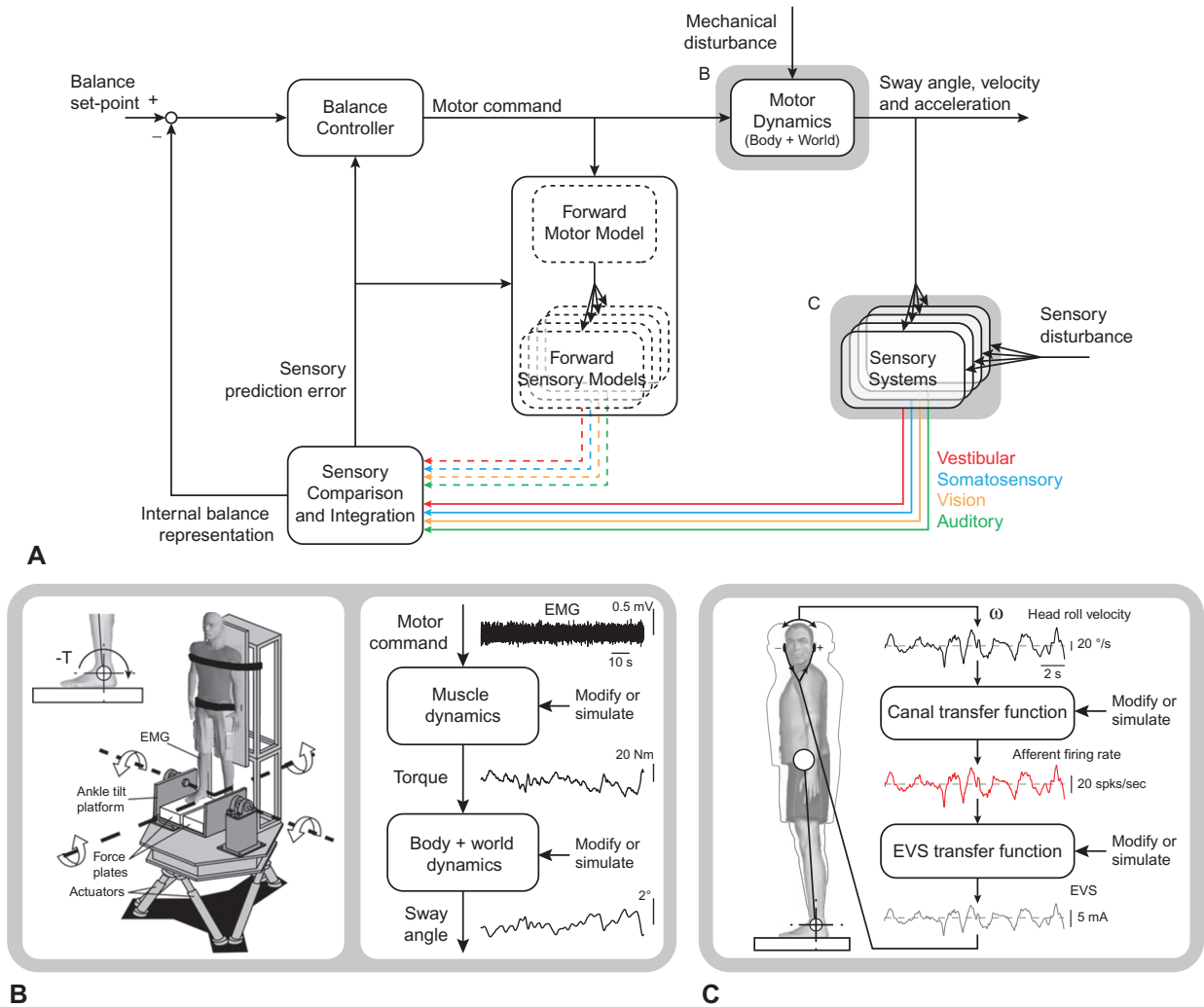


Fig. 4.3. Standing balance control loop, robotic balance simulator, and dynamic sensory manipulations. **(A)** Schematic of the balance control loop and the relationship between the motor command, sensory feedback, sensory prediction error, and internal balance representation. Sensory prediction errors occur when mechanical **(B)** and/or sensory **(C)** disturbances are imposed on the subject through external perturbations or changes in the physics of the body, world, and/or sensors. These errors are computed as the difference between sensory inflow and the sensory expectation (i.e., forward model output) of intended motor behaviors, and are used to update the balance controller as well as the forward models. An internal representation of balance is generated through the integration of sensorimotor cues, and based on this internal estimate the balance controller produces motor commands to maintain the desired balance set point. **(B)** Robotic balance simulator used to simulate and modify balance mechanics (left panel). Subjects stand on an ankle tilt platform and are securely strapped to a rigid backboard mounted on a whole-body motion platform. Both the ankle tilt platform and whole-body motion platforms can be controlled using either the net ankle torques exerted on the force plates (see upper left inset) or the net muscle activity recorded from electromyogram (EMG) electrodes. Muscle, body, and world dynamics are simulated to replicate normal standing and can be selectively modified (right panel) to produce novel balance conditions that create a mismatch between the actual and expected sensory feedback. For example, [Forbes et al. \(2016\)](#) had subjects balancing with normal or reversed vestibular consequence of balance motor commands. In the normal condition, plantarflexor torque was required to maintain the body in a forward-leaning position. In the reversed condition, dorsiflexor torque was necessary to maintain the body in a forward-leaning position and additional dorsiflexor torque would cause the body to accelerate backward. **(C)** Manipulation of vestibular sensory dynamics. Instantaneous head angular velocity is transformed into an afferent firing rate according to the canal transfer function ([Fernandez and Goldberg, 1971](#); [Schneider et al., 2015](#)), which is in turn transformed into an electrical vestibular stimulus signal according to the inverted stimulus-to-afferent transfer function ([Kwan et al., 2016](#)). The resultant electrical vestibular stimulation (EVS) replicates the afferent firing rate that would arise from head motion or can be modified to create a mismatch between the actual and expected vestibular sensory feedback ([Héroux et al., 2015](#)).

to correct the state estimate, which is in turn used for feedback control. When combined with optimal feedback control, these models are capable of replicating balance behaviors across a variety of mechanical and visual perturbation conditions (Kuo, 1995, 2005; van der Kooij et al., 1999, 2001; Kiemel et al., 2002; Carver et al., 2005).

These sensory integration models have proven useful in exploring different hypotheses about balance control. For example, van der Kooij et al. (2001) argued that the visually-induced sway at low stimulus amplitudes (see "Probing the balance controller" section, above) occurs because vestibular signal noise reduces the accuracy of the vestibular sensory prediction error within the internal model. Subsequently, Kiemel and colleagues (2002, 2006) used a similar argument (and model) to show that the inherent sway associated with quiet standing is due to noisy internal model estimates within the feedback loop rather than exploratory processes outside the feedback loop, as proposed by others (Riccio, 1993; Zatsiorsky and Duarte, 1999; van Wegen et al., 2002; Carpenter et al., 2010). Haggerty et al. (2017) presented a model of standing balance, including direct feedback with a neural integration filter, an approach commonly used to explain compensatory eye movements to combined visual and vestibular stimulation (Raphan et al., 1979; Cohen et al., 1981; Robinson, 1981; Laurens and Angelaki, 2011). By replicating the postural dynamics produced by optokinetic and electrical vestibular stimulation, these authors argued that similar sensory integration processes may govern compensatory eye and balance responses.

Finally, H  roux et al. (2015) explicitly probed internal models for standing balance to determine whether healthy volunteers can adapt to augmented (or reduced) vestibular signals of balance-related head movements. They used an electrical vestibular stimulus that was coupled to ongoing head movements based on the semi-circular canal dynamics (Fig. 4.3C), which increased sway fourfold and decreased vestibular-evoked muscle responses. After a period of visual or somatosensory recalibration, sway variability and muscle responses returned to baseline levels. The researchers concluded that other sensory cues are used to recalibrate the forward vestibular model (Fig. 4.3A), such that the predicted consequences of balance match the vestibular reafferent signal from sway, thus making it more effective for balance control.

ROBOTICS AND STANDING BALANCE

Advances in robotics have allowed researchers to investigate how we control and adapt our movements to novel physical environments, allowing the characterization of our brain's internal computations and models.

The general principle underlying the use of robotics in sensorimotor neuroscience relies on altering the dynamics of the effector (typically upper arm) and characterizing the neural signals controlling its adaptation to this manipulation.

Notterman and Weitzman (1981) followed by Ruitenbeek (1984) used an actuated lever arm to control the dynamic properties (stiffness, viscosity, and mass) associated with upper-arm motion and reported the resulting adaptations to the novel motor environment. It was the seminal work by Shadmehr and Mussa-Ivaldi (1994), however, that explicitly associated the internal model framework to robotics manipulations of the arm dynamics. Using a robotic arm manipulandum, the authors applied a velocity-dependent force field while subjects reached to a target. Over time, subjects adapted to the induced force field, performing the task similarly to before the movement-dependent perturbation was applied. When the force field was removed, subjects adopted a trajectory that mirrored (i.e., opposite direction) the velocity-dependent force field. Shadmehr and Mussa-Ivaldi (1994) proposed that the neural controller was formulating an internal model of the force-field perturbation during the adaptation period, resulting in oppositely directed aftereffects when the perturbation was removed. A similar framework has been adopted by multiple research groups (Flanagan and Wing, 1997; Shadmehr and Holcomb, 1997; Wolpert and Kawato, 1998; Kawato, 1999; Krakauer et al., 1999), replicating and expanding on the original observations by Shadmehr and Mussa-Ivaldi (1994). In this section, we propose that an analogous robotics framework can be expanded to standing balance to unravel the neural control of upright stance.

Researchers in the field of standing balance have extensively used mechanical devices to probe the balance responses to external perturbations or alter sensory feedback by sway referencing the ankle somatosensory and/or visual inputs contributing to upright stance (see section "Probing the balance controller"). A noteworthy contribution was the development of a whole-body equivalent mechanical device (Fitzpatrick et al., 1994). Their body-equivalent apparatus replicates the mechanics of standing balance with a physical inverted pendulum, enabling researchers to mimic the mechanical motion of a standing body without necessitating a subject to maintain standing balance. Fitzpatrick and colleagues and other research groups have used similar mechanical or actuated inverted pendulums to characterize the mechanics, sensory contributions, and control principles of standing balance (Fitzpatrick and McCloskey, 1994; Loram et al., 2006; Sakanaka et al., 2016; Fukuoka et al., 1999; Buettner et al., 2017). Mechanical or actuated devices have also received attention for the rehabilitation

of standing balance. Examples of balance rehabilitation devices include simple ankle actuation in an upright posture (Donaldson et al., 1997), 2-degree of freedom (anteroposterior and mediolateral) robotic balancing device to assist (simulating a spring-like motion) or perturb (torque impulse) subjects while balancing upright (Matjacić et al., 2000), as well as 3-, 4-, and 6-degree-of-freedom platforms (Lees et al., 2007; Patanè et al., 2012; Susko and Krebs, 2014; Kharboutly et al., 2015; Susko et al., 2016) that enable researchers to probe the sensorimotor control of balance and locomotion. Regardless of their technological advancements (Sinitski et al., 2015), these multidegree-of-freedom systems provide little additional opportunity to identify the internal models of standing over observations on compensatory balance responses to external perturbations.

Given these limitations, Blouin and colleagues have developed a robotic system that permits subjects to experience novel body, environment, and/or sensor dynamics while maintaining standing balance (Fig. 4.3B and C) (Huryn et al., 2010). This design was influenced by the robotic arm manipulanda and by Fitzpatrick's whole-body-equivalent mechanical device (Fitzpatrick et al., 1994), but with the specific purpose of characterizing experimentally the motor and sensory internal models of standing balance. While standing upright on the robotic device, subjects are braced by a backboard that is rigidly mounted on the robot while their standing weight is supported on top of a force plate. Conceptually, they are inside the control loop of the robotic motion, having full control of their whole-body movements based on the forces/moments applied to the ground. Resulting whole-body movements are specified by a computer simulation (or virtualization) of standing balance mechanics, mimicking normal control of standing balance (e.g., inverted pendulum) or altering the physics of the controlled body (stiffness, damping, inertia, height, mass), the environment (simulated gravity, laws of motion), and/or sensory dynamics (ankle rotation, electrical vestibular stimuli, visual field). When simulating inverted-pendulum motion for anteroposterior sway, the robotic device replicates the mechanical properties of the whole-body observed in upright balance control (Luu et al., 2011; Pospisil et al., 2012), with subjects experiencing a natural and almost effortless simulation of standing.

This robotic device has been used to re-examine the task dependence of the vestibular control of standing balance (Fitzpatrick et al., 1994). Luu et al. (2012) confirmed that whole-body balance control was a prerequisite to elicit muscle responses of vestibular origin in appendicular muscles (soleus and first dorsal interosseous). Expanding on these findings, they exposed subjects to normal balance control simulations with transient periods where subjects thought they were balancing

but robot motion was predetermined (imposed) and independent from their ankle torque. Despite being mostly unaware of these transitions, subjects exhibited rapid (< 200 ms) attenuation of vestibular responses evoked by an electrical stimulus (Fig. 4.4A). Thus, activation of the vestibular control of standing requires whole-body sensory feedback to be congruent with the predicted sensory consequences of balance-generated motor commands.

Taking further advantage of possibilities afforded by the robotic balance simulator, Forbes et al. (2016) reversed the line of action of the ankle plantar- and dorsiflexors, effectively performing a virtual muscle surgery (Berger et al., 2013). For this specific balance simulation, the expected forward-leaning body position associated with upright stance required a dorsiflexor ankle torque to stabilize the robotic balance system and increases in dorsiflexor torque greater than the gravity-induced toppling torque accelerated the body backward (Fig. 4.4B). These balancing conditions reversed the relationship between the ankle motor commands and vestibular feedback. Note that vision was occluded and that the ankle torque/ankle angle relationship was maintained by independently controlling the motion of the ankle tilt platform, isolating the sensorimotor reversal to the vestibulomotor system. Subjects adapted quickly to this reversed relationship between the balance motor commands and the vestibular feedback: all could maintain standing balance after a 30–90-second familiarization period. Subjects' motor output (torque/muscle responses) to an electrical vestibular error signal were reversed and delayed, permitting subjects to sway according to the direction of the vestibular error, i.e., in the same direction for the control and reversed balance simulations (Fig. 4.4B). Interpreting these observations in the context of response attenuation observed when control was taken away from the subjects (Luu et al., 2012) or when the plane of instability was orthogonal to the direction of the vestibular error (Forbes et al., 2016), it must be accepted that vestibular-evoked responses to electrical stimuli require computation and represent an integrated response by the balance controller. This is in stark contrast to the alternate possibility that electrical vestibular stimuli elicit direct vestibulospinal reflexes (Welgampola and Colebatch, 2001; Tax et al., 2013).

The standing balance robotic device has also made it possible to explore the plausibility of proposed control models for whole-body stabilization and the control of standing balance in the face of changing body mechanics. Huryn et al. (2014) assessed the performance of continuous and intermittent controllers (Bottaro et al., 2005; Loram et al., 2006, 2011; Asai et al., 2009) at stabilizing upright balance. Both

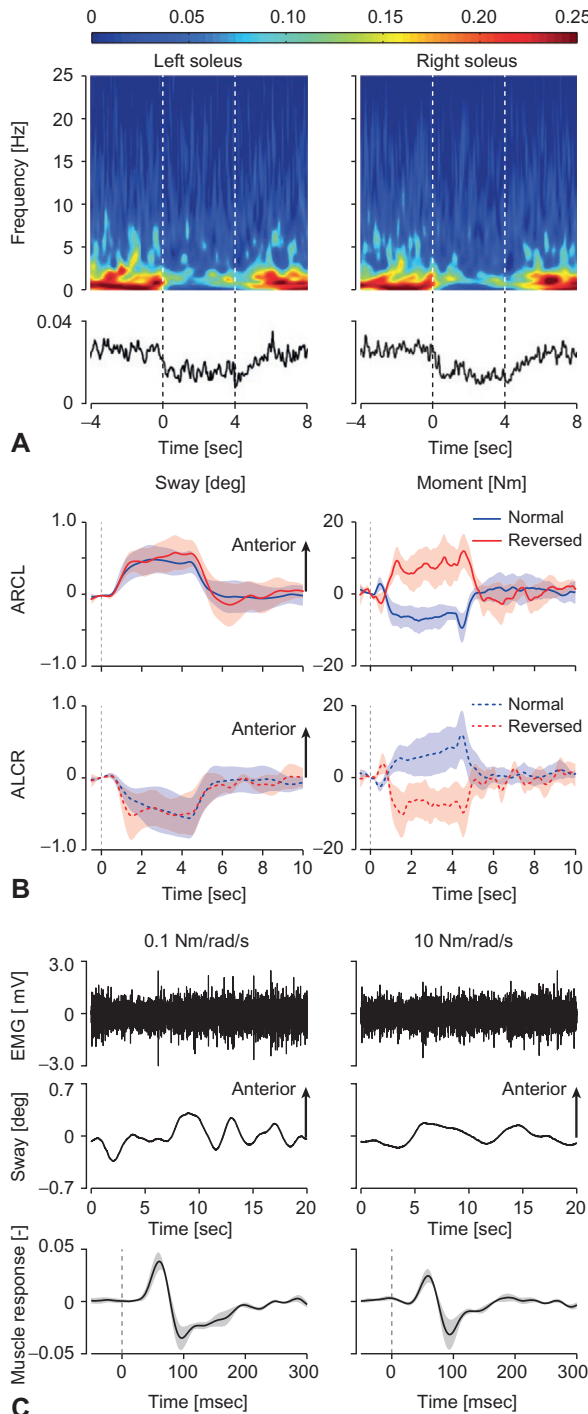


Fig. 4.4. Standing balance responses to modified motor and sensory relationships. **(A)** Subjects stood in a robotic balance simulator while the computer imperceptibly took over ($t = 0$ seconds) and eventually returned ($t = 4$ seconds) balancing control (Luu et al., 2012). Strength of the vestibular input to the soleus muscle (coherence) plotted in the time and frequency domains (colored surface plot) decreased rapidly (< 200 ms) when control was removed and increased more slowly (> 850 ms) when control was reinstated ($n = 5$). Coherence magnitude is indicated by the color bars. The mean of the

intermittent and continuous controllers could stabilize the upright body but the continuous controller replicated better the sway of natural standing while requiring more energy than the intermittent controller. The authors further explored whether a predictor overcoming the balance loop delay is beneficial to continuous and intermittent controllers (Masani et al., 2006; Vette et al., 2007; Gawthrop et al., 2009). Prediction of the balance loop delay was not a prerequisite for stability but provided some stabilization benefits for the intermittent controller.

Recent efforts explored the balance behavior under changes in viscosity of the simulated whole-body (unpublished observations). An increase in viscosity resulted in lower postural sway variance and was associated with smaller muscle responses evoked by an electrical vestibular stimulus (Fig. 4.4C). These results suggest the vestibular control of standing balance is tuned to the dynamics of the body and may depend on the variability of whole-body motion, a cautionary note when comparing balance responses from controls and patients with balance impairments or when using any sensory manipulation that interferes with whole-body sway. Future work should refine these methods to characterize how the body dynamics, sensor dynamics, and environment affect the balance controller.

CONCLUSIONS

Here, we have reviewed the mechanical and sensory contributions to standing balance from a conceptual and computational modeling perspective. The information was presented for the reader to appreciate this framework and understand how fundamental principles of operation underpinning the control of upright stance can be revealed with this approach. We further reviewed approaches to probe the balance controller, recent

coherence from 0 to 25 Hz at each time point is shown in the bottom panel. **(B)** Subjects stood in the robotic balance simulator with normal and reversed relationships between balancing motor commands and the associated vestibular feedback while being exposed to square-wave electrical vestibular stimulation (Forbes et al., 2016). Whole-body sway was in the same direction across normal and reversed conditions for each stimulus polarity (ARCL, anode-right/cathode-left; ALCR, anode-left/cathode-right), while ankle torque was reversed ($n = 8$). **(C)** Muscle activity and sway responses of a single subject during balance conditions with normal (0.1 Nm/rad/s) and increased (10 Nm/rad/s) damping properties; muscle activity remained constant but sway decreased with increased damping (unpublished observations). Vestibular-evoked muscle responses (correlation coefficient) decreased with increased damping ($n = 6$) similar to whole-body sway variability. EMG, electromyogram.

evidence supporting parallel processing of sensorimotor information for balance and perception, as well as computational approaches to standing balance. Finally, we presented advances in robotics that permit the virtualization of the balance task. These developments show the power enabled by a subject-in-the-loop robotic balance simulation approach and how it enables unique possibilities (through body, sensor, and/or environment manipulations) to probe the balance system and its adaptability. Coupled with a grounded theoretical framework, such robotic balance devices will allow researchers to address questions that could not be envisioned before. By revealing principles of operation for the balance controller, this may yield broad impacts to the specialized field of standing balance but also to the general field of movement neuroscience.

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