Chapter 2

Sensory integration for human balance control

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Abstract

The upright stance position is inherently unstable since the smallest deviation from a perfect upright orientation produces forces due to gravity that accelerate the body toward the ground. Stability is achieved by generating appropriate joint torques that correct for deviations from a desired orientation with orientation changes detected by sensory systems (primarily somatosensory/proprioceptive, visual, and vestibular systems). Functionally, balance control can be viewed as a closed-loop feedback control system with the integration of different sources of sensory orientation information being one component of the overall system, but with the system's feedback nature placing constraints on the sensory integration process. Analysis of body sway evoked by balance perturbations allows for the measurement of "sensory weights" that represent the relative contributions of different sensory systems to an internal estimate of orientation that, in turn, is used to generate corrective actions. Experiments reveal that sensory weights are not fixed quantities, but vary as a function of environmental and experimental conditions as well as neurologic disorders that affect the quality of sensory information available from different sensory systems. Because environmental conditions can change rapidly, sensory reweighting must also occur rapidly enough to prevent instability due to an under- or overproduction of corrective action.

INTRODUCTION

A complex array of peripheral sensory receptors in various sensory systems (somatosensory/proprioception, visual, vestibular (Pasma et al., 2014; Duysens et al., 2000)) contribute to balance and orientation control. Somehow all of this information is organized to provide appropriate motor actions via sensory integration and sensory-to-motor transformations that activate appropriate muscles to accomplish specific, but varying, balance-related tasks such as maintaining static balance under the destabilizing influence of gravity and resisting perturbations to balance (compensating for externally applied forces, slippery surfaces, compliant or tilted surfaces, moving visual scenes, load changes and, remarkably, all of these things potentially happening at the same time). Additionally, changing or holding differing postural configurations (poses) alters the balance control task by changing the mechanical characteristics of the body, altering the effectiveness of motor actions by changing the moment arms of muscles, and changing the site of motor action depending on support conditions (Cordo and Nashner, 1982). Finally, locomotor movements such as walking, running, hopping, and skipping gaits also require that sensory information informs motor actions that maintain consistent and stable rhythmic body motions (dynamic balance).

Early ideas considered that balance control could be explained by direct activation of reflexes to maintain posture and resist perturbations (Magnus, 1926). While this scheme might be adequate for maintaining a fixed posture, it would interfere with other aspects of balance control mentioned above and thus is an inadequate solution for maintaining stability while affording flexible

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behaviors. A reflex-based control scheme is essentially one without sensory integration except at the final motor neuron level where different reflex influences converge (e.g., stretch and vestibulospinal reflexes).

One step away from a direct reflexive control scheme is one where higher-level processing exerts influence over low-level reflexive control so that reflexive actions work more efficiently in different situations. Mathematic models were developed (Nashner, 1970) that incorporated higher-level control of reflexes with the reflex pathways incorporating the hard-won understanding of the characteristics of peripheral sensory receptors that became available in the 1960s, 1970s, and 1980s (Goldberg and Fernandez, 1971b; Fernandez and Goldberg, 1976; Matthews, 1981). Sensory integration could potentially be represented in the higher-level processing, but there were essentially no follow-up attempts to use this type of representation to predict or explain experimental outcomes, suggesting that this representation was not adequate. In retrospect, the inclusion of complex sensory receptor dynamics was not necessarily justified (see intrasensory integration section).

Advances that led to a fuller appreciation for the role of sensory integration in balance control came from two sources. One was simply recognizing the implications of the long-appreciated fact that sensory feedback contributes to balance control and that the sensory contributions to balance control should be considered in the context of a feedback control system (Talbott and Brookhart, 1980; Johansson et al., 1988). Feedback control for standing balance means that body sway is detected by sensory systems, corrective motor action is generated as a function of sensory-detected sway, and the motor action modifies the time course of sway which, in turn, is registered by sensory systems. This continuous loop of sensing – acting – sensing – acting is referred to as a closed-loop feedback control organization and is in contrast to open-loop control organization (e.g., the vestibulo-ocular reflex control of eye movements in the dark). The closed-loop feedback control organization places demands on both what particular sensory information is needed and on how central integration across different sensory systems needs to be organized for successful balance control.

The second advance that led to a clearer understanding of sensory integration is also implicit in the Johansson et al. (1988) study. This study showed that experimental results could be accounted for by the simplest possible representation of sensory feedback, which is that the nervous system has available to it accurate, wide-bandwidth sensory-derived representations of angular position and velocity. That is, it is not necessary to account for the various dynamic characteristics of individual sensory receptors or even classes of sensory receptors. Apparently, the nervous system takes care of this via intrasensory system integration mechanisms that provide the nervous system with higher-level neural representations that correspond to physical variables that are relevant for balance control. Having access to neural representations of physical variables likely simplifies the nervous system's task of combining information from different sensory systems for balance control.

This chapter begins by detailing the constraints imposed on sensory integration by the feedback nature of balance control. Evidence is presented for how intrasensory integration within individual sensory systems yields neural representations of physical variables relevant to balance control. Then various aspects of intersensory integration (combining the neural representation of physical variables derived from multiple sensory systems) are discussed. The concept, principles, and advantages of using weighted combinations of multisensory information are reviewed and methods used to measure sensory weights are outlined. Experimental results are presented to show that sensory weights adapt to changing environmental conditions via sensory reweighting mechanisms. Given that environmental conditions can change rapidly, stability of the balance system is affected by how rapidly sensory reweighting can compensate for changing conditions.

CONSTRAINTS ON SENSORY INTEGRATION DUE TO CLOSED-LOOP FEEDBACK CONTROL ORGANIZATION

The organization of balance control as a closed-loop feedback control system stabilizing a mechanically unstable body (Fig. 2.1A) places constraints on the types of motion information required from sensory systems and on the mechanisms needed to coordinate the integration of information across different sensory systems. Figure 2.1B shows a model representation of a feedback control system for balance during stance. The system maintains upright stance of an inherently unstable inverted pendulum body. The simplest body representation is as a single-segment rigid mass that rotates about an axis at ankle joint height above the stance surface and with the feet remaining in contact with the surface (Fig. 2.1A). The slightest lean away from vertical produces a gravity torque that accelerates the body further away from vertical. The system can be stabilized by applying appropriate corrective action (ankle torque) generated as a function of orientation information derived from sensory systems.

The Figure 2.1B model, when represented mathematically, makes clear that the corrective torque needs to be a
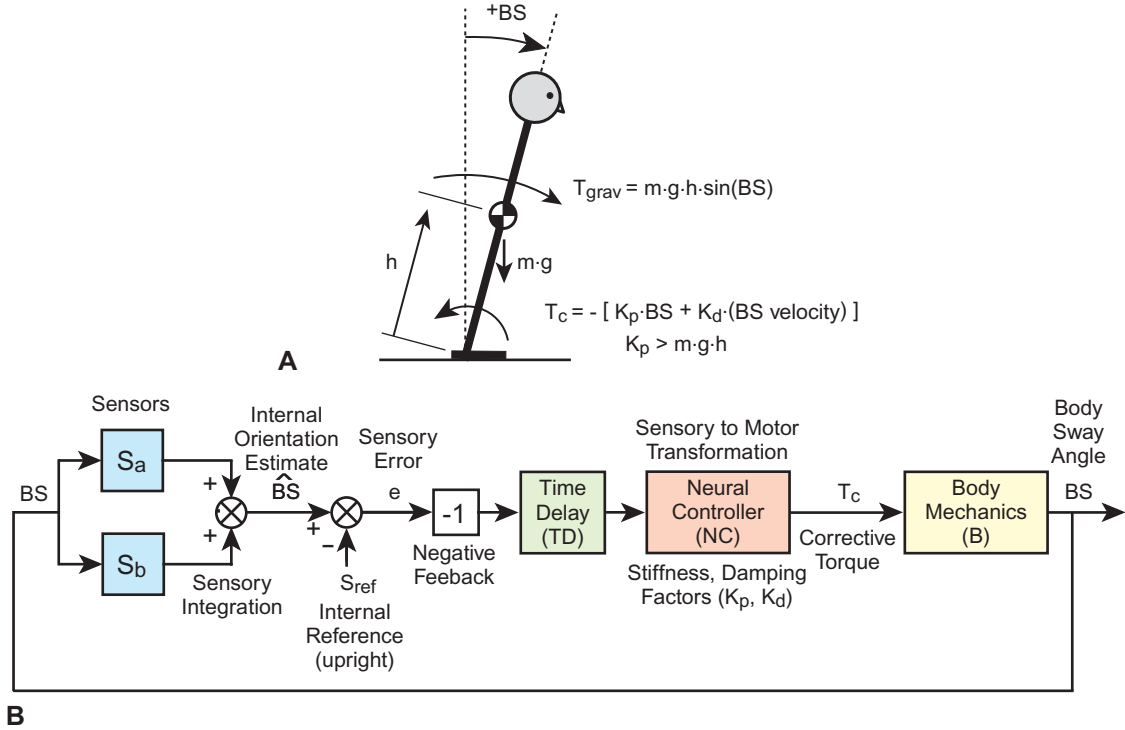
Fig. 2.1. (**A**) Body mechanics represented by a single-segment inverted pendulum defining physical variables relevant to understanding balance control with body-in-space sway angle (*BS*), body mass (*m*), and center-of-mass height (*h*), above the ankle joint. Gravity exerts a downward force $m \cdot g$ that produces a destabilizing gravity torque, T_{grav}, for sway away from a vertical orientation. The system can be stabilized if sufficient corrective torque, T_c, is applied about the ankle joint in proportion to the body sway angle (stiffness scaling factor, K_p) and angular velocity (damping scaling factor, K_d). (**B**) Block diagram showing interconnections of components of a closed-loop negative-feedback control system capable of maintaining stable upright stance. Body sway is detected by two sensory systems whose information is combined by summation to obtain an internal estimate of body orientation. The comparison of this internal estimate with a desired reference body orientation produces a sensory error. A neural controller generates a corrective ankle torque, T_c, in proportion to the sensory error. The time delay block represents time lags due to sensory transduction, afferent and efferent transmission, central processing, and muscle activation.

function of both the angular position and angular velocity of body motion with sensory systems being the source for both aspects of motion information. If corrective action (ankle torque) is only a function of deviation of angular position from the desired upright position, then a brief balance disturbance will cause the inverted-pendulum body to oscillate continuously. If corrective action is only a function of angular velocity, the pendulum will quickly fall due to the absence of the position-related torque needed to overcome the destabilizing torque due to gravity.

The sensory-to-motor transformation in the Figure 2.1B model is represented by a neural controller, *NC*, that outputs corrective ankle torque, T_c, to the inverted-pendulum body, *B*. Body sway motion is detected by sensory systems. In this case we show two different sensory systems, S_a and S_b, which redundantly sense body motion. Their motion information is combined (added) and it provides input to the neural

controller. The final component to consider is that feedback control is not instantaneous, but there are delays, represented collectively by *TD*, due to sensory transduction and transmission, central processing, motor command transmission, and muscle activation.

With this basic feedback structure defined, we can now discuss the features necessary for a robust sensory integration mechanism and we can appreciate that sensory integration and sensory-to-motor transformation components provide a functional unit that should be considered together.

First, although Figure 2.1B implies that sensory integration and sensory-to-motor transformation mechanisms are separate from one another, this is not necessarily the case. When the body is represented as a more realistic multisegment body, model structures that account for experimental data have a distributed sensorimotor configuration (Goodworth and Peterka, 2012). However, with the body modeled as a single-segment

inverted pendulum, a simple model as in Figure 2.1B can provide a very good accounting for experimental data with integration across sensory systems represented as a weighted addition of sensory signals (Peterka, 2002).

Second, the transformation from sensory input to motor output has to be scaled appropriately for good balance control. Inappropriate scaling in a closed-loop feedback control system can, in fact, cause the system to be unstable. Appropriate scaling applies to both the position-related and velocity-related signals that contribute to overall corrective torque. Scaling not only impacts stability (i.e., there are certain minimum and maximum values of position and velocity sensitivities, with sensitivity defined as torque per unit of body sway and sway velocity (Masani et al., 2008; van der Kooij and Peterka, 2011)), but also affects the dynamic characteristics of sway evoked by balance perturbations.

Third, the feedback time delay has an important influence on the dynamic response to balance perturbations. As time delay increases, the range of position and velocity sensitivities compatible with stability shrinks such that the system, assuming typical adult body anthropometrics, cannot be stabilized by the system shown in Figure 2.1B if delays are longer than about 300 ms (van der Kooij and Peterka, 2011). The deleterious effects of increased delay can be partially mitigated by decreasing position and velocity sensitivities.

Fourth, while the redundancy of orientation information from multiple sensory systems can be an advantage, there must be a mechanism in place that compensates for sudden losses of information from one or more sensory systems. For example, imagine that one of the sensory systems in Figure 2.1B is vision and that vision and the second sensory system contribute equally. Eye closure or suddenly turning off the room lights would cause loss of half of the sensory information contributing to balance and thus only half of the corrective torque per unit of body sway would be generated. Typically, an uncompensated loss of half of the corrective torque would not be compatible with stability. Therefore, some mechanism for torque normalization must exist and this mechanism must react rapidly enough to restore sufficient corrective torque to prevent instability following sudden changes in access to sensory orientation cues from one or more systems.

Fifth, the structure of the Figure 2.1B model implies that the sensory channels are independent of one another. That is, it is not necessary that the sensory integration mechanism develop a single unified percept of body motion based on all available sensory information and then respond to that unified percept. Rather, the system can respond to two different sources of sensory perturbations at the same time (Oie et al., 2002; Assländer and Peterka, 2014; Hwang et al., 2014; Logan et al., 2014), thus providing added versatility for responding to diverse changes in environmental conditions that affect orientation cues.

INTRASENSORY SYSTEM INTEGRATION

We define intrasensory integration as a process that transforms complex receptor signals encoded by primary sensory afferents from individual sensory systems into higher-level neural signals that represent physical variables such as body or limb orientation and motion in space or with respect to the environment. Psychophysical studies of the perception of body motion, limb movement, and visual motion provide evidence that humans have access to higher-level representations of physical variables that would be appropriate to generate corrective actions needed for balance control (e.g., limb position and velocity) (van Beers et al., 1998).

A well-studied example of vestibular intrasensory integration is the combination of information from the vestibular semicircular canals, sensing head angular velocity (with imperfect sensing of low-frequency motion due to biomechanics of the canals), and otolith organs, sensing both transient linear accelerations due to head movement and the sustained linear acceleration due to gravity. Information about head orientation in space can be derived from signals from the otolith organs in static, no-movement conditions, but transient linear accelerations during movement would distort a head orientation estimate derived only from otolith signals. However, there is ample evidence from studies of the vestibulo-ocular reflex that central mechanisms are able to combine canal and otolith information to derive separate internal estimates of transient linear head acceleration and head orientation with respect to gravity, and additionally improved estimates of head angular velocity (Angelaki et al., 1999, 2004; Merfeld et al., 1999; Zupan et al., 2002).

Intrasensory integration in proprioceptive/somatosensory systems is illustrated by recordings in spinal neurons that convey limb kinematic information that presumably is derived from as yet unknown mechanisms that process raw receptor information from individual muscles, joints, and various other somatosensory sources (Bosco and Poppele, 1993; Bosco et al., 2005, 2006). Additionally, neural recordings in the middle temporal area encode visual target motion information from which target velocity and acceleration can be extracted (Lisberger and Movshon, 1999).

In the following section we assume that the balance system has available to it higher-level neural representations of physical variables from various sensory systems and then consider how balance control can benefit by combining information across these sensory systems.

INTERSENSORY SYSTEM INTEGRATION

There are many potential benefits of combining sensory orientation from multiple sensory systems. These include: (1) reduction of variability and associated increase in certainty in neural representations of orientation and motion; (2) protection against sensory system dysfunction by virtue of having redundant sensory sources; (3) flexibility in organizing motor actions to meet specific behavioral goals; (4) resolving sensory conflicts by combining sensory cues to distinguish between self-motion and motion of the environment (e.g., moving surface or visual scene) or condition of the environment (e.g., firm or compliant surface); and (5) projecting sensory information across body segments via transformations that overcome limitations in individual sensory systems (i.e., combining head-referenced orientation information derived from visual and vestibular systems with head-on-body proprioception to derive body-in-space orientation information) (Mergner and Rosemeier, 1998).

Evidence for and causes of variability differences across sensory systems

A conceptual argument for understanding, and to some degree predicting, the wide variations in variability among sensory systems can be based on the varying ranges over which particular sensory systems encode orientation and motion. Figure 2.2 illustrates this for vestibular semicircular canal and otolith receptors encoding head motion and proprioceptors encoding ankle joint rotation. The semicircular canals encode angular velocity over a wide bandwidth of frequencies and with a wide range of amplitudes up to about 400°/s. The wide
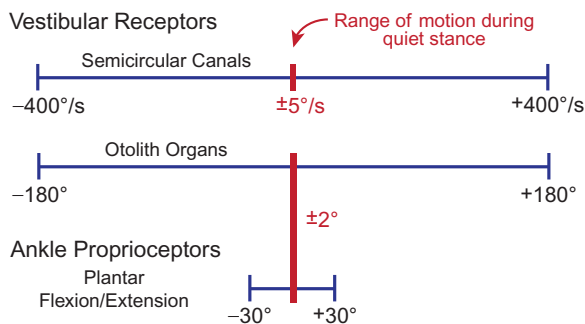

Fig. 2.2. Sensory noise is likely to have a strong influence on sway behavior during standing balance since body sway is small compared to the much wider dynamic range of sensors contributing to balance control. The width of the red vertical bars represents the narrow range of body sway motion associated with quiet stance. The horizontal bars represent the full range of motion encoded by vestibular semicircular canals and otoliths, and by ankle proprioceptors.

distribution of hair cell orientations across the two otolith organs in each ear allows the encoding of static head tilts covering the full ±180° range in head roll and pitch. However, the range of head movements that occur in standing balance and even perturbed standing balance is about two orders of magnitude smaller than the full encoding range. If the vestibular system were designed exclusively for standing balance control, this would be a horrible design flaw to have such a wide mismatch between sensor range and actual range of motion because, for a given amount of signal variability, reducing the signal range increases the noise-to-signal ratio. Of course, the vestibular system serves other purposes, such as generating vestibulo-ocular reflex eye movements during rapid head movements that require encoding a wide head velocity range.

In contrast, ankle proprioceptors are better matched to the task of standing balance. For example, the full range of extension/flexion of the ankle joint, about 60°, is a better match than the vestibular system to the range of motion that occurs during many balance tasks.

The variability associated with the visual system encoding of motion and orientation information is complex because variability is a function of visual scene properties that include contrast and spatial frequency of retinal images, physical properties defined by the distance between the viewer and the visual scene, physiologic conditions such as monocular versus binocular viewing, and cognitive processes that influence the interpretation of the visual scene. A few examples include loss of visual motion information in low-contrast environments caused by fog or whiteout conditions, or loss of motion information when the visual scene is distant (looking out from a tall bridge).

Consistent with these conceptual arguments for variations in variability across sensory systems are results from measures of motion detection thresholds. Perceptual thresholds are associated with underlying variability since reliable detection of motion depends on the neural-encoded motion signal deviating significantly from the underlying variability of the neural population (Merfeld, 2011). Fitzpatrick and McCloskey (1994) measured proprioceptive, visual, and vestibular motion detection thresholds under conditions directly relevant to standing balance control. While there were some dependencies on sway velocity for detection of body displacements (particularly for visual scene motion), results showed lowest detection thresholds for proprioception, slightly higher for vision, but vestibular thresholds were about an order of magnitude larger. Similar large differences between vestibular and proprioceptive thresholds have been found in experiments investigating perceptions related to head-in-space, head-on-trunk, and trunk-in-space movements (Mergner et al., 1991).

Principles for combining multisensory information for variability reduction

To the extent that different sensory systems may generate their own representation of the same physical variable, overall variability can potentially be decreased by combining redundant information from multiple sensory systems via intersensory system integration mechanisms.

What is the best way to combine information from multiple sensory sources? If the variability were equal among all sensory systems, the simple answer would be to average across all sensory sources. However, evidence discussed above indicates that variability differs among sensory systems. Given the convincing evidence for notably large vestibular variance, one might assume that the nervous system would just not use this information for balance control. However, this is not an optimal solution in two regards. First, the vestibular system is an inertial motion-sensing system providing motion-in-space information. In contrast, proprioception and vision provide motion information relative to body contact surfaces with the environment and to the visual world, respectively. Both contact surfaces and the visual environment can potentially move in space and thus could destabilize balance if vestibular information is ignored in conditions where proprioceptive and visual information are spatially inaccurate. Second, if multiple sensors are encoding a physical variable, estimation theory predicts that the best (lowest variability) measure of a physical variable should not exclude information from any of the sensors even if one has much higher variability than others (Ernst and Banks, 2002).

Figure 2.3 illustrates the basic concept for maximum-likelihood sensory integration for two sensory channels. Under open-loop conditions (where feedback is ignored) the lowest variance of the combined signal is achieved by a weighted summation where the weights are ratios determined by the variances of signals in the individual sensory channels. As the weighting formulas show, the sensory signal that is weighted the largest is the one with the lowest variance. The weights of the two sensory channels sum to one, meaning that the weights represent the relative contributions of information from each sensory channel.

However, as emphasized above, closed-loop feedback control is a feature of balance control. The closed-loop nature complicates predictions for what might be optimal sensory weights. Imagine a subject standing with eyes closed on a flat surface and the subject's vestibular system is 10 times more variable than the proprioceptive system if measured separately. Because of these noisy measures from the sensory systems, the subject is not able to stand perfectly still. The body sway caused by the inherent vestibular noise is sensed by the proprioceptive system and combines with the inherent variability of the proprioceptive system. Similarly, the inherent variability of the proprioceptive system will produce body sway that is encoded by the vestibular system and combined with the inherent variability of vestibular system. These signals circulate in the closed-loop balance control system, eventually achieving a steady-state condition with a certain level of body sway variability that will depend on the weighting factors used in the internal sensory integration process. One can expect that the balance control system may be able to select sensory weights to optimize some behavioral goal; that is, to minimize some physical aspect related to spontaneous body sway (e.g., sway displacement, velocity, acceleration, or energy expenditure, or joint torque production) (van der Kooij and Peterka, 2011).

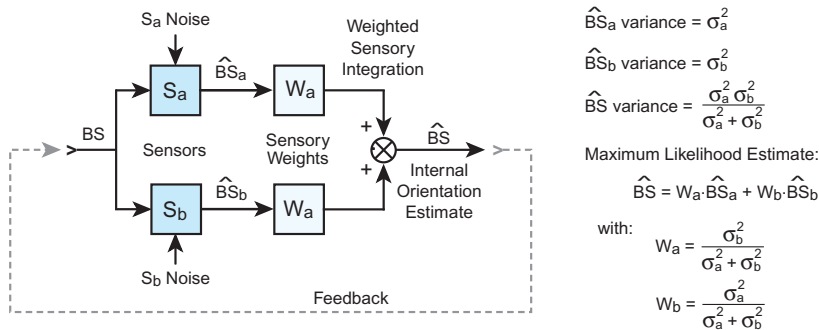There is additional complexity in that external stimuli or environmental conditions also can be expected to

$$\widehat{BS}_a \text{ variance} = \sigma_a^2$$

$$\widehat{BS}_b \text{ variance} = \sigma_b^2$$

$$\widehat{BS} \text{ variance} = \frac{\sigma_a^2 \sigma_b^2}{\sigma_a^2 + \sigma_b^2}$$

Maximum Likelihood Estimate:

$$\widehat{BS} = W_a \cdot \widehat{BS}_a + W_b \cdot \widehat{BS}_b$$

with:

$$W_a = \frac{\sigma_b^2}{\sigma_a^2 + \sigma_b^2}$$

$$W_b = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_b^2}$$

Fig. 2.3. For open-loop systems a weighted average of noisy sensory signals can provide a maximum likelihood orientation estimate with lower variance than either signal from the individual sensory systems using the formulas shown. However, when the feedback loop is closed (dashed line) the situation is more complex because variability in the signal from each sensor is affected by noise in both sensors as well as other sources of variability (e.g., motor noise, external perturbations). (Modified from van der Kooij H, Peterka RJ (2011) Non-linear stimulus–response behavior of the human stance control system is predicted by optimization of a system with sensory and motor noise. J Comput Neurosci 30: 759–778.)

influence the selection of sensory weights and the inter-mixing of different sensory signals. For example, variable motion of the stance surface acts directly to increase the variability of ankle proprioception, and then indirectly to other sensory channels due to closed-loop control. Another example would be stance on a compliant surface where compensatory ankle torque also produces foot and ankle joint motion that would appear to the balance control system as an increase in variability of ankle joint proprioception.

Evidence of multisensory contributions and sensory weighting

Experimental methods for demonstrating and quantifying multisensory contributions to balance follow two main paradigms. One is to withdraw or distort potential sources of sensory orientation information and look for changes in some behavioral measure of balance control. The other is to perturb the balance control system using stimuli that target one particular sensory system (or a limited set of sensory systems) and record responses correlated with the stimulus. For both methods, a wide variety of experimental measures can be used to quantify behavior (angular or linear displacements, velocities, or accelerations of body segments, center-of-mass angular or linear motion, center of pressure, joint torques, muscle activation commands recorded by surface or intramuscular electromyograms, or ultrasound imaging of muscle movements (Loram et al., 2005)). And for each of these measures, a variety of parameters that summarize performance can be calculated (Prieto et al., 1996; Maurer and Peterka, 2005).

The simplest sensory withdrawal experiments are based on measures of spontaneous sway. Generally, sway levels are smallest when subjects have full access to multiple accurate sensory sources of orientation information (i.e., stance on flat, level surface with eyes open and viewing a rich visual environment). In this condition all sensory systems are providing congruent information. We presume that information across systems is appropriately combined to reduce variability of an internal estimate of orientation, and this reduced variability is reflected in reduced sway levels. With eye closure, vision no longer contributes and sway levels increase, indicating that vision is contributing to balance control. Stance on a compliant foam surface with eyes open distorts proprioceptive cues, causing increases in sway levels, indicating that proprioceptive cues are important contributors to balance control. Finally, eyes-closed stance on foam forces a major reliance on the noisy orientation information from the vestibular system (consistent with vestibular threshold measures discussed above) causing further increases in recorded sway.

Perturbation methods for demonstrating multisensory contributions to balance are based on the concept that if a particular sensory system makes a contribution to balance control, then a perturbation that primarily stimulates a particular sensory system would be expected to evoke a correlated response. The magnitude of the response provides information about the relative, but not absolute, strength (weight) of the sensory contribution to balance. For example, visual scene motion evokes body sway (Lee and Lishman, 1975; Lestienne et al., 1977; Jeka et al., 2000), indicating a visual system contribution to balance control and, for a given magnitude of scene motion, scenes with more contrast and complexity evoke larger sways, indicating a relatively greater reliance on vision (greater visual weight) under those conditions (van Asten et al., 1988). Similarly, stationary visual scenes with increasingly complex configurations provide greater suppression of sway evoked by galvanic vestibular stimulation (Day and Guerraz, 2007).

Sensory weight measures

Experimental results can be used to derive quantitative measures of sensory system contributions to balance control using a model-based interpretation of experimentally evoked body sway. Figure 2.4 shows an extended version of the simple model shown in Figure 2.1B. This extended model includes multiple sensory contributions and a sensory integration mechanism consisting of a weighted summation of orientation information from proprioceptive, visual, and vestibular systems. Each sensory weight represents the proportion of the total of all of these sensory contributions such that the sum of all weights contributing to balance control in a given condition is 1 ($W_{prop} + W_{vis} + W_{vest} = 1$ when all three sensory systems are contributing). Additionally, the model diagram shows how external stimuli can be used to perturb the system to evoke a body sway response. By appropriate selection of a stimulus, analysis of stimulus–response data can identify the dynamic characteristics of the balance control system, and then parameters of the Figure 2.4 model can be adjusted to account for the stimulus–response behavior. These parameters include the sensory weights as well as other system components such as time delay and neural controller parameters representing the sensory-to-motor transformation. Given the complexity of individual components of sensory and motor systems contributing to balance control, it is incredible that this relatively simple model accounts quite well for body center-of-mass motion evoked by balance perturbations (Peterka, 2002, 2003; Cenciarini and Peterka, 2006).

An important assumption about the sensory integration mechanism is that the proprioceptive, visual, and vestibular systems are equivalent in the sense that they
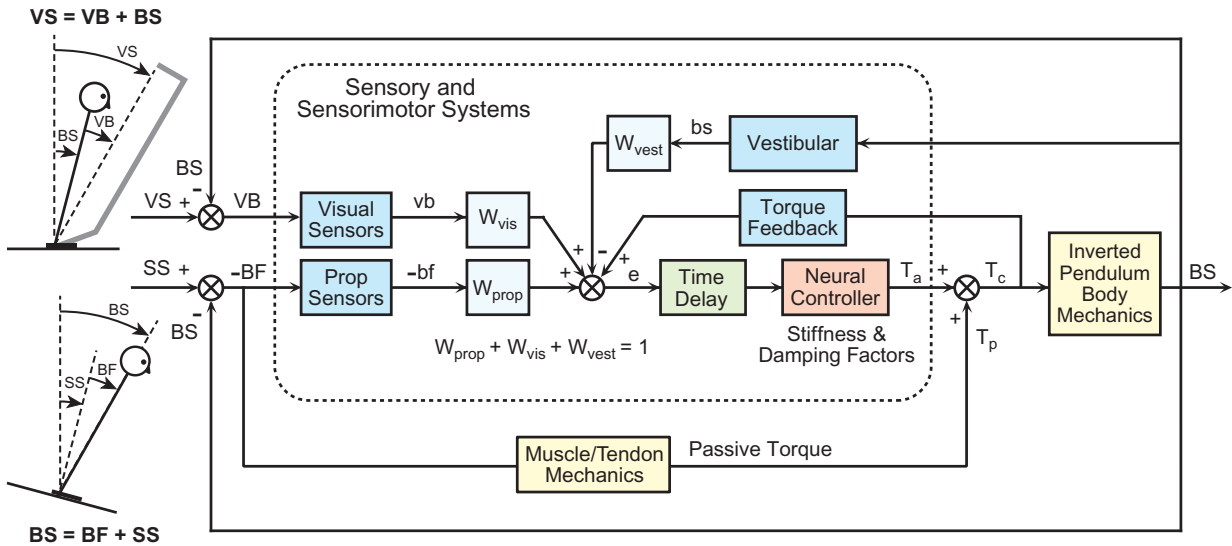
Fig. 2.4. Block diagram of the balance control model used for the estimation of sensory weights and other parameters. Experimentally applied support surface (*SS*) tilt stimuli or visual surround (*VS*) tilt stimuli evoke body sway (*BS*). Model parameters are optimally adjusted to account for the stimulus-evoked sway. *VB*, visual surround tilt angle relative to body sway angle; *BF*, body sway angle relative to the angle of the feet on the support surface. (Modified from Peterka RJ (2002) Sensorimotor integration in human postural control. J Neurophysiol 88: 1097–1118 and Cenciarini M, Peterka RJ (2006) Stimulus-dependent changes in the vestibular contribution to human postural control. J Neurophysiol 95: 2733–2750.)

all provide wide-bandwidth, accurate encoding of their respective physical variables with proprioception encoding body motion with respect to surface orientation, vision encoding body motion with respect to the visual scene, and vestibular encoding body motion in space.

In addition to proprioceptive, visual, and vestibular sensory feedback, the Figure 2.4 model includes torque feedback. The nature of the feedback from sensors of torque is different from feedback of the other sensory systems in two ways. First, the torque feedback is organized to provide a positive-feedback contribution while the other sensory systems provide negative-feedback contributions (Prochazka et al., 1997a, b). Second, the torque feedback does not carry wide-bandwidth information about rapid, instantaneous changes in the physical variable it encodes (muscle/tendon force), but rather is limited to slow, low-frequency information. Golgi tendon organs are a likely source of muscle/tendon force information contributing to balance control. However, afferent recordings show wide-bandwidth encoding of force and even the rate of change of force at higher frequencies (Anderson, 1974). The direct feedback of this afferent force information would not account for experimental observations. Thus the model assumes that the raw receptor signals from Golgi tendon organs (and other potential sources of force information) are processed by central mechanisms that greatly limit their bandwidth.

The two differences between torque feedback and other sensory system contributions to balance control cause torque feedback to have unique behavioral effects. The

negative-feedback control organization of proprioceptive, visual, and vestibular systems causes body movement toward alignment with the physical variable encoded by these sensory systems. For example, imagine a subject who only has proprioception for balance control. A toe-down tilt of the surface produces a proprioceptive "error" signal equal to the difference between the sensor-derived measure of body orientation and the desired orientation. For ankle proprioception the desired orientation is alignment of the body perpendicular to the surface. This proprioceptive error generates an ankle torque that initially moves the body toward alignment with the tilted surface.

When the body is actually aligned perpendicular to the tilted surface, the system generates no ankle torque (because the error is zero) and, therefore, this aligned orientation cannot be maintained. Gravity pulls the body further forward, causing the proprioceptive error signal to increase, but with opposite sign, producing a backward-directed ankle torque that slows the forward motion of the body. The body continues to move forward until the backward corrective torque generated by ankle proprioception balances the forward destabilizing torque due to gravity. If this subject's balance control system also includes positive torque feedback, the sustained backward torque would be sensed (Golgi tendon organs, pressure sensors in the feet) and used to generate an even larger magnitude backward ankle torque via the positive feedback organization. This increased backward torque overcomes the torque due to gravity and gradually moves the body back toward an upright position. As the

body moves toward an upright position, the backward torque diminishes and the contribution of the positive torque feedback loop declines. The net effect is that this positive torque feedback provides a mechanism that favors body alignment with gravity (or, more specifically, alignment with gravito-inertial force direction in the case of accelerating environments like an accelerating train) and this mechanism does not rely on the inertial reference provided by the vestibular system.

Two external stimuli that are useful in experimental investigations of sensory integration are represented in Figure 2.4. One is a rotation of the stance surface and the other a rotation of the visual scene viewed by the test subject. These rotational stimuli are particularly useful since proprioceptive and visual systems, respectively, are directly affected while all other sensory systems are only indirectly affected by the feedback nature of the balance control system. For a visual stimulus, for example, the stimulus–response behavior can be described mathematically by the equation:

$$BS(f)/VS(f) = W_{\text{vis}}$$
$$\cdot \frac{NC \cdot B \cdot TD}{1 - TF \cdot NC \cdot B + P \cdot B + NC \cdot B \cdot TD}$$

The term $BS(f)/VS(f)$ is a measure of the body sway response normalized to the visual tilt stimulus as a function of stimulus frequency, f. Without going into details (which can be found in Peterka, 2002, 2003, 2016), one can see that W_{vis}, which represents the visual contribution to balance, multiplies the remainder of the equation that includes frequency-dependent factors representing body mechanics (B), neural controller properties (NC), time delay (TD), passive muscle/tendon properties (P), and torque feedback (TF). These remaining parts of the equation define the dynamic properties of the system that determine, for example, the time course of body sway evoked by a given visual tilt stimulus. Assuming that all of the parameters that define the dynamic properties are not affected by properties of the stimulus (e.g., visual scene properties such as contrast, complexity, distance from subject), then if a visual stimulus of a given amplitude and frequency with one set of properties evokes a larger response than another visual stimulus of the same amplitude and frequency with different properties, then the response difference can be attributed to a change in W_{vis}.

A similar analysis applies when a surface tilt stimulus is used. But instead of W_{vis} being the multiplier, W_{prop} is the multiplier and, additionally, the influence of passive muscle/tendon properties is different in the equation defining $BS(f)/SS(f)$ because a surface tilt stimulus directly stretches ankle muscles (Peterka, 2002, 2003, 2016). Because the W_{vis} and W_{prop} parameters are standalone multipliers in the equations defining responses to visual and surface tilt stimuli, respectively, results from experiments using visual and surface tilt stimuli can be used to measure W_{vis} and W_{prop} values, respectively. Then, depending on the test conditions, the contributions of other sensory systems can be calculated using the sensory integration constraint that the sum of the weights equals 1. For example, for eyes-closed tests using surface stimuli, the analysis gives an estimate of W_{prop} and then the vestibular contribution is given by $W_{\text{vest}} = 1 - W_{\text{prop}}$.

We have used wide-bandwidth pseudorandom surface rotations and/or visual surround rotations to evoke body sway responses (with the response considered to be the body center-of-mass tilt angle from upright), analyzed the stimulus–response data to characterize the dynamic properties of the balance control system, and then optimally adjusted parameters of the Figure 2.4 model to account for the experimentally observed dynamic properties. Experiments were performed using stimulus amplitudes ranging from 0.5 to 8° (peak-to-peak) and in different conditions that provided different access to sensory information (eyes open, eyes closed, stance on a sway-referenced surface where the surface in real time rotates in direct proportion to the body sway angle such that proprioception encodes no change in body orientation relative to the surface (Nashner et al., 1982)). The vestibular contribution to balance was investigated by performing tests in subjects with bilaterally absent or unilaterally absent vestibular function.

Figure 2.5 shows sensory weight measures as a function of stimulus amplitude for two different test conditions and for subjects with normal sensory function and 4 individual subjects with bilaterally absent vestibular function. W_{prop} and sway amplitude measures were obtained using surface tilt stimuli during eyes-closed stance (Fig. 2.5A) and W_{vis} and sway amplitude measures using visual tilt stimuli during stance on a fixed and level surface (Fig. 2.5B). Both show that, for subjects with normal sensory function, the weights are largest when the stimulus amplitude is smallest, and weights decline with increasing stimulus amplitude. That is, there is an amplitude-dependent sensory reweighting. Declines in W_{prop} and W_{vis} mean that the balance control system becomes relatively less sensitive to the surface and visual stimulus motions, respectively, as the stimulus amplitude increases, with the result that the sway response amplitude asymptotes at a certain level (lower panels of Fig. 2.5A and B). In the case of eyes-closed stance with a surface stimulus, subjects with normal sensory function are easily able to maintain stability at the highest stimulus amplitude. In contrast, vestibular loss subjects in this condition show 100% reliance on proprioception for balance control across all stimulus amplitudes ($W_{\text{prop}} = 1$, implying $W_{\text{vest}} = 0$ consistent with their diagnosis of bilateral vestibular loss). This means that their evoked body sway increased in direct proportion to the stimulus amplitude such that their
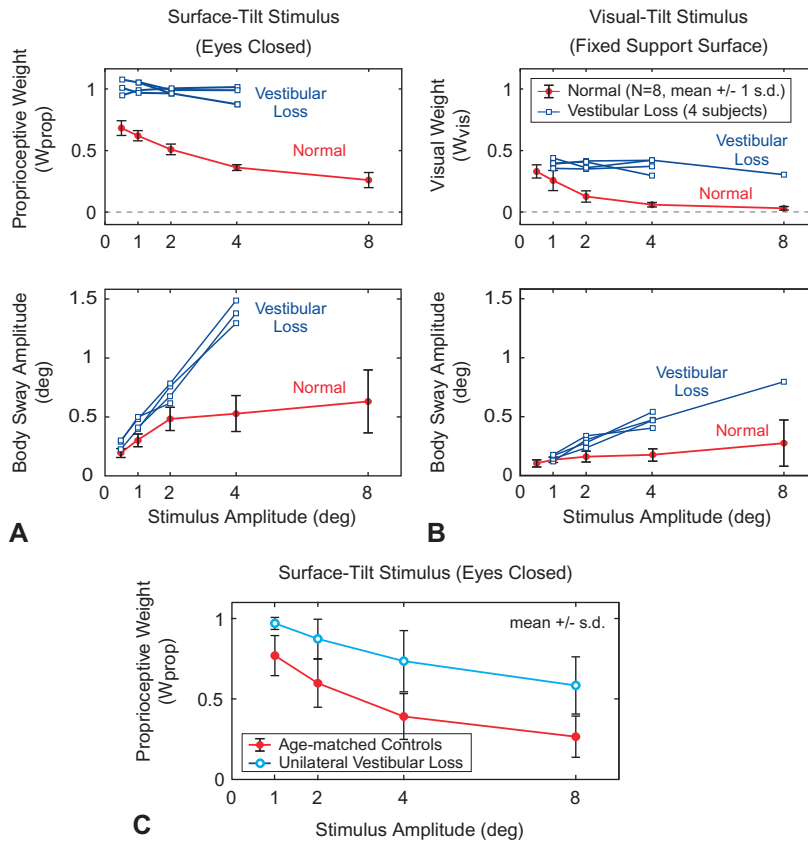
Fig. 2.5. Experimentally determined sensory weights and center of mass sway amplitude as a function of stimulus amplitude. (**A**) Proprioceptive weights and sway amplitude (root mean squared values) measured with eyes closed using a surface tilt stimulus evoking anterior–posterior sway in subjects with normal sensory function and 4 subjects with bilaterally absent vestibular function. (**B**) Visual weights and sway amplitude measured with eyes open using a visual tilt stimulus evoking anterior–posterior sway in subjects with normal sensory function and 4 subjects with bilaterally absent vestibular function. (**C**) Proprioceptive weights measured with eyes closed using a surface tilt stimulus evoking medial–lateral sway in 11 subjects with unilateral vestibular loss and 11 age-matched controls. ((**A**) and (**B**) modified from Peterka RJ (2002) Sensorimotor integration in human postural control. J Neurophysiol 88: 1097–1118. (**C**) Modified from Peterka RJ, Statler KD, Wrisley DM, et al. (2011). Postural compensation for unilateral vestibular loss. Frontiers in Neurology 2.)

evoked sway was too large to maintain stance for the 8° stimulus. At the lowest stimulus amplitudes, W_{prop} values in vestibular loss subjects were about 30% larger than in subjects with normal sensory function.

The combination of low stimulus amplitude and similar W_{prop} values means that evoked sway levels were small and only moderately larger for vestibular loss subjects. Thus, behaviorally the vestibular loss and normal subjects were quite similar at low stimulus amplitudes. However, when balance was challenged by larger perturbations, the benefits of having a vestibular system and of having a sensory reweighting mechanism that is able to shift towards increasing reliance on vestibular information become evident.

In bilateral vestibular loss subjects tested in conditions without access to visual information, it is completely understandable that they are 100% reliant on proprioception and no sensory reweighting is possible

(Fig. 2.5A). But does reweighting occur when vestibular loss subjects have access to both proprioceptive and visual cues and one of those sensory modalities is perturbed by a surface or visual stimulus? For example, if a visual stimulus is presented to a vestibular loss subject standing on a level unmoving surface, vision is providing inaccurate information that evokes body motion away from an upright orientation. If the visual weight W_{vis} could be reduced, then sway amplitude and balance control effort could be reduced by increasing reliance on the accurate proprioceptive information. However, experimental results showed that vestibular loss subjects in the visual stimulus condition have a reduced ability to reweight sensory information as the stimulus amplitude changed compared to subjects with normal sensory function (Fig. 2.5B). The amplitude-independent W_{vis} values for vestibular loss subjects suggests that their balance control system was unable to determine which of the

two sources of orientation information was accurate and then shift toward increased reliance on the more accurate source. That this reweighting did not happen hints at the potential importance of having inertial, space-referenced cues provided by the vestibular system to mediate the sensory reweighting process.

A final data set consistent with variability management as a driver of sensory weighing is from a study comparing sensory weighting in subjects with unilateral absent vestibular function with age-matched controls (Peterka et al., 2011). There is reason to expect that vestibular information from a single ear can accurately encode the relatively small head motions evoked by balance perturbations because vestibular afferents have high discharge rates that allow for bidirectional encoding of head motion (Goldberg and Fernandez, 1971a; Fernandez and Goldberg, 1976). However, to the extent that information from both ears is normally combined to derive an overall internal vestibular estimate of orientation, one would expect there to be higher variability in an internal vestibular orientation estimate when half of the vestibular system is lost. If the vestibular variability is higher in unilateral loss subjects the expectation is that reliance on proprioceptive cues should be greater (larger W_{prop}) than in subjects with normal sensory function. Sensory weight measures from eyes-closed tests using surface tilt stimuli show a consistent shift toward increased reliance on proprioceptive information for balance (Fig. 2.5C).

Clinical screening tests of balance control often rely on measures of spontaneous body sway in a variety of conditions that vary the availability of sensory cues (stance with eyes open or closed on firm or compliant surfaces) (Agrawal et al., 2009) or more sophisticated versions such as sensory organization tests (Nashner and Peters, 1990) that use sway referencing to manipulate the accuracy of proprioceptive and/or visual cues. Because these nonperturbed test conditions do not provide quantitative measures of sensory contributions to balance, it may be of interest to know the approximate sensory weights in subjects with normal sensory function in conditions like those used in clinical screenings. We found that the lowest-amplitude 0.5° stimuli reliably evoked body sway even though subjects were typically unaware that their balance was being perturbed (Peterka, 2002). Thus the sensory weights measured from responses to the 0.5° stimuli are likely to be representative of the sensory contributions to balance control in unperturbed, quiet stance conditions.

Table 2.1 compiles these sensory weight measures for a variety of test conditions that are typically used in studies that rely on measures of quiet stance to judge balance performance. One feature is the relatively small contribution of vestibular information to balance. This

Table 2.1

Sensory contributions (sensory weights expressed as percentages) to balance control under three test conditions that provided full access to sensory orientation information (condition 1), absent visual information (condition 2), or inaccurate proprioceptive information (condition 3)

	Sensory contribution to balance control		
Sensory system	Condition 1	Condition 2	Condition 3
Proprioception	50%	68%	SR (0%)
Visual	33%	EC (0%)	77%
Vestibular	17%	32%	23%

Results derived from Peterka (2002), where sensory weights were measured by analysis of body sway evoked by low-amplitude (0.5°) surface tilt or visual tilt perturbations.
EC, eyes closed; SR, sway reference surface.

small contribution is consistent with the notion that vestibular sensory information is noisy relative to other sensory systems such that a sensory integration process assigns a relatively low weight to the vestibular contribution. One caveat for the visual weight estimates is that the visual scene used in the experiments had high contrast and was located close to the subjects. With a less rich visual environment, one would expect a lower visual contribution.

Mechanisms for automatic reweighting

While the analysis of experimental results with reference to the balance control model in Figure 2.4 allows estimates of functionally relevant parameters such as sensory weights, this model does not include a mechanism that makes condition-dependent adjustments in sensory weights. Two classes of weight-adjusting models of balance control are described below.

Model reference control schemes are widely considered to be relevant to understanding motor control systems (Borah et al., 1988; Bhushan and Shadmehr, 1999; Wolpert and Ghahramani, 2000). In this case the "model" refers to the idea that the nervous system embodies internal models of the physical and neural systems involved in movement control (limbs, body, neuromuscular properties, sensory properties). These internal models serve multiple functions, including translating higher-level desired movements into distributed motor commands, predicting expected movements and expected sensory feedback based on the motor commands, comparing expected to actual sensory feedback, and using sensory comparisons to drive corrective motor actions. This control scheme can take into consideration the noise properties of sensory and motor systems such that the

overall system displays condition-dependent behavior consistent with sensory reweighting (Kuo, 2005; van der Kooij et al., 1999, 2001; Carver et al., 2005). Model reference control also can incorporate adaptive mechanisms that calibrate the internal models to account for changes that alter the responsiveness of the system to motor commands or the encoding of motion by sensory systems (Forbes et al., 2016).

An alternative concept is the disturbance estimation and compensation (DEC) model that uses hypothesized threshold-determined combinations of sensory information to estimate external and internal balance disturbances and then generates corrective actions to compensate for these disturbances (Mergner and Rosemeier, 1998). Implementation of the DEC model accounts for experimentally determined condition and stimulus-dependent sensory reweighting (Maurer et al., 2006) and the DEC concept can be extended to control balance in multisegment bodies (Hettich et al., 2014).

Transient effects of sensory reweighting

There are many instances in everyday life when access to accurate orientation information changes suddenly (e.g., room lights turned on or off, standing next to a train that begins to move, stepping onto or off a pliant or slippery surface). These changes can remove or restore accurate sensory information. Sudden changes in conditions initiate dynamic postural adjustments as balance control processes are altered for optimal behavior in the new conditions. These dynamic adjustments are centrally mediated and thus cannot occur instantaneously, leaving subjects potentially vulnerable to transient instability.

Two general methods have been used to investigate the transient effects of condition changes on balance control. One is to measure the time course of changes in spontaneous sway following loss or restoration of sensory cues (Teasdale et al., 1991; Hay et al., 1996; Sozzi et al., 2011, 2012; Honeine et al., 2015). The other is to apply a continuous (often sinusoidal), low-amplitude perturbation that primarily affects a particular sensory system (e.g., surface tilt, visual tilt, or galvanic vestibular stimulation) and measure the time course of changes in the sway response to the perturbation (Jeka et al., 2008; Assländer and Peterka, 2014, 2016).

It is intuitive that a sudden loss of access to sensory information without some compensatory process that adjusts for this loss can be destabilizing. With reference to the Figure 2.4 model, sudden loss of one source of sensory information results in a reduced generation of corrective torque. If the corrective torque is reduced to less than the destabilizing gravity torque, the system becomes unstable. Even if the corrective torque reduction is less than an amount that causes instability, the

system becomes very sensitive to small external perturbations such that small disturbances result in large sway responses.

The compensation that restores normal corrective torque generation following loss of sensory information can be viewed as a sensory reweighting process where weights of the remaining sensory systems increase. There is some time urgency to this reweighting since the system may be frankly unstable until sufficient reweighting has occurred.

Now consider what might happen when the system is operating optimally (weights optimally set) in an environment where one sensory source of orientation is missing and then this sensory source is suddenly restored. One could hypothesize that the time urgency of reweighting to make use of the restored information is not so urgent since the system is already stable and seemingly not at risk of instability (but see below). The balance system could initially ignore the new information and then more gradually incorporate it in order to optimize balance. This hypothesis would predict that central mechanisms that drive sensory reweighting should make more rapid adjustments following the loss of sensory information than following the restoration of sensory information.

An example consistent with this is shown in Figure 2.6A where proprioceptive cues for balance control were suddenly removed or restored by periodically turning on and off surface sway referencing. Subjects with eyes closed had their balance perturbed by a constant-amplitude sinusoidal galvanic vestibular stimulus that evoked medial-lateral sway. The evoked sway rapidly increased when sway-referencing was turned on consistent with a rapid reweighting toward increased reliance on vestibular information for balance. There was also a rapid increase in sway variability (lower panel in Fig. 2.6A) consistent with use of noisier vestibular information. When sway referencing was turned off, the evoked sway amplitude and sway variability gradually declined consistent with a slower shift back toward increased reliance on proprioceptive cues. This reweighting asymmetry has been observed in a number of experiments (Jeka et al., 2008; Sozzi et al., 2012; Honeine et al., 2015), but not in all (Assländer and Peterka, 2016).

An unexpected consequence of reweighting dynamics is that sudden restoration of sensory orientation information actually can make the balance control system unstable. This goes against the intuitive expectation that restoration of accurate orientation cues would always lead to improvements in balance control, as indicated, for example, by a reduction in spontaneous sway levels. However, this is not necessarily the case, as illustrated by an experiment described below.
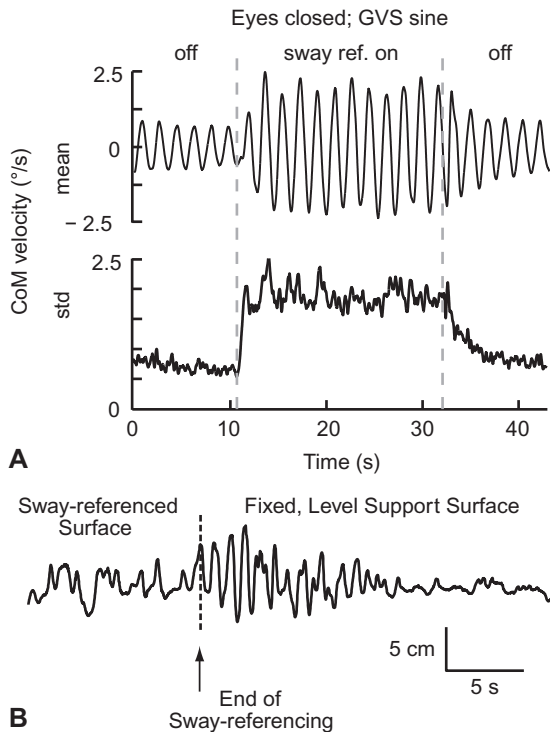
Fig. 2.6. (**A**) Upper plot shows dynamic changes in sway velocity evoked by a continuously applied constant-amplitude sinusoidal galvanic vestibular stimulus (*GVS*) while proprioceptive cues for balance control were periodically removed or restored by turning on or off surface sway-referencing, respectively. Lower plot show corresponding dynamic changes in sway velocity variability with an increase in variability during the sway-referencing on period consistent with increased reliance on noisy vestibular cues for balance control. *CoM*, center of mass. (**B**) Center of pressure recording showing transient instability associated with 1 Hz body oscillation following restoration of accurate proprioceptive orientation cues in a naïve subject. ((**A**) Modified from Assländer L, Peterka RJ (2014) Sensory reweighting dynamics in human postural control. J Neurophysiol 111: 1852–1864. (**B**) Modified from Peterka RJ, Loughlin PJ (2004) Dynamic regulation of sensorimotor integration in human postural control. J Neurophysiol 91: 410–423.)

Figure 2.6B shows body sway measured following a transition where accurate proprioceptive cues were suddenly restored following a period where accurate proprioception was greatly reduced by sway referencing the stance surface. In eyes-closed, sway-referenced conditions, subjects must rely entirely on vestibular information for balance control. Referring to Table 2.1 for eyes-closed conditions, we expect that when surface sway referencing ends, subjects will eventually transition from using 100% vestibular information to using about 70% proprioception and 30% vestibular information. If the sensory reweighting was accomplished by ramping down the vestibular contribution from 100% to 30% while simultaneously ramping up the proprioceptive contribution from 0% to 70%, we would expect a systematic reduction in spontaneous sway levels as the system shifted from reliance on noisy vestibular to less noisy proprioceptive information.

In contrast to this prediction of a systematic sway reduction, many subjects when first experiencing sway-referencing transitions demonstrated a prominent oscillatory body sway at 1 Hz with the amplitude of this oscillation declining over time but lasting tens of seconds in some subjects (Peterka and Loughlin, 2004). Our explanation for this result relies on the Figure 2.4 model, some peculiarities of sway referencing, and on the feedback nature of balance control where dynamic behavior depends on the sensitivity of the overall sensory-to-motor transformation.

Briefly, eyes-closed surface sway referencing requires the subject to rely entirely on vestibular information. The representation of this reliance in the Figure 2.4 model is that a reweighting mechanism sets $W_{vest} = 1$. However, it is not necessarily true that $W_{prop} = 0$ during sway referencing because the proprioceptive signal itself is zero (signaling no ankle motion). Perhaps W_{prop} remained at a value of 0.7 (as expected for eyes-closed stance on a level surface). When sway referencing ends, suddenly both vestibular and proprioceptive signals are present and contributing to an overall sensory sensitivity of $W_{vest} + W_{prop} = 1.7$. Thus the high sensory sensitivity in combination with a normal sensitivity of the neural controller produces an overall feedback loop gain that is too high. Effectively, torque normalization has transiently failed such that too much corrective torque is generated per unit of body sway. Consistent with experimental results, the Figure 2.4 model actually predicts that a too high feedback loop gain results in a system with 1 Hz resonant dynamics, meaning that 1-Hz components of any internal sensory noise will be greatly amplified, resulting in body sway dominated by this frequency. Additionally, the resonant dynamics also indicate that the system is very close to instability. Thus we have an example where a change in environmental conditions that restores access to accurate sensory orientation information produces the paradoxic result of transiently jeopardizing stability.

It may seem that the above example is too unusual to have real-world relevance. However, evidence for transient instability has been reported in elderly subjects following restoration of visual cues (Teasdale et al., 1991) and restoration of accurate proprioceptive cues following periods where tendon vibration disrupted proprioception (Hay et al., 1996). The possibility exists that neurologic diseases that disrupt the dynamic regulation of sensory integration could leave subjects vulnerable to falls following restoration as well as loss of accurate orientation cues.

CONCLUSIONS

This chapter emphasizes the importance of considering the balance control system as a whole when evaluating sensory contributions to balance. In particular, the feedback nature of the balance control system places constraints on how sensory information is combined and transformed into corrective motor actions, and on the dynamic regulation of sensory integration following environmental changes that withdraw or restore access to accurate sensory information. System identification methods are available for the appropriate analysis of closed-loop control systems (van der Kooij et al., 2005). Future application of these methods to patients with balance disorders due to sensory deficits and neurologic disorders may provide insights into their disorders and help to focus and evaluate rehabilitation efforts (Engelhart et al., 2014; Pasma et al., 2014).

REFERENCES

Agrawal Y, Carey JP, Della Santina CC et al. (2009). Disorders of balance and vestibular function in US adults. Arch Intern Med 169: 938–944.

Anderson JH (1974). Dynamic characteristics of Golgi tendon organs. Brain Res 67: 531–537.

Angelaki DE, McHenry MQ, Dickman JD et al. (1999). Computation of inertial motion: Neural strategies to resolve ambiguous otolith information. J Neurosci 19: 316–327.

Angelaki DE, Shaikh AG, Green AM et al. (2004). Neurons compute internal models of the physical laws of motion. Nature 430: 560–564.

Assländer L, Peterka RJ (2014). Sensory reweighting dynamics in human postural control. J Neurophysiol 111: 1852–1864.

Assländer L, Peterka RJ (2016). Sensory reweighting dynamics following removal and addition of visual and proprioceptive cues. J Neurophysiol 116: 272–285.

Bhushan N, Shadmehr R (1999). Computational nature of human adaptive control during learning of reaching movements in force fields. Biol Cybern 81: 39–60.

Borah J, Young LR, Curry RE (1988). Optimal estimator model for human spatial orientation. Ann N Y Acad Sci 545: 51–73.

Bosco G, Poppele RE (1993). Broad directional tuning in spinal projections to the cerebellum. J Neurophysiol 70: 863–866.

Bosco G, Eian J, Poppele RE (2005). Kinematic and non-kinematic signals transmitted to the cat cerebellum during passive treadmill stepping. Exp Brain Res 167: 394–403.

Bosco G, Eian J, Poppele RE (2006). Phase-specific sensory representations in spinocerebellar activity during stepping: evidence for a hybrid kinematic/kinetic framework. Exp Brain Res 175: 83–96.

Carver S, Kiemel T, van der Kooij H et al. (2005). Comparing internal models of the dynamics of the visual environment. Biol Cybern 92: 147–163.

Cenciarini M, Peterka RJ (2006). Stimulus-dependent changes in the vestibular contribution to human postural control. J Neurophysiol 95: 2733–2750.

Cordo PJ, Nashner LM (1982). Properties of postural adjustments associated with rapid arm movements. J Neurophysiol 47: 287–302.

Day BL, Guerraz M (2007). Feedforward versus feedback modulation of human vestibular-evoked balance responses by visual self-motion information. J Physiol 582: 153–161.

Duysens J, Clarac F, Cruse H (2000). Load-regulating mechanisms in gait and posture: Comparative aspects. Physiol Rev 80: 83–133.

Engelhart DE, Pasma JH, Schouten AC et al. (2014). Impaired standing balance in elderly: a new engineering method helps to unravel causes and effects. JAMDA 15: 227. e221-227.e226.

Ernst MO, Banks MS (2002). Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415: 429–433.

Fernandez C, Goldberg JM (1976). Physiology of peripheral neurons innervating otolith organs of the squirrel monkey. I. Response to static tilts and to long-duration centrifugal force. J Neurophysiol 39: 970–984.

Fitzpatrick R, McCloskey DI (1994). Proprioceptive, visual and vestibular thresholds for the perception of sway during standing in humans. J Physiol (Lond) 478: 173–186.

Forbes PA, Luu BL, van der Loos HF et al. (2016). Transformation of vestibular signals for the control of standing in humans. J Neurosci 36: 11510–11520.

Goldberg J, Fernandez C (1971a). Physiology of peripheral neurons innervating semi-circular canals of the squirrel monkey. I. Resting discharge and response to constant angular accelerations. J Neurophysiol 34: 635–660.

Goldberg JM, Fernandez C (1971b). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. III. Variations among units in their discharge properties. J Neurophysiol 34: 676–684.

Goodworth AD, Peterka RJ (2012). Sensorimotor integration for multisegmental frontal plane balance control in humans. J Neurophysiol 107: 12–28.

Hay L, Bard C, Fleury M et al. (1996). Availability of visual and proprioceptive afferent messages and postural control in elderly adults. Exp Brain Res 108: 129–139.

Hettich G, Assländer L, Gollhofer A et al. (2014). Human hip-ankle coordination emerging from multisensory feedback control. Hum Mov Sci 37: 123–146.

Honeine JL, Crisafulli O, Sozzi S et al. (2015). Processing time of addition or withdrawal of single or combined balance-stabilizing haptic and visual information. J Neurophysiol 114: 3097–3110.

Hwang S, Agada P, Kiemel T et al. (2014). Dynamic reweighting of three modalities for sensor fusion. PLoS One 9: 1–8.

Jeka J, Oie KS, Kiemel T (2000). Multisensory information for human postural control: integrating touch and vision. Exp Brain Res 134: 107–125.

Jeka JJ, Oie KS, Kiemel T (2008). Asymmetric adaptation with function advantage in human sensorimotor control. Exp Brain Res 191: 453–463.

Johansson R, Magnusson M, Akesson M (1988). Identification of human postural dynamics. IEEE Trans Biomed Eng 35: 858–869.

Kuo AD (2005). An optimal state estimation model of sensory integration in human postural balance. J Neural Eng 2: S235–S249.

Lee DN, Lishman JR (1975). Visual proprioceptive control of stance. J Hum Movem Stud 1: 87–95.

Lestienne F, Soechting J, Berthoz A (1977). Postural readjustments induced by linear motion of visual scenes. Exp Brain Res 28: 363–384.

Lisberger SG, Movshon JA (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. J Neurosci 19: 2224–2246.

Logan D, Kiemel T, Jeka JJ (2014). Asymmetric sensory reweighting in human upright stance. PLoS One 9: 1–10.

Loram ID, Maganaris CN, Lakie M (2005). Non-invasive tracking of contractile length. J Appl Physiol 100: 1311–1323.

Magnus R (1926). Some results of studies in the physiology of posture. Lancet 208: 531–536; 585–588.

Masani K, Vette AH, Kawashima N et al. (2008). Neuromuscular torque-generation process has a large destabilizing effect on the control mechanism of quiet standing. J Neurophysiol 100: 1465–1475.

Matthews PBC (1981). Muscle spindles: their messages and their fusimotor supply. In: VB Brooks (Ed.), Handbook of physiology, section 1: The nervous system, vol. II. Motor control, Part 1. American Physiological Society, Bethesda, MD.

Maurer C, Peterka RJ (2005). A new interpretation of spontaneous sway measures based on a simple model of human postural control. J Neurophysiol 93: 189–200.

Maurer C, Mergner T, Peterka RJ (2006). Multisensory control of human upright stance. Exp Brain Res 171: 231–250.

Merfeld DM (2011). Signal detection theory and vestibular thresholds: I. Basic theory and practical considerations. Exp Brain Res 210: 173–184.

Merfeld DM, Zupan L, Peterka RJ (1999). Humans use internal models to estimate gravity and linear acceleration. Nature 398: 615–618.

Mergner T, Rosemeier T (1998). Interaction of vestibular, somatosensory and visual signals for postural control and motion perception under terrestrial and microgravity conditions – a conceptual model. Brain Res Rev 28: 118–135.

Mergner T, Siebold C, Schweigart G et al. (1991). Human perception of horizontal trunk and head rotation in space during vestibular and neck stimulation. Exp Brain Res 85: 389–404.

Nashner LM (1970). Sensory feedback in human posture control. Sc.D. thesis. In: Massachusetts Institute of Technology.

Nashner LM, Peters JF (1990). Dynamic posturography in the diagnosis and management of dizziness and balance disorders. Neurol Clin 8: 331–349.

Nashner LM, Black FO, Wall III C (1982). Adaptation to altered support and visual conditions during stance: Patients with vestibular deficits. J Neurosci 2: 536–544.

Oie KS, Kiemel T, Jeka JJ (2002). Multisensory fusion: simultaneous re-weighting of vision and touch for the control of human posture. Brain Res Cogn Brain Res 14: 164–176.

Pasma JH, Engelhart DE, Schouten AC et al. (2014). Impaired standing balance: the clinical need for closing the loop. Neuroscience 267: 157–165.

Peterka RJ (2002). Sensorimotor integration in human postural control. J Neurophysiol 88: 1097–1118.

Peterka RJ (2003). Simplifying the complexities of maintaining balance. IEEE Eng Med Biol Mag 22: 63–68.

Peterka RJ (2016). Model-based interpretation of experimental data related to the control of balance during stance and gait in humans. In: BI Prilutsky, DH Edwards (Eds.), Neuromechanical modeling of posture and locomotion. Springer, New York.

Peterka RJ, Loughlin PJ (2004). Dynamic regulation of sensorimotor integration in human postural control. J Neurophysiol 91: 410–423.

Peterka RJ, Statler KD, Wrisley DM et al. (2011). Postural compensation for unilateral vestibular loss. Frontiers in Neurology 2: 57.

Prieto TE, Myklebust JB, Hoffman RG et al. (1996). Measures of postural steadiness: Differences between healthy young and elderly adults. IEEE Trans Biomed Eng 43: 956–966.

Prochazka A, Gillard D, Bennett DJ (1997a). Implications of positive feedback in the control of movement. J Neurophysiol 77: 3237–3251.

Prochazka A, Gillard D, Bennett DJ (1997b). Positive force feedback control of muscles. J Neurophysiol 77: 3226–3236.

Sozzi S, Monti A, De Nunzio AM et al. (2011). Sensori-motor integration during stance: Time adaptation of control mechanisms on adding and removing vision. Hum Mov Sci 30: 172–189.

Sozzi S, Do M-C, Monti A et al. (2012). Sensorimotor integration during stance: Processing time of active or passive addition or withdrawal of visual or haptic information. Neuroscience 212: 59–76.

Talbott RE, Brookhart JM (1980). A predictive model study of the visual contribution to canine postural control. Am J Physiol 239: R80–R92.

Teasdale N, Stelmach GE, Breunig A (1991). Postural sway characteristics of the elderly under normal and altered visual and support surface conditions. J Gerontol 46: B238–B244.

van Asten WNJC, Gielen CCAM, van der Gon JJ Denier (1988). Postural adjustments induced by simulated motion of differently structured environments. Exp Brain Res 73: 371–383.

van Beers RJ, Sittig AC, Gon JJ (1998). The precision of proprioceptive position sense. Exp Brain Res 122: 367–377.

van der Kooij H, Peterka RJ (2011). Non-linear stimulus–response behavior of the human stance control system is predicted by optimization of a system with sensory and motor noise. J Comput Neurosci 30: 759–778.

van der Kooij H, Jacobs R, Koopman B et al. (1999). A multisensory integration model of human stance control. Biol Cybern 80: 299–308.

van der Kooij H, Jacobs R, Koopman B et al. (2001). An adaptive model of sensory integration in a dynamic environment applied to human stance control. Biol Cybern 84: 103–115.

van der Kooij H, van Asseldonk E, van Der Helm FCT (2005). Comparison of different methods to identify and quantify balance control. J Neurosci Methods 145: 175–203.

Wolpert DM, Ghahramani Z (2000). Computational principles of movement neuroscience. Nature 3: 1212–1217.

Zupan LH, Merfeld DM, Darlot C (2002). Using sensory weighting to model the influence of canal, otolith and visual cues on spatial orientation and eye movements. Biol Cybern 86: 209–230.