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Human upright posture control models based on multisensory inputs; in fast and slow dynamics

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Review article

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ABSTRACT

Posture control to maintain an upright stance is one of the most important and basic requirements in the daily life of humans. The sensory inputs involved in posture control include visual and vestibular inputs, as well as proprioceptive and tactile somatosensory inputs. These multisensory inputs are integrated to represent the body state (body schema); this is then utilized in the brain to generate the motion. Changes in the multisensory inputs result in postural alterations (fast dynamics), as well as long-term alterations in multisensory integration and posture control itself (slow dynamics). In this review, we discuss the fast and slow dynamics, with a focus on multisensory integration including an introduction of our study to investigate “internal force control” with multisensory integration-evoked posture alteration. We found that the study of the slow dynamics is lagging compared to that of fast dynamics, such that our understanding of long-term alterations is insufficient to reveal the underlying mechanisms and to propose suitable models. Additional studies investigating slow dynamics are required to expand our knowledge of this area, which would support the physical training and rehabilitation of elderly and impaired persons.

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1. Introduction

The “posture control” needed to maintain an upright stance is a very important and basic requirement in daily human life (Wallmann, 2009). Adequate posture control requires the sensory and central nervous systems (CNS), and for the human body to function appropriately against gravity and environmental forces (Runge et al., 1999). Posture control requires visual and vestibular inputs, as well as both proprioceptive and tactile somatosensory inputs, to control posture-regulating muscles in the whole body, especially in the lower limbs and trunk (Horak and Macpherson, 1996). Thus, the CNS needs to control multiple muscles simultaneously based on corresponding multisensory inputs. Because of the complexity of the CNS, the mechanism by which this regulation occurs is still unknown despite researchers’ best efforts.

Changes in multisensory inputs elicit immediate changes in posture corresponding to the sensory information. These immediate alterations, referred to as the *fast dynamics* in the CNS, occur when the brain predicts sensory inputs and corrects the body’s motion based on the error between the predicted and actual sensory inputs. In this process, the multisensory inputs are integrated to represent the body state (body schema); this is then utilized by the brain to generate motion. Though an interesting phenomenon in its own right, how the brain integrates multisensory inputs in the CNS is still unknown. The “weight and reweight” concept is an important framework for describing the ability of multisensory integration to calculate body state, including parameters such as the center of mass (CoM) and heading. In general, the sensory inputs include signal noise, and the multisensory “integrator” decides which inputs are reliable, and to what degree, as the “weighting” process. Then the CNS reweights (changes the weights) the inputs according to the internal and external conditions of the body and around the body such as light level, bodily acceleration, etc. The details of this concept will be introduced in the fourth section.

Another interesting aspect of posture control is that multisensory integration and the posture controller undergo long-term alterations for a variety of reasons, including aging and learning. These long-term alterations are referred to as the *slow dynamics* in the CNS.

In this review, we will focus on both fast and slow dynamics of multisensory integration in posture control. In this section, we introduced the background of posture control studies and summarized the current gaps in our understanding. Next, we will introduce the detailed sensory inputs related to posture. In the third section, we will follow that up by introducing studies investigating the relationship between multisensory inputs and postural alterations (fast dynamics), including our study investigating “internal force control” to evoke postural alterations when the multisensory inputs are changed. In the fourth section, we will introduce the available modeling and simulation approaches to explain postural alterations, including the results of those studies introduced in the third section. Finally, we will also describe the findings of studies examining long-term alterations in posture in relation to aging, learning, and rehabilitation, which is a field of research that has increasingly been garnering attention. In closing, we will summarize the key points of this review.

2. Contributions of individual sensory inputs

As mentioned above, visual, vestibular, proprioceptive, and tactile sensory inputs are the primary contributors to the maintenance of upright posture. Several studies have examined the contribution of each sensory input to posture maintenance using a variety of experimental methodologies. Due to the large number of studies related to these sensory systems, we introduce only review papers with experimental methods in this section. For each sensory input, we will describe the ways the input can be altered, and the resulting changes in postural control.

2.1. Visual sensory input

Visual sensory input can be easily modified by opening and closing the eyes, which results in changes in postural stability (Horak and Macpherson, 1996). Another method of modifying visual sensory input is by projecting scenes onto a moving screen. Wade and Jones (1997) have reviewed the effects of visual stimulation on posture control. Recent studies of visual alteration discuss the contribution of vision in multisensory reweighting and the human posture control model. Such studies will be introduced in the third section.

2.2. Vestibular sensory input

Vestibular input cannot be easily changed, because it cannot be consciously controlled. Vestibular information transmitted to the brain provides the head orientation relative to gravity (vertical) and, in conjunction with neck proprioception, makes it possible to estimate body orientation. The head orientation, in turn, affects eye movements. Changes in vestibular inputs can be elicited by electrical stimulation, including galvanic vestibular stimulation (GVS). Contribution of the vestibular input to postural control has also been investigated by studying patients with disorders that result in loss of vestibular function. Vestibular mechanisms and their relationship to posture control, including head movement and whole body sway, are reviewed by Green and Angelaki (2010). For a general overview of vestibular function, please refer to the review paper (Forbes et al., 2015).

2.3. Proprioceptive somatosensory input

Proprioception, like vestibular sensation, is difficult to modulate in experiments. Proprioception gives us information on the static and dynamic components of joint position/orientation; for posture control, information about lower limb and ankle orientation is especially important. This sensory input can be decreased experimentally by using a tilting platform to adjust the ankle joint angle with a referring body sway of the subjects. The reduced proprioceptive input due to the tilting platform evokes a postural sway better than that related to a normal, fixed platform. Proprioception can be altered through the vibration of muscles such as the soleus. Proprioceptive alteration alone does not evoke body sway, but rather requires alterations of visual, vestibular, or tactile sensations as well. Allum et al. (1998) have reviewed studies that investigated proprioceptive contributions using this method. To find the contribution of the proprioception, neck and ankle muscles

were stimulated by vibration to analyze the relationship between neck and ankle proprioception (Kavounoudias et al., 1999).

2.4. Tactile somatosensory input

In the upright stance, tactile cues are conveyed to the brain from the soles of the feet. The information is based on the pressure on the sole, and the center of pressure (CoP) is a very important cue for the maintenance of a stable stance. Sole-derived tactile input can be easily changed in experiments by covering the floor with foam or similar soft material. Another study noted that a light touch anywhere on a subject's body can attenuate postural sway, even when the touch is not physical but electrical stimulation (e.g., of a finger) (Shima et al., 2013). The effects of a light touch are very interesting, but the mechanism by which they work is still unknown. Some data suggest the mechanism may relate to the attention, which is near concept to "reweighting", dedicated by the brain to the sensory inputs maintaining posture (Woollacott and Shumway-Cook, 2002; Soto-Faraco et al., 2004).

3. Experimental approach for multisensory integration

In this section, we discuss studies that experimentally investigated the effects of multisensory input alterations. We also introduce our study as an example of the experimental investigation.

3.1. Experimental method for investigation of multisensory integration

Visual and proprioceptive sensory inputs can be changed simultaneously using the Sensory Organization Test (SOT), which examines how subjects utilize combinations of those sensory feedback to maintain an upright stance (Fig. 1) (Nashner et al., 1982; Nashner and Peters, 1990). In the SOT, a screen in front of the subject and a platform on which the subject stands can both tilt according to the body sway of subjects. In one study focusing on fast dynamics, brain function was measured using functional near-infrared spectroscopic (fNIRS) imaging to identify the region(s) associated with sensory input processing during alterations of the conditions of the SOT (Karim et al., 2013). This study found bilateral activation in temporal-parietal areas in conditions of visual and proprioceptive inhibition, in which this test and fNIRS potentially utilized the measurements of the brain function for quiet standing. This test is utilized in many studies to investigate aging, learning,

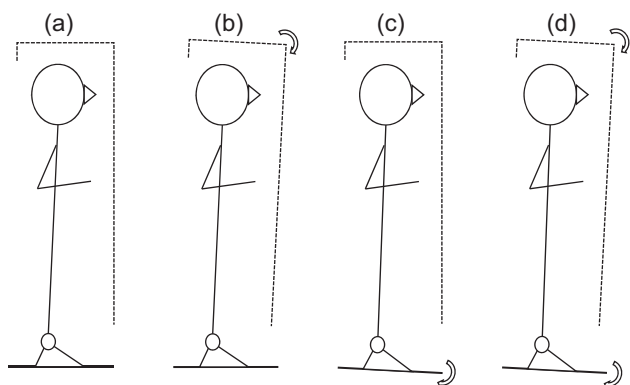


Fig. 1. Sensory organization test: the subjects' CoP, CoM, and the other measurements are calculated using a (a) fixed screen in front of subjects with a fixed platform, (b) rotating screen referenced subjects' body sway (visual alteration), (c) rotating platform referenced subjects' body sway (proprioception alteration), (d) rotating screen and platform referenced subjects' body sway (visual and proprioception alteration). The posture control is scored based on the measurements.

multisensory-integrated modeling, and posture control modeling, all of which are discussed in the following section.

Under conditions of visual stimulation by projection of a moving pattern, and proprioceptive perturbation by vibration to the bilateral Achilles tendons, the postural maintenance of young adult subjects was perturbed, while the disturbance was rescued by galvanic vestibular stimulation (Eikema et al., 2014). This result suggests that vestibular input has less of an effect than the other sensory inputs, since the subjects could not hold their postures without artificial vestibular stimulation. A similar experiment used GVS to alter vestibular input, screen transition to alter visual input, and vibration to alter proprioception (Hwang et al., 2014). In this study, when one of the sensory inputs was disturbed, the weights of the other sensory inputs increased as per a feedback control model. The data indicated that the sensory inputs were clearly independent, and that the weight of each sense's reliability would be required for correct modeling. The combined effect of the visual and vestibular sensory inputs on posture control has been reviewed elsewhere (Coelho and Balaban, 2015).

As mentioned, a light touch increased postural stability of the upright stance in the presence of visual disturbances (Jeka et al., 2000; Oie et al., 2001; Allison et al., 2006). The effect is still observed in patients with vestibular loss (Horak, 2009). These data suggested that the contribution of each of the multisensory inputs is not integrated linearly, because a light touch did not increase information of posture parameters (e.g., CoP). Rather, this input possibly induce the reweighting of information from each sensory input. Moreover, posture can be maintained by light touch whether given or received, and even in the presence of vestibular disturbances (Chiba et al., 2013). In addition, proprioceptive disturbance using a foam surface with visual stimulation still increases body sway compared to a fixed surface with normal vision (Bronstein, 1986). However, experiments comparing postures with eyes closed on a fixed surface versus a foam surface found no significant differences of posture control between on the fixed and foam surfaces (Creath et al., 2005).

Finally, one study noted that vibration of the soleus that elicited a disturbance of ankle joint orientation under an eyes-closed condition induced a variable postural body sway that varied with the vibration frequency (Capicikova et al., 2006). However, the multisensory reweighting was unclear in this study, making interpretation difficult.

3.2. A multisensory integrated control model (Chiba et al., 2013)

Here, as one example of fast dynamics studies, we introduce our study examining changes in posture by alterations in multisensory inputs in this subsection. This work was done to show that muscular tonus control and tactile inputs from not only the foot, but any part of the body, play important roles in postural stability.

For this study, we recruited 12 male subjects in their twenties without any impairments. We measured the CoP and muscle activities as shown in Fig. 2. We used 8 experimental conditions, with different combinations of modulated visual, vestibular, and tactile stimulation. Vision was occluded by closing the eyes, vestibular sensation was disturbed by a caloric test that upset the vestibular system through introduction of cold water into the left ear cavity, and tactile stimulation was introduced by the touch of a body part by another person. Specifically, the 8 conditions were: condition1, normal; condition2, visual occlusion; condition3, tactile stimulation; condition4, visual occlusion and tactile stimulation; condition5, vestibular disturbance; condition6, visual occlusion and vestibular disturbance; condition7, vestibular disturbance and tactile stimulation; condition8, visual occlusion, vestibular disturbance, and tactile stimulation. The participants were just required to maintain an upright stance under all conditions.

Table 1

Muscle activities in each condition: The combined change of visual and vestibular inputs results in high activities in almost all of the muscles (condition 6). Adding light touch does not decrease these activities, although the posture recovers (condition 8).

Conditions	1	2	3	4	5	6	7	8
Soleus (left)	1.00	1.19	1.18	1.34	1.38	1.71	1.40	1.84
Soleus (right)	1.00	1.12	1.11	1.21	1.29	1.48	1.32	1.60
Tibialis anterior (l)	1.00	1.26	1.40	1.33	2.29	4.51	2.47	4.41
Tibialis anterior (r)	1.00	1.29	1.25	1.23	2.35	4.44	2.15	4.33
Quadriceps femoris (l)	1.00	1.16	1.21	1.20	1.64	3.61	1.91	4.49
Quadriceps femoris (r)	1.00	0.91	0.90	1.10	1.88	2.81	1.93	3.35
Hamstring (l)	1.00	1.44	1.64	1.68	1.44	1.75	1.62	1.94
Hamstring (r)	1.00	1.38	1.39	1.60	1.38	1.64	1.47	1.64
Erector spinae (l)	1.00	1.03	1.04	1.05	1.12	1.16	1.14	1.23
Erector spinae (r)	1.00	1.02	1.01	1.04	1.15	1.21	1.15	1.26

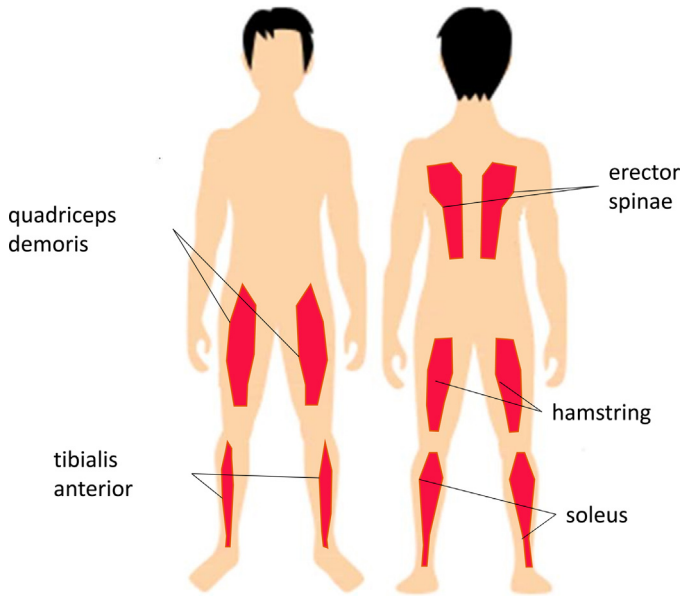


Fig. 2. Measured muscles: we recorded the electromyographs of the tibialis anterior, soleus, quadriceps demoris, hamstring, and erector spinae on both sides of the body.

Outside of the control condition, their postures were markedly altered, as shown in Fig. 3. Fig. 3(A) shows the postural alteration in each condition, and Fig. 3(B) shows the CoP in each condition. Briefly, posture was inclined by vestibular disturbance without

vision, though most interestingly, the inclined posture was rescued with a light touch. However, the muscle activities did not show the same effect. Table 1 shows the muscle activities in each condition. The activities of the tibialis anterior and quadriceps femoris were enhanced, as were the other muscles in condition6 and condition8, when compared with condition1 (control). In other words, to maintaining upright posture, the activities of many muscles are required, and not only the ankle muscles of the left side (the main CoP side). Moreover, the muscle activations in condition8 do not differ much from those in condition6, although posture is recovered by leaning to the left (the disturbed vestibular side). This indicates that the CNS simultaneously controls the stiffness of the human body as well as the posture which means regulating the joint angles. It further indicates that it is important to measure the muscle activities of the whole body to assess posture control.

An overview of the feedback model that we propose is shown in Fig. 4. The integrated sensory feedback was input into two kinds of controllers, a posture-maintaining controller for joint angles and a stiffness-adjusting controller for moment of joint inertia (referred to as an “internal force controller” here). A stiffness control model in Winter et al. (1998) lacked accuracy, because the model did not include multisensory input alterations. We considered that the existence of this internal force should not be ignored when designing this posture control model, and that the stiffness of each joint in the body model should be adjustable. It seems that this controller functions in a manner similar to an intermittent controller (Bottaro et al., 2008; Suzuki et al., 2012; Nomura et al., 2013), to control the torque and the phase of each joint. Future studies expanding on this model should investigate the relationship between stiffness control and phase control.

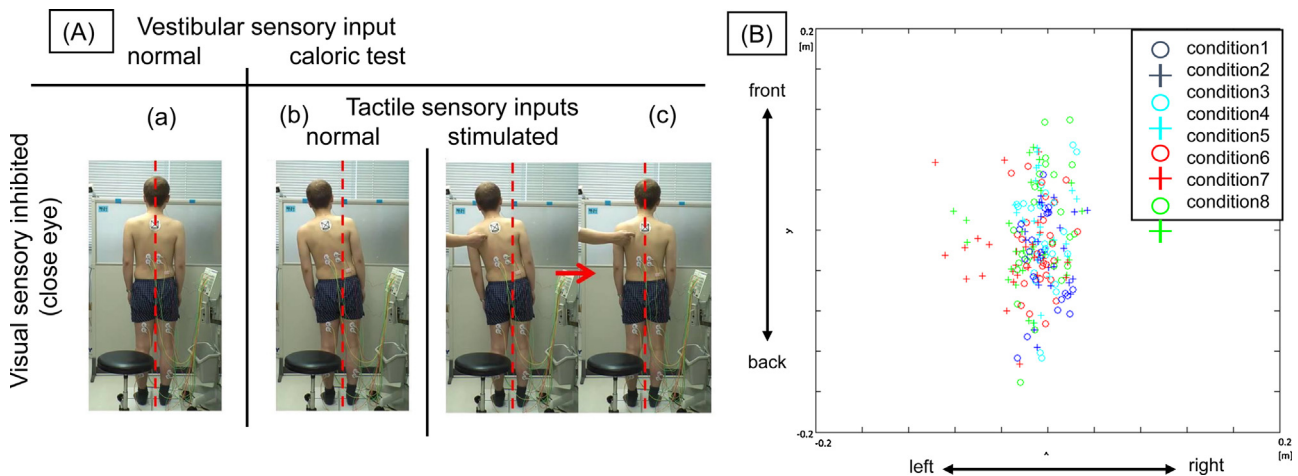


Fig. 3. Posture alteration (A) and average CoP (B) by the multisensory inputs change: the sole visual or vestibular changes result in lesser alterations (A (a) and B (condition 2, 3)). The combined change of visual and vestibular inputs results in marked alterations (A (b) and B (condition 6)). However, the light touch at the condition results in recovery to near normal posture (A (b) and B (condition 8)).

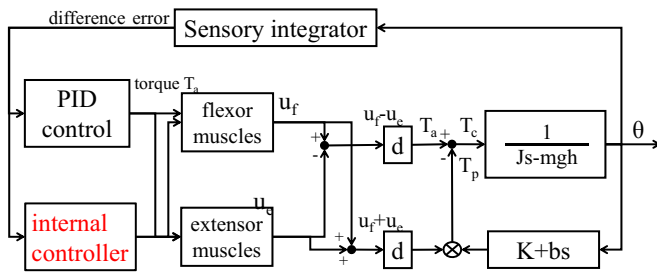


Fig. 4. Feedback models with stiffness controlling: sensory inputs are feedback to 2 controllers, a PID controller, which provides the torque at each joint for the posture maintenance, and an internal force controller, which provides the stiffness of each joint.

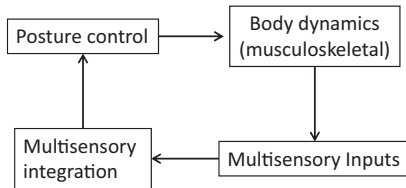


Fig. 5. The simplest concept of basic feedback control with multisensory integration: the posture controller induces muscle activities and the posture is configured by these muscle activities. When the body configuration changes, sensory inputs the body and environment are altered. The sensory inputs integrate into the information that is then used by the posture controller.

4. Modeling and simulation of multisensory integration

The feedback loop of posture control described in Fig. 5 can be used to understand multisensory input modeling, because multisensory integration can be evaluated computationally using the body model parameters. These parameters include the number of segments that equal the number of joints or degrees of freedom, segment mass, segment inertia, segment length, and others in the posture control model. The body model parameters are described in studies that investigated posture alterations by measuring motion capture data, force plate data, and EMG data. To understand the multisensory integration model, we first must introduce the studies of the posture control model and the body model.

4.1. Posture control model

Modeling the controller helps us understand the internal mechanism underlying the human upright posture. If we can estimate the internal state of the controller by modeling, it would be useful for rehabilitation, because we could estimate how much impairment could be recovered. The basic model of posture control is the sensory feedback model that is utilized in machine control (for an investigation of this theory in the muscle activities in cats, see He et al. (1991)). This model is able to explain the motion of patients with balance loss in relation to the time delays in the control loop (Van der Kooij et al., 1999; Lockhart and Ting, 2007; Vette et al., 2010; Li et al., 2012). Other studies have proposed a feedforward mechanism for predictive control or strategy selection (Barin, 1989; Wolpert et al., 1995; Fitzpatrick et al., 1996; Gatev et al., 1999; Morasso and Sanguineti, 2002). A model with both feedback and/or feedforward activity was proposed by Kuo (1995). The continuous feedback models are proposed with determined parameters to account for the experimental results in several studies (for example, muscle stiffness (Morasso et al., 1999; Morasso and Sanguineti, 2002)). The feedback models are extended to the models including estimation of sensory inputs that is reconstructed during task (Diekmann et al., 2004). In Hettich et al. (2011), Mahboobin (2007), and Mergner et al. (2009), upright standing robots using vestibular

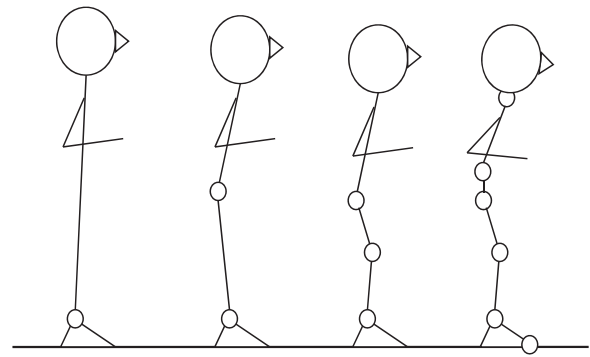


Fig. 6. Body link models: the ankle is the basic joint utilized in all link models. The hip, knee, waist, toe, and neck joints are included for additional models. These are modeled as the inverted pendulum that can be mechanically formulated in mathematics.

input were proposed, with multiple joints using a feedback mechanism similar to that in humans, which verified the stability of the robot stance. These models were constructed based on a one-joint, inverted pendulum, which will be introduced in the next subsection. A feedback model with a two-joint body model was proposed in Park et al. (2004) to represent a more complex postural alteration with the hip joint. In Hettich et al. (2014), the posture alterations were also obtained using a feedback controller with a two-joint body model.

According to a feedback control model, humans may stabilize posture in order to minimize muscle activities, rather than to minimize body sway (Kiemel et al., 2011). One study also considered ankle states (angle and torque) as the minimized index in the feedback control model (Qu et al., 2009). Posture control feedback models with multisensory inputs are discussed in another review (Mergner, 2010). Finally, intermittent feedback control has also been proposed to account for posture control (Bottaro et al., 2008; Suzuki et al., 2012; Nomura et al., 2013).

Currently, the control model of human posture remains to be established; the proposed models still depend on the tasks, which include target posture, environment, adding force, and sensory inhibition. In addition, these also depend on the target indices being optimized in motion. The target indices are measured properties in experiments, for example CoM, CoP, EMGs, and heading, then the studies try to construct necessary and sufficient models to explain the measured properties. Database and big data analyses may be needed to resolve this issue because of the extensive coupling between these dependent variables.

4.2. Body model

It is also important to represent body segments mathematically and computationally for simulations. The basic model is the single inverted pendulum model (e.g., Peterka, 2002; Maurer et al., 2006). This model has one segment with one joint at the ankle, and no joint at the knee or hip. However, the hip and the knee joints play an important role in maintaining posture for the trunk, and for relative head movement (Creath et al., 2005; Hsu et al., 2007). Therefore, models including two or more joints have been proposed (Fig. 6) (Alexandrov et al., 2005; Kuo, 2005; Hsu et al., 2007; Kilby et al., 2015). During quiet standing, the CoM can be represented with two joints: the ankle and the hip joint (Gage et al., 2004). Kilby et al. (2015) calculated the CoM in 3, 4, 5 and higher degrees of freedom (DoFs) models. Not only the DoFs, but also the tendon modeling, are important for constructing a realistic body model to verify the controller (Loram et al., 2004, 2005a,b). Recently, with advances in computing technology, detailed musculoskeletal models such as OpenSim (Delp et al., 2007) have been proposed and utilized to

simulate human motions. In one study, 3 DoF models with muscles were constructed with optimized posture control using the Genetic Algorithm (Pasha Zanoosi et al., 2015). Although models with additional DoFs can represent complex motion, they require complex controllers to reproduce motions that were observed and measured in experiments. Therefore, it is important to find the simplest body models that can adequately represent the empirically derived motions. For example, unperturbed standing can be adequately represented with one joint (Pinter et al., 2008).

4.3. Multisensory integration model

Dealing with multisensory feedback and state estimation are challenges encountered during modeling of posture control. Several studies have attempted to construct a Kalman filter as a multisensory integration of the inputs of the posture controller in humans (Van der Kooij et al., 1999, 2001; Kiemel et al., 2002). Sensory weighting and reweighting models are very common feedback models. The multisensory reweighting models for condition changes in humans are proposed in many studies using Bayesian models or linear summation. Reweighting of proprioception and graviception is discussed in terms of continuous feedback control (Peterka and Loughlin, 2004; Van der Kooij and Peterka, 2011). The multisensory inputs are integrated linearly as weights of each sensory input in the model, and the model can then represent alterations of body sway in experiments. The model is extended to separate models of the upper and lower body in Goodworth and Peterka (2012). Some studies (Mahboobin et al., 2005; Mahboobin, 2007) also utilize the linear reweighting model with visual and proprioceptive inputs. In Hwang et al. (2014), the visual, vestibular, and proprioceptive inputs are disturbed in the quiet standing posture, and the gain of each sensory input is calculated repeatedly as both the weight and reweight. Estimation and threshold are important contributors to posture control in several commonly occurring human conditions of the sensory disturbances, and some researchers have proposed a reweighting method with thresholds to estimate these conditions (Blümle et al., 2006; Maurer et al., 2006). An optimal estimation method with minimal prediction error has been proposed by Kuo (2005). In the Bayesian models, the reliability of each sensory input is obtained by day-to-day experience, and then used by the controller to weight each sense (Dokka et al., 2010; Vilares and Kording, 2011). This method can represent a nonlinear integration of the multisensory inputs, and is adequate for representing the effects of aging. Therefore, this method is currently considered the most effective available for modeling slow dynamics. A computational model of the control and sensory integration of posture, as well as other kinds of motions, has been previously reviewed in Franklin and Wolpert (2011).

5. Long-term alteration in posture

The postural alterations mentioned above are considered fast dynamics because of their related immediate sensory changes. However, alterations are also caused over the long term, producing slow dynamics.

5.1. Aging and posture disorders

Aging is one of the factors involved in long-term alterations in posture. Compared to younger individuals, the reweighting of sensory inputs is altered in elderly individuals (Eikema et al., 2014). Therefore, the relationship between the multisensory reweighting and aging has been investigated recently using various sensory input alterations. According to reports of experimental posture control studies, the likelihood of falling down increases exponentially with age, especially after the age of 60 (Horak et al., 1989).

Furthermore, an increase in body sway in the SOT was observed in the elderly (Speers et al., 2002), especially in the absence of visual and proprioceptive cues (Cohen et al., 1996). The patterns of joint movement in elderly individuals are similar to that in young adults, but larger proximal joint rotations in elderly individuals induce larger sway (Tsai et al., 2014). Backward transition platform experiments indicate that elderly individuals experience more body sway and employ different posture control strategies compared to younger individuals (Kasahara et al., 2015). Moreover, a study using a variety of methods to inhibit multisensory inputs reported differences in CoP between elderly and young individuals in several conditions (Maitre et al., 2013). Similar to reports of experimental sensory reweighting, studies reporting that proprioception can be altered in elderly individuals have been reviewed by Goble et al. (2009) and Shaffer and Harrison (2007). Recently, it was reported that the effects of visual cues with oscillation, as well as with oscillation and transition, show only marginal differences between young, elderly, and fall-prone elderly individuals (Jeka et al., 2006). Vestibular dysfunction in elderly, healthy elderly, and healthy younger adults has been compared using SOT, and the results indicated that visual and vestibular functions exhibited significantly more age-related weakening than did proprioception (Pedalini et al., 2009). Furthermore, GVS is less effective on elderly subjects compared with young subjects (Eikema et al., 2014). Several studies of age-related alterations at the cortical and spinal levels have been conducted (see Papegaaij et al., 2014 for a review).

The model-based approach of posture control indicates that with Proportional-Integral-Derivative (PID) control, which is basic feedback control method in engineering, improving hip and ankle stiffness may increase the lateral stability of elderly individuals (Nishihori et al., 2012). In addition to the differences in sensory inputs, the time delay in the feedback loop is also significantly different between a young group and an elderly group (Qu et al., 2009; Davidson et al., 2011). The model-based approach of sensory reweighting indicates that proprioception, rather than other cues, is primarily utilized in elderly individuals (Wiesmeier et al., 2015). Reduction of both the visual and proprioceptive cues results in significant differences of the postures between the young and elderly (Mahboobin, 2007). The above studies provide evidence that multisensory integration undergoes an age-related decline resulting in alterations in posture control. On the other hand, multisensory integration in children also differs from that in adults (Peterson et al., 2006). This means that the alteration of multisensory integration is induced by aging and development.

Certain disorders also cause alterations in multisensory integration. For example, Yozu and Haga found that the patients of hereditary sensory and autonomic neuropathy (HSAN) type 4 or 5 have significantly different gait parameters (Zhang et al., 2013). Patients with a loss of vestibular function can maintain an upright posture when visual and somatosensory cues are altered by long-term adaptation (Bronstein, 1986; Herdman, 1997). Similarly, individuals with vestibular dysfunction do not differ from normal subjects in their responses to visual inhibition or a foam platform (Cohen et al., 2014). In addition, individuals with loss of somatosensory function do not exhibit changes in posture compared to healthy individuals during quiet standing (Horak et al., 1990). However, limitations in other sensory substitutions are observed in patients with loss of vestibular input (Nashner et al., 1982; Bronstein, 1986; Maurer et al., 2000, 2006; Blümle et al., 2006), and they do not employ the hip strategy that human utilize movement of hip joint for postural maintenance. Elderly patients with loss of vestibular input exhibit more significant differences in posture control (Pedalini et al., 2009). Patients with a loss of vestibular input can be divided into two groups, depending on how prone they are to falling in response to visual changes and a light touch (Horak, 2009). The authors hypothesized that this difference

may have been caused by training and learning in the individuals' daily lives. The postural stability of patients with Parkinson's disease has also been analyzed, and a significant difference in posture was observed in multisensory alteration, but not in single-sensory alteration (Bertolini et al., 2015). On exposure to visually congruent stimulation, patients with Alzheimer's disease showed a decrease in balance, but patients with Parkinson's disease did not (Chong et al., 1999). A balance test for hemiplegia diagnosis has in fact been proposed (Di Fabio and Badke, 1990), which indicates that the SOT may be a candidate test for such patients. It is very difficult to propose a common theory to explain the observations in all these patients, because of inter-individual variations.

5.2. Learning and rehabilitation

A learning effect in posture control has been previously demonstrated, revealing that healthy adults improve their posture control significantly in the SOT (Wrisley et al., 2007). The archers (archery players) can be in a stable position compared with normal subjects because of training (Stambolieva et al., 2015). A learning effect was also observed in Peterka and Loughlin (2004).

Recent studies have focused on the learning and rehabilitation applications of motion control, including posture control. A recent study (Nardone et al., 2010) reported rehabilitation in patients with disorders of peripheral neuropathy, as well as vestibular disorders, using a moving platform. The improvement of balance control provided by this intervention is similar to that seen with the application of Frankel exercises. For vestibular rehabilitation therapy, please refer to the following review (Han et al., 2011). Recently, robot-aided neurorehabilitation has been proposed (Krebs et al., 2000), but recovery of posture with this method (model) is still insufficient. One of the reasons for this is that the relationship or correspondence between the model parameters and the endpoint goal of rehabilitation are still unclear. The difference in the parameters should be based on the motion or measurable values from the rehabilitation.

6. Conclusion

In this review, we introduced studies of posture control for the maintenance of an upright stance. Multisensory inputs play important roles in the stability of human posture. The studies presented investigated multisensory inputs and observed postural alterations. They also constructed models that include not only posture control models, but also body models and sensory integration models. These models are still dependent on the tasks involved, and conditions that include impairments of subjects and environmental conditions, and measurements such as CoP, CoM, EMGs, and brain images. In this field, the researchers have collected evidence to provide insight into human internal control, for which they propose models to be able to explain the results of the human postural experiments.

Fast dynamics of posture alteration by changes in multisensory inputs have been investigated and modeled in many studies. However, slow dynamics, the long-term alteration, has not been sufficiently investigated. We suggest that the researches should focus on the "body representation in the brain" that is utilized to estimate the state of the body via the integration of sensory inputs. Any difference between this "body representation in brain" and the real body will result in inappropriate body control. This difference may result from aging or other impairments and can be partly reduced by rehabilitation, using the long-term alteration model. To achieve this, an interdisciplinary approach combining the fields of neuroscience, biomechanics and rehabilitation will be required.

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