BALANCE CONTROL MECHANISMS DO NOT BENEFIT FROM SUCCESSIVE STIMULATION OF DIFFERENT SENSORY SYSTEMS

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ABSTRACT

In humans, to reduce deviations from a perfect upright position, information from various sensory cues is combined and continuously weighted based on its reliability. Combining noisy sensory information to produce a coherent and accurate estimate of body sway is a central problem in human balance control. In this study, we first compared the ability of the sensorimotor control mechanisms to deal with altered ankle proprioception or vestibular information (i.e., the single sensory condition). Then, we evaluated whether successive stimulation of difference sensory systems (e.g., Achilles tendon vibration followed by electrical vestibular stimulation, or vice versa) produced a greater alteration of balance control (i.e., the mix sensory condition). Electrical vestibular stimulation (head turned ~90°) and Achilles tendon vibration induced backward body sways. We calculated the root mean square value of the scalar distance between the center of pressure and the center of gravity as well as the time needed to regain balance (i.e., stabilization time). Furthermore, the peak ground reaction force along the anteroposterior axis, immediately following stimulation offset, was determined to compare the balance destabilization across the different conditions. In single conditions, during vestibular or Achilles tendon vibration, no difference in balance control was observed. When sensory information returned to normal, balance control was worse following Achilles tendon vibration. Compared to that of the single sensory condition, successive stimulation of different sensory systems (i.e., mix conditions) increased stabilization time. Overall, the present results reveal that single and successive sensory stimulation challenges the sensorimotor control mechanisms differently.

Key words: sensorimotor control; human balance control; sensory stimulation; sensory reintegration.

INTRODUCTION

Human upright balance is inherently unstable. To reduce the small deviations from a perfect upright body position, information from proprioceptive, vestibular and visual systems are combined (Bronstein, 1986; Bronstein and Hood, 1986; Kavounoudias et al., 1999; Magnusson et al., 1990). These sensory signals are continuously reweighted based on their reliability and specificity to maintain the upright standing position (Maurer et al., 2006; Oie et al., 2002; Peterka, 2002). To assess the role of each sensory cue, it is common to experimentally induce sensory illusions. Electrical vestibular stimulation (EVS) with the cathode electrode located on the right mastoid and the anode electrode located on the left mastoid induces an increase in the firing rate of the right vestibular nerve (cathode) and a decrease in in the firing rate of the left vestibular nerve (anode), leading to a body sway towards the anode (Fitzpatrick and Day, 2004; Goldberg et al., 1984). Ankle tendon vibrations also induce body sway resulting from the activation of the primary endings of muscle spindles (Burke et al., 1976). When vibration is applied to the Achilles tendon, the firing rates of the gastrocnemius and soleus muscle spindles increase (i.e., as if these muscles stretched), suggesting a forward body sway. To counterbalance this illusion, the body sways backward (Eklund, 1972). Previous results suggest that vestibular stimulation influences the processing of somatosensory signals (Ferre et al., 2011; Ferre et al., 2013; Hlavačka et al., 1995). Moreover, human neuroimaging studies have revealed vestibular projections in the primary and secondary somatosensory cortex (Bottini et al., 1994; Fasold et al., 2002) and the primary motor cortex and premotor cortex (Bense et al., 2001; Emri et al., 2003; Fasold, et al., 2002). The overlap in brain activation of the vestibular and somatosensory inputs is not simply anatomical but also reflects a functional crossmodal perceptual interaction. Psychophysical studies have revealed that vestibular stimulation facilitates the detection of cutaneous stimuli, suggesting a vestibular-somatosensory perceptual interaction (Ferre, et al., 2011). Consequently, it is possible that successive stimulation of these two senses improves balance control.

The first aim of this study was to compare the ability of the sensorimotor mechanisms to control balance during alterations in vestibular information or ankle

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proprioception. A mathematical model was used to assess the effects of sensory and motor noise on balance control; the results indicate that the magnitude of noise in the vestibular system is ~10 times greater than that of noise in the proprioceptive system (van der Kooij and Peterka, 2011). Furthermore, balance control mainly relies on ankle proprioception (Diener et al., 1984; Horak et al., 2002), and its contribution represents more than 60% of balance control (Lord et al., 1991; Peterka and Benolken, 1995; Simoneau et al., 1992; Simoneau et al., 1995). Thus, we hypothesize that body sway should be larger during Achilles tendon vibration compared to EVS.

The second aim of this study was to assess whether successive stimulation of different sensory systems alters the performance of the sensorimotor integration mechanisms. During upright standing, a sudden alteration in one sensory information source normally leads to an increase in body sway. When a sensory stimulation is repeated over time, however, the amplitude of body sway decreases (Bronstein, 1986; Caudron et al., 2010; Holmberg et al., 2003). During simultaneous sensory stimulation, the attenuation of body sway is limited or it not necessarily transferred to other senses or other muscles during ankle tendons vibration (Caudron, et al., 2010; Fransson et al., 2007). It is unclear, however, whether the sensorimotor integration mechanisms can benefit from successive stimulation of different sensory modalities. To address the second aim, we compared balance control performance to a condition in which a single sensory system was altered to a condition in which different sensory systems were stimulated in a chronological sequence. An increase in body sway following the subsequent stimulation would suggest that the error signal from different senses alters the performance of the sensorimotor integration mechanisms.

METHODS

Participants

Thirty-two participants (16 men, 16 women, age = 23.1 ± 4.5 years, weight = 69.0 ± 13.2 kg, height = 168.6 ± 10.7 cm) with no known history of neurological or vestibular dysfunction took part in two separate experiments (16 participants in each experiment). Prior to participation, participants provided informed consent. The study was approved by the Biomedical research Ethics Committee at Laval University and conformed to the Declaration of Helsinki standards.

Experimental set-up and protocol

Participants stood barefoot on a force platform (model Optima, Advanced Mechanical Technology, Inc., Watertown, MA, USA) with their feet parallel at 10 cm inter-malleoli and their arms alongside. Their eyes were closed, and their head was turned left at approximately 90° and extended approximately 18°. This head orientation parallels the EVS-evoked rotational vector with the horizontal, thus maximizing the balance response to EVS along the anteroposterior (AP) axis (Cathers et al., 2005; Lund and Broberg, 1983). The force platform signals were sampled at 1000 Hz using a 16-bit A/D converter (model NI PCIe-6531, National Instrument, Austin, TX, USA). The center of pressure (COP) displacements along the mediolateral (ML) and anteroposterior (AP) axes were calculated from the reaction forces and moments of the force platform. All data were filtered using a zero-lag 4th order low-pass Butterworth filter (cut-off frequency 10 Hz). The center of gravity (COG) along the AP axis was estimated using a zero-point-to-zero-point double integration technique (King and Zatsiorsky, 1997; Zatsiorsky and King, 1998) with the assumption that the COP coincides with the vertical line passing through the COM when the horizontal ground reaction force is zero.

Experimental conditions

Applying vibration to a muscle tendon specifically activates the primary endings of the muscle spindle (Burke, et al., 1976; Roll and Vedel, 1982). In this study, vibration (n = 2, Freq.: 70 Hz, amplitude: ~1 mm) was applied to the Achilles tendon to cause a backward body sway, which is known as a vibration-induced postural response (Eklund, 1972; Simoneau et al., 2006; Teasdale and Simoneau, 2001). Vestibular stimulation was delivered by applying electrical stimulation to the eighth cranial nerve (i.e., vestibulocochlear). Electrical vestibular stimulation (EVS) activates all the primary afferents of the semicircular canals and otoliths, with a cathodal current increasing the firing rate of the afferent and an anodal current decreasing the firing rate (Goldberg, et al., 1984; Kim and Curthoys, 2004). EVS induces a net equivalent motion vector (EVS vector) based on the vectorial summation of all the activated vestibular afferents (Fitzpatrick and Day, 2004). According to this model, EVS applied bilaterally over the mastoid processes (i.e., in a binaural bipolar configuration) results in a net rotation around a vector pointing posteriorly and ~18.8° above Reid's plane (Day et al., 2010; Mian et al., 2010). Thus, altering the firing rate of the vestibular afferent results in a perceptual illusion of a tilt of falling towards the cathode electrode. To counter this vestibular illusion, muscles are activated creating body sway toward the anode, that is, a backward body sway in the present experiment. To induce vestibular stimulation, a binaural EVS was delivered from a constant-current stimulator (Model DS-5, Digitimer Ltd., Hertfordshire, UK) to electrodes (5 cm^2, ValuTrode® X Cloth Neurostimulation Electrodes, Model VTX5050, Axelgaard Manufacturing Co., Ltd., Fallbrook, CA) located over both mastoid processes and stabilized with a headband. The stimulus was a 1 mA current step that lasted 5 s (see the explanation of the conditions below).

Throughout the two experiments, we alternated the sequence of sensory stimulation. In both experiments, there were two conditions: single and mix. Under the single sensory condition, sensory information from one sensory system was altered, whereas under the mix sensory condition, information from the two sensory systems was altered in sequence. Thus, during the first experiment, under the single sensory condition (Fig. 1 – upper panel) Achilles tendon vibration created a backward body sway. This condition served as a basis of comparison with the mix sensory condition. Under the mix condition,

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information from the vestibular and proprioceptive systems was altered in sequence (Fig. 1 – upper panel).

For the second experiment (Fig. 1 – lower panel), different participants were involved. Experiment 2 was like experiment 1, but under the single sensory condition, the vestibular apparatus was stimulated first to create a backward body sway. Then, under the mix sensory condition, the Achilles tendon was vibrated after the vestibular apparatus was stimulated. Trials under the single condition lasted for 20 s and were divided into three different epochs: prestimulation (5 s), stimulation (5 s) and poststimulation (10 s). Under the mix sensory condition, trials lasted for 40 s and contained six epochs: prestimulation (10 s), first stimulation (5 s), post first stimulation (5 s), prestimulation (5 s), second stimulation (5 s), and post second stimulation (10 s). Participants performed, in blocks, 10 trials of each of the two conditions.
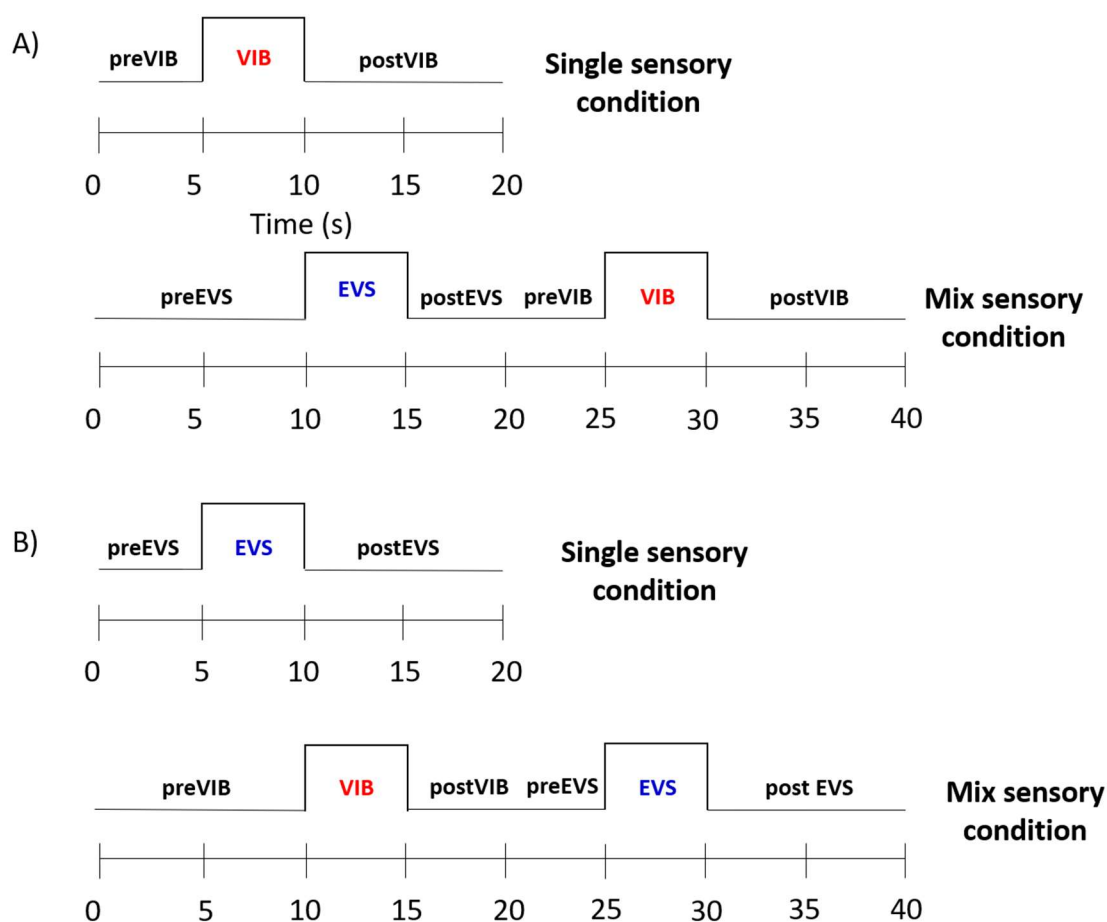
Figure 1: A) Time course of experiment 1 that contained two experimental conditions: single and mix sensory conditions. Under the single sensory condition, electrical vestibular stimulation (EVS) was applied to induce backward body sway. There were three epochs: preEVS (0–5 s), EVS (5–10 s) and postEVS (10–20 s). Under the mix sensory condition, Achilles tendon vibration (VIB) was applied first to create a backward body sway. Then, EVS was applied. B) The time course of experiment 2, which also contained two experimental conditions: single and mix sensory conditions. The epoch durations were as in Experiment 1, but under the single sensory condition, the Achilles tendons were vibrated to create a backward body sway. Under the mix sensory condition, first an electrical vestibular stimulation was applied and then the Achilles tendons were vibrated.

Data analysis

Balance control performance was assessed by calculating the scalar distance between the time series of the COP and COG displacements (Fig. 2 – upper panel) and then calculating the root mean square (RMS) value of the COP-COG scalar distance in each interval. This measure reflects the linear acceleration of the COM, an indicator of balance control performance (Masani et al., 2007; Winter, 1995). We also calculated the stabilization time, which was the time needed to recover balance when sensory information returned to normal (i.e., poststimulation interval). We considered that balance was recovered when the COP-COG scalar distance was below a defined threshold for 500 ms consecutively. For each participant, the threshold was defined as the mean of the RMS value of the COP-COG scalar distance during the prestimulation intervals (dashed line in Fig. 2 – lower left panel). Furthermore, we determined the amplitude of balance destabilization immediately following sensory stimulation by identifying the peak force along the AP axis (Fig. 2 – lower right panel). Visual inspection of every time series showed that peaks occurred at less than 1.5 s following the stimulation offset. Comparison of the peaks between conditions allowed us to verify whether balance destabilization differed when vestibular and ankle proprioception returned to normal.
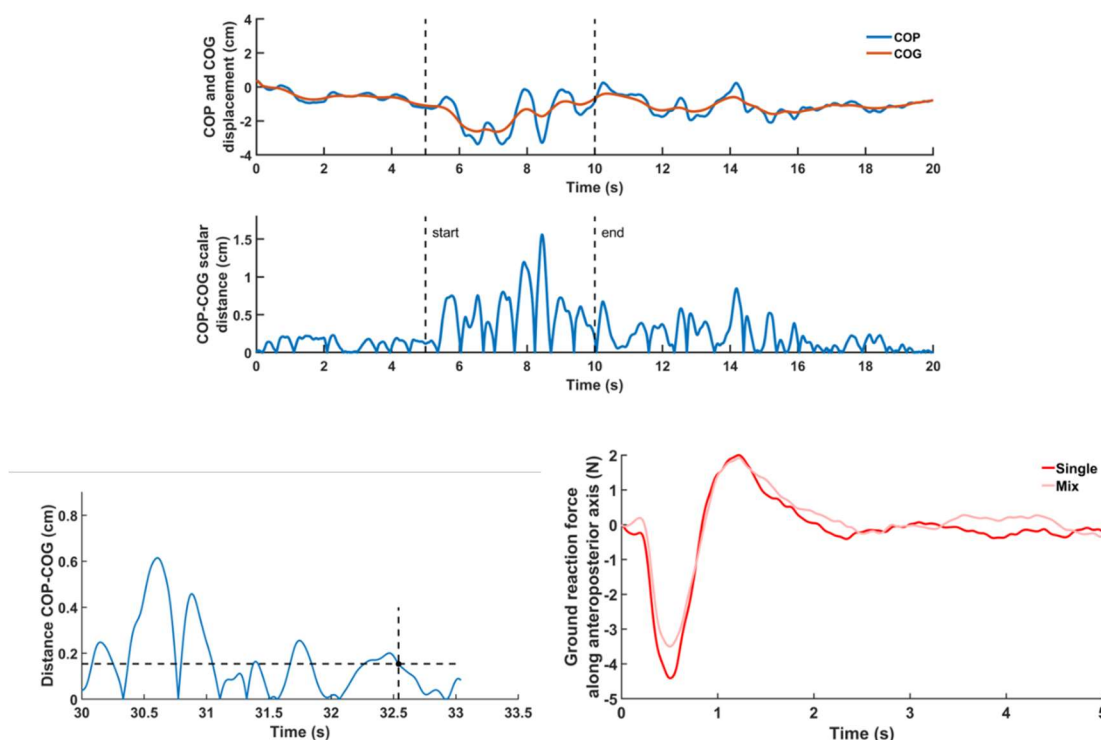
Figure 2: Upper panel) Representative time series of the center of pressure (COP) and center of mass (COM) displacements along the anteroposterior axis. Time-series of the corresponding COP-COG scalar difference. Lower left panel) Determination of the stabilization time following sensory alteration. The blue line represents the time series of the COP-COG scalar distance, the horizontal black dashed line represents the stability threshold and the crossing vertical black line with the dot depicts the time when the COP-COG scalar distance is below the stability threshold for the next 0.5 s. Lower right panel) Mean time-series of the ground reaction force along the anteroposterior axis following Achilles tendon offset for the single and mix conditions.

Statistical analysis

To compare balance control under the single sensory conditions, the RMS values of the COP-COG scalar distance were submitted to analysis of variance (ANOVA) with repeated measures on the factors epoch (prestimulation, stimulation and poststimulation) and condition (VIB, EVS). To contrast balance control performance under the single and mix sensory conditions, the RMS values of the COP-COG scalar distance between the

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single and mix sensory stimulation were compared through separate ANOVAs with repeated measures on two factors (condition: single, mix; epoch: prestimulation, stimulation and poststimulation). Post-hoc analyses were realized using Tukey's honest significant difference (HSD) test. To assess whether the stabilization time differed between the single and mix conditions, paired t-tests were performed. We evaluated whether balance destabilization (i.e., peak force along the AP axis, following stimulation offset) differed among the single conditions using unpaired T-tests. To compare balance destabilization between the single and mix conditions, paired T-tests were used.

RESULTS

Comparison of single sensory conditions

The results of the analysis of the RMS value of the COP-COG scalar distance (Fig. 3) during single sensory stimulation partly confirmed our hypothesis, suggesting that balance control should be poorer when ankle proprioception is altered compared to EVS (significant interaction of Epoch by Condition: $F(2,60) = 6.82$, $p = 0.002$). Decomposition of the interaction revealed that balance control was similar before and during the alterations in vestibular or ankle proprioceptive signals ($ps > 0.05$). When sensory information returned to normal, however, as hypothesized, the RMS value of the COP-COG scalar distance was greater following Achilles tendon vibration ($p = 0.009$). Balance control worsened across epochs (main effect of epoch: $F(2,60) = 47.19$, $p = 0.000$). The RMS value of the COP-COG scalar distance increased from the prestimulation to stimulation epochs ($p = 0.0001$) and from the stimulation to poststimulation epochs ($p = 0.01$). Overall, balance control performance was worse in VIB compared to EVS conditions (main effect of condition: $F(1,30) = 9.78$, $p = 0.004$).
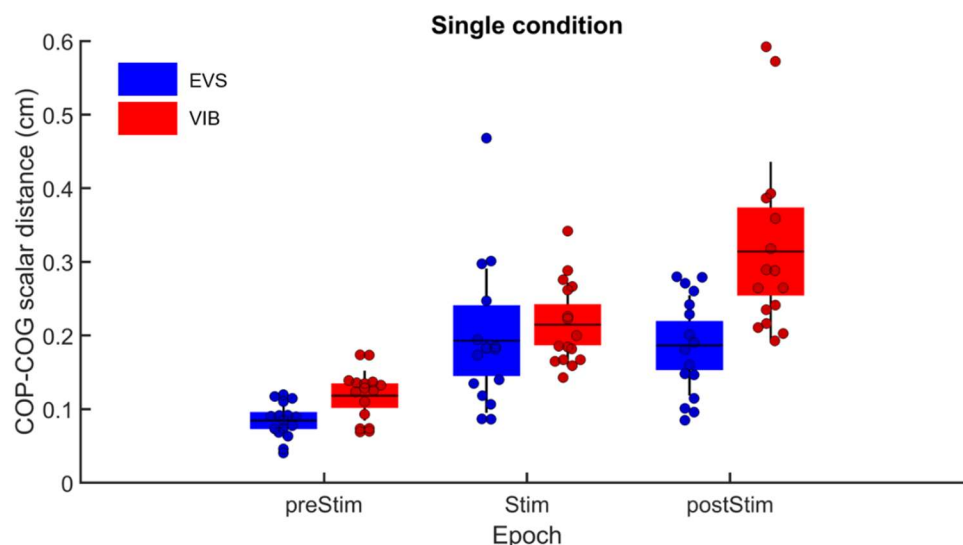
Figure 3: Comparison of the RMS values of the COP-COG scalar distance before (preSTIM), during (STIM) and after (postSTIM) electrical vestibular stimulation and Achilles tendon vibration under the single sensory condition. The dots depict the mean results for each participant. The horizontal lines illustrate the group means, the boxes denote the group standard error of the mean and the lines depict one standard deviation. The blue data and boxes are for the electrical vestibular stimulation (EVS) condition, and the red data and boxes are for the Achilles tendon vibration (VIB) condition.

Balance destabilization under the single sensory condition

Analysis of the peak force along the AP axis revealed that balance destabilization was larger when ankle proprioception returned to normal (mean = −6.24, sd = 22.95) compared to when vestibular information returned to normal (mean = −3.15, sd = 1.52; $t(30) = 3.71$, $p = 0.0008$).

Comparison of the mix sensory conditions

Comparison of the single to mix conditions when vestibular signals were altered (Fig. 4 – left panel) revealed worse balance control under the mix compared to single conditions (main effect of condition: $F(1,15) = 6.94$, $p = 0.02$). Furthermore, balance control differed across epochs (main effect of epoch: $F(2,30) = 31.94$, $p = 0.000$). During and following EVS, balance control was similar ($p = 0.98$); however, the RMS values of

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the COP-COG scalar distance in these epochs were greater than in the preEVS epoch. The analysis reported no difference in balance control performance between conditions across epochs (interaction condition by epoch: $F(2,30) = 1.74$, $p = 0.19$). Comparison of the single to mix sensory conditions when ankle proprioception was altered (Fig. 4 – right panel) revealed no difference (main effect of condition: $F(1,15) = 0.05$, $p = 0.81$). Across epochs, however, the RMS value of the COP-COG scalar distance varied (main effect of epoch: $F(2,30) = 32.19$, $p = 0.000$). Post-hoc tests showed that the RMS value of the COP-COG scalar distance increased across epochs (preStim vs Stim, $p < 0.001$ and Stim vs postStim, $p < 0.01$). Across epochs, however, no difference between conditions was observed (interaction condition by epoch: $F(2,30) = 2.53$, $p = 0.09$).

Balance destabilization under the mix sensory condition

The peak forces when vestibular information returned to normal were similar between the single (mean = −3.16, sd = 1.52) and mix (mean = −3.47, sd = 1.55; $t(15)$ = 1.14, $p = 0.27$) conditions. Following Achilles tendon vibration, the peak force did not differ between the single (mean = −6.24, sd = 2.95) and mix (mean = −5.65, sd = 2.97; $t(15) = −1.84$, $p = 0.09$) conditions.
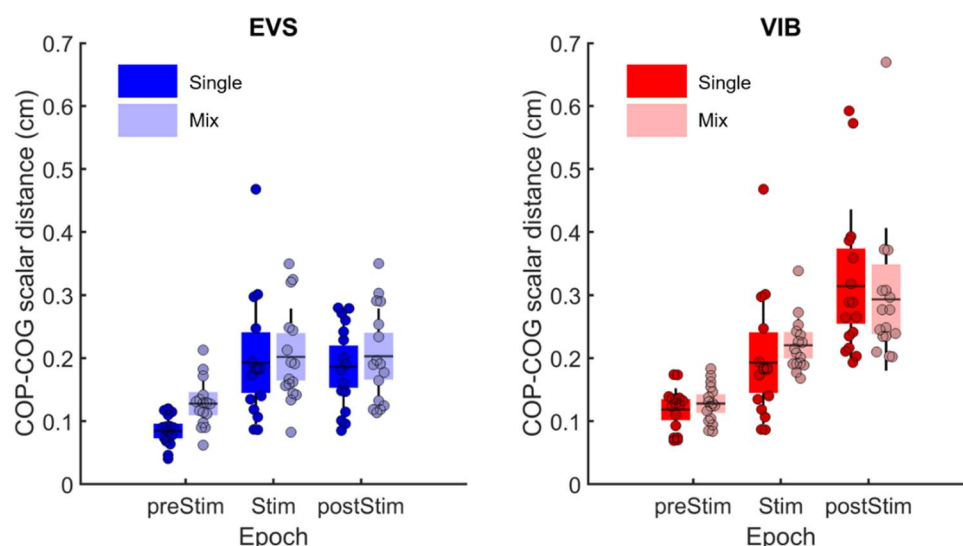

Figure 4: Left panel) Comparison of the RMS values of the COP-COG scalar distance between single sensory and mix sensory conditions, before (preSTIM), during (STIM) and after (postSTIM) electrical vestibular stimulation (EVS). The blue data and boxes represent the single sensory condition, while the light blue data and boxes depict the mix

sensory condition. Right panel) Comparison of the RMS values of the COP-COG scalar distance between the single sensory and mix sensory conditions for the same epochs for the Achilles tendon vibration (VIB) condition. In each panel, the dots depict the mean results for each participant. The horizontal lines illustrate the group means, the boxes denote the group standard error of the mean and the lines depict one standard deviation. The red data and boxes represent the single sensory condition, while the light red data and boxes depict the mix sensory condition.

Time required to reduce the body sway amplitude

Analysis of the stabilization time between the single and the mix sensory conditions revealed that the stabilization time was longer under mix compared to single sensory conditions when either vestibular or ankle proprioception information returned to normal (Fig. 5 – left and right panels: paired T-tests: $t(15) = -4.29$, $p < 0.001$ and $t(15) = -6.86$, $p < 0.001$, respectively).
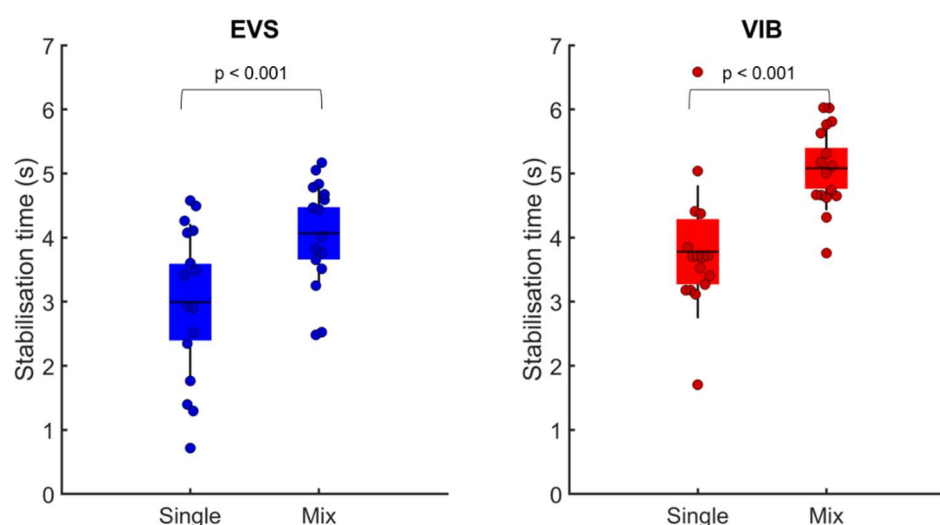

Figure 5: Left panel) Comparison of the stabilization time following electrical vestibular stimulation (EVS) under the single and mix sensory conditions. Right panel) Comparison of the stabilization time following Achilles tendon vibration (VIB) under the single and mix sensory conditions. In each panel, the dots depict the mean results for each

participant. The horizontal lines illustrate the group means, the boxes denote group standard error of the mean and the blue lines depict one standard deviation.

The RMS of the scalar distance between the COP and the COG approximates the center of mass acceleration. Thus, the fact that the peak forces immediately following sensory stimulation were alike between the single and mix sensory conditions was not surprising as no difference was observed for the RMS value of the COP-COG scalar distance. Balance destabilization (i.e., peak force) immediately following sensory stimulation was a good predictor of the RMS value of the COP-COG scalar distance; the variance explained by the linear model was larger than 80% (Fig. 6). Peak force was, however, not a good predictor of the stabilization time (Fig. 7) as the variance ranged from 16% to 51%.
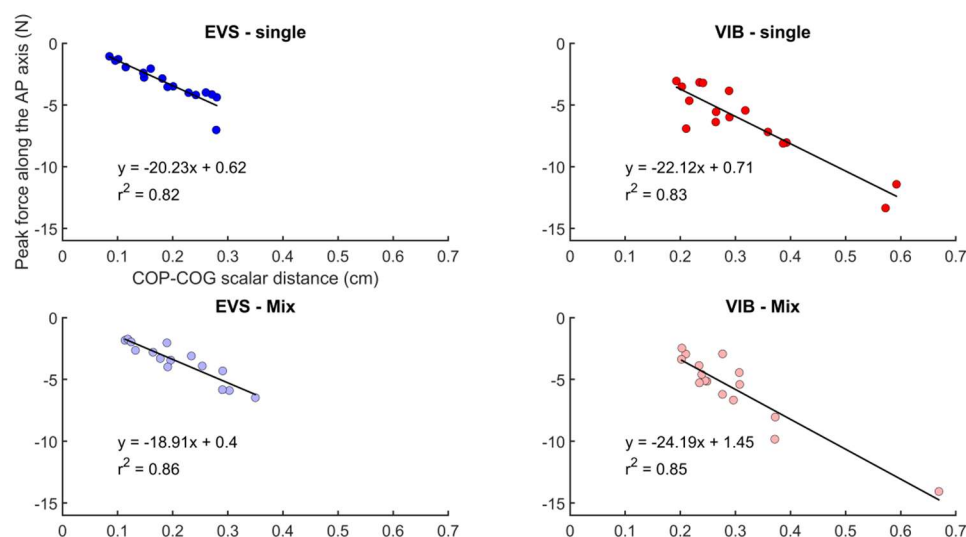

Figure 6: Left column) Linear relationship between the peak forces and RMS values of the COP-COG scalar distance for the single (upper left panel) and mix sensory conditions (lower left panel) when vestibular information returned to normal (i.e., post stimulation epoch). Right column) Linear relationship between peak forces and RMS values of the COP-COG scalar distance for the single (upper left panel) and mix sensory conditions

(lower left panel) when ankle proprioception returned to normal (i.e., post stimulation epoch).
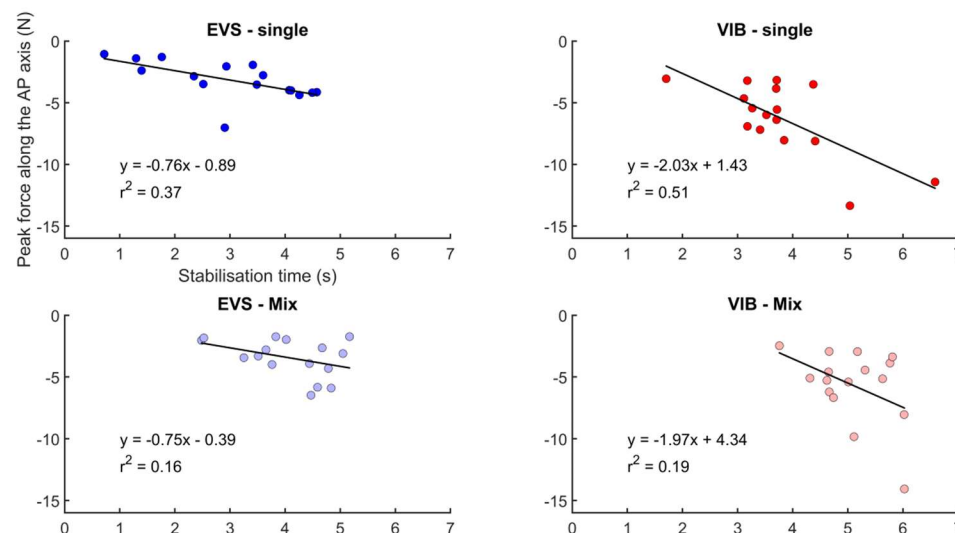

Figure 7: Left column) Linear relationship between the peak force and stabilization time for the single (upper left panel) and mix sensory conditions (lower left panel) when vestibular information returned to normal (i.e., poststimulation epoch). Right column) Linear relationship between the peak force and stabilization time for the single (upper left panel) and mix sensory conditions (lower left panel) when ankle proprioception returned to normal (i.e., poststimulation epoch).

DISCUSSION

Not much is known about the time course of sensory reintegration following a sudden change in a sensory state. Rapid and effective sensory reweighting is crucial to alter the balance motor commands and to reduce instability. The aim of the present study was two-fold. First, to compare the ability of the sensorimotor mechanisms to reintegrate ankle proprioception and vestibular cues. Second, to investigate whether successive stimulation of different sensory systems altered balance control performance. Contrary to our hypothesis, the results revealed no difference in balance control performance when ankle proprioception or vestibular information was altered. As expected, however, when sensory information returned to normal, balance control performance was poorer during

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the reintegration of ankle proprioception compared to vestibular information. This difference was caused by a larger peak of the ground reaction force, that is, balance destabilization, following Achilles tendon vibration offset. Following successive changes in the sensory state (i.e., the mix sensory condition), the amplitude of body sway did not differ between the single and mix conditions, but the time needed to recover balance was longer under the mix condition.

Comparison of the single sensory conditions

Under the single sensory condition, contrary to our hypothesis, balance control performance was similar during ankle proprioception and vestibular alteration. Poorer balance control performance during Achilles tendon stimulation was expected as balance control mainly relies on ankle proprioception (Lord, et al., 1991; Peterka and Benolken, 1995; Simoneau, et al., 1992; Simoneau, et al., 1995) and the vestibular system is approximately 10 times noisier than the proprioceptive system (van der Kooij and Peterka, 2011). We reasoned that during ankle proprioception alterations in the absence of vision, participants would assign larger weights to vestibular information. Since vestibular sensory information is noisy, this should cause poorer balance control. The absence of a difference between ankle proprioception and vestibular alteration may be due to biomechanical constraints. During this stimulation epoch, the amplitude of the backward body sway was restricted by the posterior stability limit. It is tempting to suggest that in the absence of a stability limit, the body sway amplitude could have been larger during Achilles tendon vibration compared to EVS. Furthermore, to reduce balance destabilization during Achilles tendon vibration, it has been suggested that a participant could adopt a forward tilt posture since such a strategy stretches the Achilles tendon and increases ankle stiffness (Tjernstrom et al., 2002). It is worth noting, however, that the center of mass accelerations (i.e., RMS value of the COP-COG scalar distance) were similar under both conditions, ruling out this latest suggestion. During ankle proprioception alteration, it is possible that proprioceptive information from other lower limb muscles combined with vestibular cues contributed to improving the state estimates of body sway. This multisensory process likely reduces the overall variance within noisy sensory systems, attenuating body sway (Ernst and Banks, 2002), which could explain

why balance control performance was not poorer during Achilles tendon vibration compared to EVS. However, it is unclear why balance control performance was not better during EVS. Under this condition, unaltered ankle proprioception could sense body sways, leading to better balance control. One explanation could be that the fusion of ankle proprioception with altered vestibular information led to a noisy unified perception of body sway dynamics and inaccurate state estimation.

When sensory information returned to normal, balance control performance was poorer following Achilles tendon vibration than following EVS. This observation suggests that vestibular reweighting, contrary to ankle proprioception reweighting, could mainly occur at the subcortical level. The vestibular system differs from the proprioceptive system in many ways. First, the same neurons receiving direct afferent inputs can send direct projections to motoneurons, and the first stage of central processing is multimodal (Cullen, 2016). In addition, the vestibular system unambiguously senses head acceleration. Thus, changes in the firing rate of vestibular nerves necessarily provide information about self-motion (Guerraz and Day, 2005). By contrast, ankle proprioception either signals the whole-body orientation with respect to the feet or the orientation of the feet with respect to the shin. During ankle dorsiflexion, the brain must determine whether the body sways forward or the feet are tilted upward. These two situations require balance responses that are fundamentally different, and therefore, such processes should imply complex interactions between cortical and subcortical structures (Nashner, 1976; Taube et al., 2006; Tokuno et al., 2009). This complex interaction likely causes a slower reweighting. Studies assessing the long-stretch reflexes in lower limbs, due to unexpected surface translation, have reported that these responses are mediated in part by cortical mechanisms (Golanov et al., 2001; Stelmach et al., 1989; Taube, et al., 2006). Furthermore, the similarity of the postural responses when different muscles are vibrated means that the motor responses are not caused by the tonic vibration reflex. On the contrary, cortical processing of afferences from all body segments from the feet to the head allows a coherent perception of the whole-body state to be built (Proske and Gandevia, 2012; Roll et al., 1989), which is supported by the fact that postural responses, during muscle vibration, are altered by various factors, such as the availability of other sensory cues or balance stability (Adamcova and Hlavacka, 2007;

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Grasso et al., 2000; Ivanenko et al., 1999; Lackner and DiZio, 2000; Popov et al., 1999). Thus, we suggest that when ankle proprioception returns to normal, the brain must assess the reliability of proprioception, primarily at the cortical level. During the processing of accurate cues, the sum of sensory weight could be transiently larger than one (Assländer and Peterka, 2016). The slow adjustment of the ankle proprioception weight likely led to an improper corrective ankle torque and therefore a larger center of mass acceleration, which was confirmed by the larger peak force following Achilles tendon vibration offset. Despite the difference between the center of mass acceleration (i.e., RMS value of the scalar distance between the COP and COG) between both single sensory conditions, the similar stabilization time suggests that immediately after Achilles tendon vibration, the balance motor commands were effective in reducing the center of mass acceleration.

Comparison of the single versus mix sensory conditions

In humans, when the vestibular and proprioceptive systems are simultaneously probed, the amplitude of body sway corresponds to the sum of body sway evoked by the stimulation of the two systems alone (Hlavačka, et al., 1995), and multiple muscle co-vibration does not represent a linear summation of the combined effects (Roll, et al., 1989). Moreover, neuroimaging studies have found vestibular projections in the primary and secondary somatosensory cortices (Bottini, et al., 1994; Fasold, et al., 2002) and the primary motor cortex and premotor cortex (Bense, et al., 2001; Emri, et al., 2003; Fasold, et al., 2002). Psychophysical studies have revealed that vestibular stimulation facilitates the detection of cutaneous stimuli, suggesting a vestibular-somatosensory perceptual interaction (Ferre, et al., 2011). Thus, there is growing evidence for a functional crossmodal perceptual interaction between vestibular stimulation and the processing of somatosensory inputs. Altering ankle proprioception before stimulating the vestibular system could enhance the sensorimotor mechanisms.

Under the mix sensory conditions, the increase in stabilization time suggests that the sensorimotor mechanisms did not benefit from successive stimulation of different sensory systems. The results of the center of mass acceleration (i.e., RMS value of the COP-COM scalar distance) mitigate the latest affirmation. Nonetheless, it is important to distinguish the RMS value of the COP-COM scalar distance from the stabilization time. The RMS

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value of the COP-COG scalar distance was calculated over a time window and provided information about the amplitude of the center of mass acceleration. The stabilization time represents a discrete event and provides about the time needed to recover a baseline-like balance control performance. Balance destabilization (i.e., peak force) was a good predictor of the RMS value of the COP-COG scalar distance (variance explained > 80%), while it was not a good predictor of the stabilization time (range of variance explained: 16%–51%). These results suggest that these parameters convey different information about the performance of the sensorimotor control mechanisms.

A limitation of the mix sensory conditions was the delay between sensory stimulations. Previous studies have assessed how ankle proprioception and vestibular information interact with each other when altered simultaneously (e.g., Hlavačka, et al., 1995; Inglis et al., 1995). The direction and amplitude of body sway during ankle proprioception alterations are influenced by simultaneous changes in the vestibular input. In our study, the aim was to verify whether successive stimulation of two sensory systems involved in balance control could be beneficial for the sensorimotor mechanisms. We added a delay of 5 s between sensory stimulations to avoid a transient effect of the previous stimulation on the following stimulation. Furthermore, the delay needed to be short enough to assure that sensorimotor information was shared over time. Neural responses are improved when different sensory cues are temporally and spatially congruent (Fetsch et al., 2013; Meredith and Stein, 1983; Meredith and Stein, 1986). EVS and Achilles tendon vibration evoked body sways in the same direction. However, it seems that the short delay between sensory stimulation prevented a balance control improvement.

CONCLUSION

Understanding how the brain combines sensory information to quickly adapt its motor commands to sudden changes in sensory states represents a challenge. In the present study, when ankle proprioception returned to normal, the peak of ground reaction force was larger, leading to a faster body sway (i.e., a larger RMS value of the COP-COG scalar distance). However, even though balance control mainly relies on ankle

proprioception (Lord, et al., 1991; Peterka and Benolken, 1995; Simoneau, et al., 1992; Simoneau, et al., 1995), balance control performance did not differ during alterations of ankle proprioception and vestibular information. Moreover, successive alterations of different sensory systems (i.e., mix sensory condition) worsen balance control performance as the time needed to recover balance is longer compared to that under the single sensory condition. The amplitude of the center of mass acceleration and the time required to regain balance control seem to convey complementary information about the performance of the sensorimotor control mechanisms.

ACKNOWLEDGEMENTS

AUTHOR CONTRIBUTIONS

JPC, NA and MS: conception and design of research; JPC and NA: performed the experiments; JPC, NA and MS: analyzed data; JPC and MS: prepared the figures; JPC and MS: drafted the manuscript; all the authors edited, revised and approved the final version of the manuscript.

REFERENCES

Adamcova N, Hlavacka F (2007) Modification of human postural responses to soleus muscle vibration by rotation of visual scene. Gait Posture 25:99-105.

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

Bense S, Stephan T, Yousry TA, Brandt T, Dieterich M (2001) Multisensory cortical signal increases and decreases during vestibular galvanic stimulation (fMRI). J Neurophysiol 85:886-899.

Bottini G, Sterzi R, Paulesu E, Vallar G, Cappa SF, Erminio F, Passingham RE, Frith CD, et al. (1994) Identification of the central vestibular projections in man: a positron emission tomography activation study. Exp Brain Res 99:164-169.

Bronstein AM (1986) Suppression of visually evoked postural responses. Experimental Brain Res 63:655-658.

Bronstein AM, Hood JD (1986) The cervico-ocular reflex in normal subjects and patients with absent vestibular function. Brain Res 373:399-408.

Burke D, Hagbarth KE, Lofstedt L, Wallin BG (1976) The responses of human muscle spindle endings to vibration of non-contracting muscles. J Physiol 261:673-693.

Cathers I, Day BL, Fitzpatrick RC (2005) Otolith and canal reflexes in human standing. J Physiol 563:229-234.

Caudron S, Nougier V, Guerraz M (2010) Postural challenge and adaptation to vibration-induced disturbances. Exp Brain Res 202:935-941.

Cullen KE (2016) Physiology of central pathways. Handb Clin Neurol 137:17-40.

Day BL, Marsden JF, Ramsay E, Mian OS, Fitzpatrick RC (2010) Non-linear vector summation of left and right vestibular signals for human balance. J Physiol 588:671-682.

Diener HC, Dichgans J, Guschlbauer B, Mau H (1984) The significance of proprioception on postural stabilization as assessed by ischemia. Brain Res 296:103-109.

Eklund G (1972) General features of vibration-induced effects on balance. Ups J Med Sci 77:112-124.

Emri M, Kisely M, Lengyel Z, Balkay L, Marian T, Miko L, Berenyi E, Sziklai I, et al. (2003) Cortical projection of peripheral vestibular signaling. J Neurophysiol 89:2639-2646.

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

Fasold O, von Brevern M, Kuhberg M, Ploner CJ, Villringer A, Lempert T, Wenzel R (2002) Human vestibular cortex as identified with caloric stimulation in functional magnetic resonance imaging. Neuroimage 17:1384-1393.

Ferre ER, Bottini G, Haggard P (2011) Vestibular modulation of somatosensory perception. Eur J Neurosci 34:1337-1344.

Ferre ER, Day BL, Bottini G, Haggard P (2013) How the vestibular system interacts with somatosensory perception: a sham-controlled study with galvanic vestibular stimulation. Neurosci Lett 550:35-40.

Fetsch CR, DeAngelis GC, Angelaki DE (2013) Bridging the gap between theories of sensory cue integration and the physiology of multisensory neurons. Nat Rev Neurosci 14:429-442.

Fitzpatrick RC, Day BL (2004) Probing the human vestibular system with galvanic stimulation. J Appl Physiol 96:2301-2316.

Fransson PA, Gomez S, Patel M, Johansson L (2007) Changes in multi-segmented body movements and EMG activity while standing on firm and foam support surfaces. Eur J Appl Physiol 101:81-89.

Golanov EV, Christensen JR, Reis DJ (2001) Neurons of a limited subthalamic area mediate elevations in cortical cerebral blood flow evoked by hypoxia and excitation of neurons of the rostral ventrolateral medulla. J Neurosci 21:4032-4041.

Goldberg JM, Smith CE, Fernandez C (1984) Relation between discharge regularity and responses to externally applied galvanic currents in vestibular nerve afferents of the squirrel monkey. J Neurophysiol 51:1236-1256.

Grasso R, Ivanenko YP, McIntyre J, Viaud-Delmon I, Berthoz A (2000) Spatial, not temporal cues drive predictive orienting movements during navigation: a virtual reality study. Neuroreport 11:775-778.

Guerraz M, Day BL (2005) Expectation and the vestibular control of balance. J Cogn Neurosci 17:463-469.

Hlavačka F, Križková M, Horak FB (1995) Modification of human postural response to leg muscle vibration by electrical vestibular stimulation. Neurosci Lett 189:9-12.

Holmberg J, Karlberg M, Fransson PA, Magnusson M (2003) Phobic postural vertigo: body sway during vibratory proprioceptive stimulation. Neuroreport 14:1007-1011.

Horak FB, Dickstein R, Peterka RJ (2002) Diabetic neuropathy and surface sway-referencing disrupt somatosensory information for postural stability in stance. Somatosens Mot Res 19:316-326.

Inglis JT, Shupert CL, Hlavacka F, Horak FB (1995) Effect of galvanic vestibular stimulation on human postural responses during support surface translations. J Neurophysiol 73:896-901.

Ivanenko YP, Talis VL, Kazennikov OV (1999) Support stability influences postural responses to muscle vibration in humans. Eur J Neurosci 11:647-654.

Kavounoudias A, Gilhodes JC, Roll R, Roll JP (1999) From balance regulation to body orientation: two goals for muscle proprioceptive information processing? Exp Brain Res 124:80-88.

Kim J, Curthoys IS (2004) Responses of primary vestibular neurons to galvanic vestibular stimulation (GVS) in the anaesthetised guinea pig. Brain Res Bull 64:265-271.

King DL, Zatsiorsky VM (1997) Extracting gravity line displacement from stabilographic recordings. Gait Posture 6:27-38.

Lackner JR, DiZio PA (2000) Aspects of body self-calibration. Trends Cogn Sci 4:279-288.

Lord SR, Clark RD, Webster IW (1991) Postural stability and associated physiological factors in a population of aged persons. J Gerontol 46:M69-76.

Lund S, Broberg C (1983) Effects of different head positions on postural sway in man induced by a reproducible vestibular error signal. Acta Physiol Scand 117:307-309.

Magnusson M, Enbom H, Johansson R, Wiklund J (1990) Significance of pressor input from the human feet in lateral postural control. The effect of hypothermia on galvanically induced body-sway. Acta Otolaryngol 110:321-327.

Masani K, Vette AH, Kouzaki M, Kanehisa H, Fukunaga T, Popovic MR (2007) Larger center of pressure minus center of gravity in the elderly induces larger body acceleration during quiet standing. Neurosci Lett 422:202-206.

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

Meredith MA, Stein BE (1983) Interactions among converging sensory inputs in the superior colliculus. Science 221:389-391.

Meredith MA, Stein BE (1986) Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. J Neurophysiol 56:640-662.

Mian OS, Dakin CJ, Blouin JS, Fitzpatrick RC, Day BL (2010) Lack of otolith involvement in balance responses evoked by mastoid electrical stimulation. J Physiol 588:4441-4451.

Nashner LM (1976) Adapting reflexes controlling the human posture. Exp Brain Res 26:59-72.

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.

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

Peterka RJ, Benolken MS (1995) Role of somatosensory and vestibular cues in attenuating visually induced human postural sway. Exp Brain Res 105:101-110.

Popov KE, Kozhina GV, Smetanin BN, Shlikov VY (1999) Postural responses to combined vestibular and hip proprioceptive stimulation in man. Eur J Neurosci 11:3307-3311.

Proske U, Gandevia SC (2012) The proprioceptive senses: their roles in signaling body shape, body position and movement, and muscle force. Physiol Rev 92:1651-1697.

Roll JP, Vedel JP (1982) Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. Exp Brain Res 47:177-190.

Roll JP, Vedel JP, Ribot E (1989) Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. Exp Brain Res 76:213-222.

Simoneau GG, Leibowitz HW, Ulbrecht JS, Tyrrell RA, Cavanagh PR (1992) The effects of visual factors and head orientation on postural steadiness in women 55 to 70 years of age. J Gerontol 47:M151-158.

Simoneau GG, Ulbrecht JS, Derr JA, Cavanagh PR (1995) Role of somatosensory input in the control of human posture. Gait Posture 3:115-122.

Simoneau M, Mercier P, Blouin J, Allard P, Teasdale N (2006) Altered sensory-weighting mechanisms is observed in adolescents with idiopathic scoliosis. BMC Neurosci 7:68.

Stelmach GE, Teasdale N, Di Fabio RP, Phillips J (1989) Age related decline in postural control mechanisms. Int J Aging Hum Dev 29:205-223.

Taube W, Schubert M, Gruber M, Beck S, Faist M, Gollhofer A (2006) Direct corticospinal pathways contribute to neuromuscular control of perturbed stance. J Appl Physiol 101:420-429.

Teasdale N, Simoneau M (2001) Attentional demands for postural control: the effects of aging and sensory reintegration. Gait Posture 14:203-210.

Tjernstrom F, Fransson PA, Hafstrom A, Magnusson M (2002) Adaptation of postural control to perturbations--a process that initiates long-term motor memory. Gait Posture 15:75-82.

Tokuno CD, Taube W, Cresswell AG (2009) An enhanced level of motor cortical excitability during the control of human standing. Acta Physiol 195:385-395.

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.

Winter DA (1995) Human balance and posture control during standing and walking. Gait Posture 3:193-214.

Zatsiorsky VM, King DL (1998) An algorithm for determining gravity line location from posturographic recordings. J Biomech 31:161-164.