

CHANGE IN THE NATURAL HEAD-NECK ORIENTATION MOMENTARILY
ALTERED SENSORIMOTOR CONTROL DURING SENSORY TRANSITION

Isabelle Xu¹

Simon Laurendeau^{2,3}

Normand Teasdale^{2,3}

Martin Simoneau^{2,3}

¹Faculté de médecine, Université Laval

²Faculté de médecine, Département de kinésiologie, Université Laval

³Centre de recherche du CHU de Québec, Québec, Québec, Canada

*Corresponding author:

Martin Simoneau
Faculté de médecine, Département de kinésiologie
Université Laval
2300, rue de la Terrasse
Quebec, Qc, Canada G1V 0A6
Telephone: 1-418-656-2131 ext. 7788
Email: martin.simoneau@kin.ulaval.ca

ABSTRACT

Achilles tendon vibration generates proprioceptive information that is incongruent with the actual body position; it alters the perception of body orientation leading to a vibration-induced postural response. When a person is standing freely, vibration of the Achilles tendon shifts the internal representation of the verticality backward thus the vibration-induced postural response realigned the whole body orientation with the shifted subjective vertical. Because utricular otoliths information participates in the creation of the internal representation of the verticality, changing the natural orientation of the head-neck system during Achilles tendon vibration could alter the internal representation of the earth vertical to a greater extent. Consequently, it was hypothesized that compared to neutral head-neck orientation, alteration in the head-neck orientation should impair balance control immediately after Achilles tendon vibration onset or offset (i.e., sensory transition) as accurate perception of the earth vertical is required. Results revealed that balance control impairment was observed only immediately following Achilles tendon vibration offset; both groups with the head-neck either extended or flexed showed larger body sway (i.e., larger root mean square scalar distance between the center of pressure and center of gravity) compared to the group with the neutral head-neck orientation. The fact that balance control was uninfluenced by head-neck orientation immediately following vibration onset suggests the error signal needs to accumulate to a certain threshold before the internal representation of the earth vertical becomes incorrect.

INTRODUCTION

Human upright standing is inherently unstable. Small changes in body orientation with respect to gravitational acceleration produce a destabilizing torque that tends to accelerate the body away from the earth vertical. To detect small deviations from an upright body position, multimodal integration of vestibular, visual and somatosensory information is required [1-3]. Thereafter, corrective torques are produced to reduce body deviation with respect to vertical [4]. As a result, misinterpreting the direction of the gravitational acceleration because of an incorrect reference orientation can lead to perceptual errors that threaten balance control. To ascertain proper balance control, accurate perception of the earth vertical is crucial. It is likely that stimulation of one of the sensory systems (i.e., visual, proprioceptive or vestibular) or impairment in one of these sensory systems could alter the internal representation of the earth vertical [5-7]. Barbieri et al. [8] demonstrated that Achilles tendon vibration alters the postural perception of vertical; it tilts the subjective vertical backward. Mechanical vibration to muscles or tendons generates proprioceptive information that is incongruent with the actual body position. Therefore, while standing upright, ankle tendon vibration leads to body sways known as vibration-induced postural response [9]. The direction of the vibration-induced postural sway depends upon the vibration side [9]. This has been observed with the vibration of several muscles along the body axis [10-14]. For instance, when vibration is applied to the Achilles tendon, muscle spindles of the gastrocnemius and soleus muscles respond as if stretched, that is, as if the individual was leaning forward. To compensate for this illusion, the individual sways backward. In contrast, vibration applied to the tibialis anterior muscles causes forward sway. It has been

suggested that this vibration-induced postural response aligns the whole body with the backward or forward tilted of the subjective vertical [8].

Among the sensory signals allowing to build an internal representation of the earth vertical, the vestibular system, through utricular otoliths, provides information about head alignment with respect to gravity. Extension of the head-neck system alters the optimal working range of the utricular otoliths [15]. Thus, during Achilles tendon vibration, altering the orientation of the head-neck system should reduce the accuracy of the internal representation of the vertical and perception of body sways. It is acknowledged that standing upright in absence of vision with the head-neck extended alters balance control more than with the head-neck flexed [16, 17]. The reduced effect of head-neck flexion on balance control could entail that in this posture, the subjective perception of body sway is less influenced compared to head-neck extension. It is unknown, however, whether changing the orientation of the head-neck during Achilles tendon vibration reduces the accuracy of the internal representation of the earth vertical to a greater extent compared to neutral head-neck orientation. When Achilles tendon vibration starts or stops, the sudden change in sensory signals (i.e., sensory transition) requires sensory reweighting to adjust the weight of each sensory signal, and produce corresponding balance motor commands (i.e., corrective torque) to reduce body sway [18-20]. During sensory transition, it is likely that the sensory reweighting mechanisms need an accurate perception of body sways with respect to earth vertical to assign proper weight to vestibular, visual and somatosensory information [21].

The aim of the present study was to assess if modifying the orientation of the head-neck alters balance control during a sensory transition. It is suggested that altering the

head-neck orientation should create uncertainty about the alignment of the head-centric and the body-centric coordinate systems resulting in a less accurate internal representation of the earth vertical and perceived body sways. Because sensory transition requires rapid sensory reweighting, it is hypothesized that misinterpretation of the earth vertical during this period, thus suboptimal subjective perception of body sway, should lead to larger body sway immediately following vibration onset or offset. To assess balance control, we calculated the root mean square (RMS) value of the scalar distance between the center of pressure (*COP*) and the center of gravity (*COG*); it has been suggested that this parameter is sensitive to changes in the control system [22]. When the head-neck orientation is flexed or extended compared to the normal head orientation, a larger RMS value of the scalar distance between the *COG* and the *COP* immediately following the onset or the offset of Achilles tendon vibration, would confirm that inaccurate internal representation of the earth vertical during a sensory transition alters the sensorimotor control mechanisms leading to larger body sway.

METHODS

Participants

Thirty-five young adults, who were unaware of the hypothesis, were recruited. Participants reported no history of neurological diseases, vestibular disorders or signs or symptoms of cervical spine diseases. They all gave their informed consent according to the institutional review board. Participants were randomly assigned to one of three groups: head flexion (n=12: 7 females, mean (\pm SD) height = 1.68 ± 0.07 m, mean weight = 62.9 ± 5.6 kg, mean age = 23.8 ± 9.3 years), head extension (n=11: 8 females, mean height = 1.70 ± 0.07 m, mean weight = 74.1 ± 11.4 kg, mean age = 21.6 ± 4.0 years), and head normal (n=12: 6 females, mean height = 1.75 ± 0.10 m, mean weight = $67.8.0\pm 10.9$ kg, mean age = 21.5 ± 3.5 years). The vibration-evoked postural response decreases drastically within 1-2 trials [23]. When using a within-subject design, the results of each condition are influenced by the other conditions that were presented previously [24, 25]. This effect of sequence has been observed in the study of Barbieri et al. [8]. Therefore, different participants were involved in each group to avoid an effect of sequence. Head orientation was monitored using an inertial unit sensor, fixed on a headband (model MTx, Xsens Technologies, Enschede, Netherlands). This procedure ascertained proper head orientation before the beginning of each trial. Participants in the head extension group had to keep their head extended backward by 30° and the participants in the head flexion group had to keep their head flexed forward by 30° . For the normal group, participants kept their head in a neutral orientation. Throughout the duration of each trial, participants kept their eyes closed but they opened them between trials.

Procedure

Participants stood barefoot on the force platform with their feet 15 cm apart and arms along the body. They performed 24 trials and each trial lasted 45 seconds. Trials were divided into three intervals: Pre-vibration (0 - 5.02 s), Vibration (5.03 - 34.81 s), and Post-vibration (34.82 - 45 s). Because a change in head orientation could cause neck muscle tension, a 2-min rest period was allowed every eight trials or whenever the participant expressed a desire to rest. In addition, a head support (i.e., a modified rigid collar) was used to minimize neck muscle fatigue for the head extension group only. Participants were instructed to close their eyes before the trial onset and to adopt a relaxed standing posture.

During the Vibration interval, Achilles tendons were vibrated to evoke a vibration-induced postural response. The vibrators ($n=2$) consisted of unbalanced masses fixed at both extremities of DC motors rotating at 70 Hz; each motor was inserted into a plastic cylinder and the amplitude of the mechanical oscillation was ~ 1 mm. The vibrators were fixed on the Achilles tendons by means of rubber bands. Applying vibration to a muscle tendon specifically activates the muscle spindle primary endings [26, 27]. The activation and the deactivation of the vibrators were computer controlled. None of the participants had experienced tendon vibration before.

Data acquisition and processing

An AMTI (model OR6-5) force platform was used to assess balance control. The force platform signals were amplified (AMTI, model MSA-6) prior to being sampled at 100 Hz using a 16-bit A/D converter (Measurement Computing Corporation, DAS-6402).

The *COP* displacements along the medio-lateral (ML) and anterior-posterior (AP) axes were calculated from the reaction forces and moments of the platform. An electromagnetic sensor (TrakStar model, Ascension Technology, Milton, VT, USA) was attached at the sacrum (height of the superior iliac crest) to estimate the kinematics of the center of mass (*COM*). Another electromagnetic sensor was fixed to the headband worn by the participants. Data were analyzed using Matlab 2014b (Mathworks, Natick, MA, USA). All data were filtered using a zero-lag 4th order low-pass Butterworth filter (cut-off frequency 6 Hz). Although *COP* data along the ML and AP axes were computed, only those along the AP direction were analyzed because vibratory stimulation of the Achilles tendon induces body sway mostly along this axis [28].

For the extension and flexion groups, to verify the head-neck orientation for each trial, we calculated the orientation of the vector between the sensor located on sacrum and the sensor located on the head. The vector was divided by its norm to get a unit vector pointing in the same direction as the vector between the sacrum and the head. The angle of the unit vector with respect to the anteroposterior axis (i.e., x-axis) was determined by calculating the inverse cosines of the x component of the unit vector. Then, we calculated the range of the angle of the vector. If the range was within $\pm 5^\circ$, we considered that that participant kept his head-neck orientation. On average, the range of the angle of the vector was 4.23 (SEM = 0.55) and 3.11 (SEM = 0.36) for the Extension and the Flexion groups, respectively. For the normal group, the orientation of the Frankfort plane was assessed visually during each trial.

The position of the center of gravity (*COG*) along the AP axis was estimated throughout each trial using a zero-point-to-zero-point double integration technique, also known as the gravity line projection technique [29, 30]. The underlying assumption of this method is that the *COP* coincides with the vertical line passing through the *COM* (*COG* is the vertical projection of the *COM*) when the horizontal ground reaction force is zero.

Modeling upright balance control as an inverted pendulum reveals that the horizontal acceleration of the *COM* is proportional to the scalar distance between the *COP* and the *COG* position [31]:

$$COP - COG = \frac{-J}{mgh} \times \ddot{x}COM_{estimated} \quad (Eq. 1)$$

To determine the scalar distance between the *COP* and *COG* position, we estimated the height of the *COM* ($h = 0.547 \times H$, where H is the participant's height), the mass without the mass of the feet ($m = 0.971 \times M$, where M is the participant's mass), and the moment of inertia around the ankle joint ($J = 0.319 \times M \times H^2$) according to Winter [32]. Before the Achilles tendon vibration onset, the scalar distance between the *COP* and *COG* position was close to zero (Fig. 1, right panel). Immediately following vibration onset and offset (i.e., ~2.5-s windows), however, the scalar distance increased suggesting that altering ankle proprioception momentarily impaired balance control.

Because ankle tendon vibration induces larger body sway than during normal upright standing, the assumption that participants swayed as an inverted pendulum first needed to be verified. Using the equation describing the inverted pendulum model (Eq. 1), the

horizontal acceleration of the *COM* (i.e., $\ddot{x}COM_{estimated}$) was estimated. In addition, the experimental horizontal acceleration of the center of gravity ($\ddot{x}COG_{experimental}$) was calculated using the time series of the horizontal anterior-posterior ground reaction force (F_y) recorded with the force platform and the mass of the participant (m):

$$\ddot{x}COG_{experimental} = \frac{F_y}{m} \text{ (Eq. 2)}$$

Then, we determined if the RMS value of the estimated horizontal acceleration of the center of mass ($\ddot{x}COM_{estimated}$) was correlated with the RMS value of the experimental horizontal acceleration of the center of gravity ($\ddot{x}COG_{experimental}$). A linear regression analysis was performed between the RMS value of $\ddot{x}COM_{estimated}$ and the RMS value of $\ddot{x}COG_{experimental}$. Results of the Pearson's correlation revealed that participants swayed as an inverted pendulum; the coefficient of determinations for the normal, head extension and head flexion groups were 0.85, 0.95 and 0.98, respectively. These values are consistent with those observed in previous studies [22, 33].

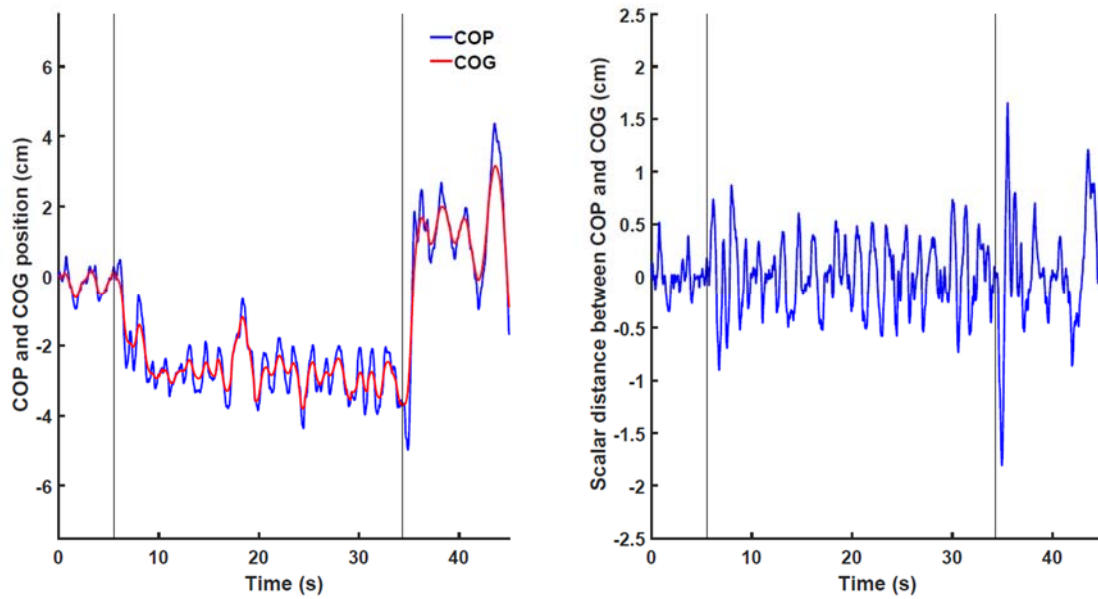


Figure 1: Left panel: Representative time series of the center of pressure (COP, blue line) and the center of gravity (COG, red line) displacement along the anterior-posterior axis. Data are from one typical trial of a participant from the Extension group. Negative displacements of the COP and COG indicate backward movements. Right panel: Representative time series of the scalar distance between the center of pressure and center of gravity displacements along the anterior-posterior axis. On each panel, the vertical black lines indicate Achilles tendon vibration onset and offset, respectively.

Although it is likely that the brain performs sensorimotor control continuously, intense sensorimotor control must occur when a sensory transition is presented, that is, immediately following the onset and the offset of ankle vibration. As well, it is known that a drastic decrease in the amplitude of the vibration-induced postural response is observed within the first three trials [e.g., 23, 34]. To assess the performance of the sensorimotor control mechanisms during sensory transition (i.e., following a sudden change in sensory condition), we computed the RMS value of the scalar distance (*COP-COG*) for 2.5-s windows immediately following the Achilles tendon vibration onset and offset for the first three trials (sensorimotor integration epoch). This time window was

chosen because the peak of the *COG* acceleration occurred within this period (see Fig. 1) and the time course of sway variability for sensory transition is approximately 2 s [35, 36]. Data for the mean of the first three trials of the RMS value of the scalar distance (*COP-COG*) for the three groups were submitted to a Group by Sensory transition epoch (2.5-s window after vibration onset and offset) ANOVA. A group difference in the RMS value of the scalar distance (*COP-COG*) immediately following vibration onset and offset would indicate that changing the orientation of the head-neck system impairs sensorimotor control. If necessary, planned comparisons were performed to decompose the interaction. Furthermore, because following the first three trials, change in the natural orientation of the head-neck could be short-lived, we compared the RMS value of the scalar distance (*COP-COG*) (2.5 s immediately following vibration offset) for all trials following vibration offset (Post-vibration interval). If a group difference is present even after 24 trials, it would indicate that the sensorimotor control impairment is long lasting. To check for this possibility, a one-way ANOVA compared group means.

RESULTS

The analysis of the RMS value of the scalar distance (*COP-COG*) for the 2.5-s windows for the first three trials immediately following Achilles tendon vibration onset and offset indicated that the extension and flexion groups showed a greater RMS value of the scalar distance (*COP-COG*) compared to the normal group [Fig. 2 – left panel; interaction of Group by Interval: $F(2,32) = 21.28, p < 0.001$]. Post-hoc analyses revealed that the RMS value of the scalar distance (*COP-COG*) immediately following Achilles tendon vibration onset (Vibration) was similar across groups ($p > 0.05$). However, immediately after the Achilles tendon vibration offset (Post-vibration), the extension and

flexion groups exhibited a large RMS value of the scalar distance (*COP-COG*). The increases in the RMS value of the scalar distance (*COP-COG*) were significant ($p < 0.001$). To assess whether these group differences persisted beyond the first three trials, the group means (all trials) for the RMS value of the scalar distance (*COP-COG*) immediately after Achilles tendon vibration offset were compared (Fig. 2 – right panel). The ANOVA demonstrated that altering the head-neck orientation influenced sensorimotor control even across trials [main effect of Group: $F(2,32) = 8.57, p < 0.01$]. A post-hoc analysis revealed no difference between the extension and flexion groups ($p > 0.05$) and a difference between Normal and Flexion groups ($p < 0.01$) and Normal and Extension groups ($p < 0.001$).

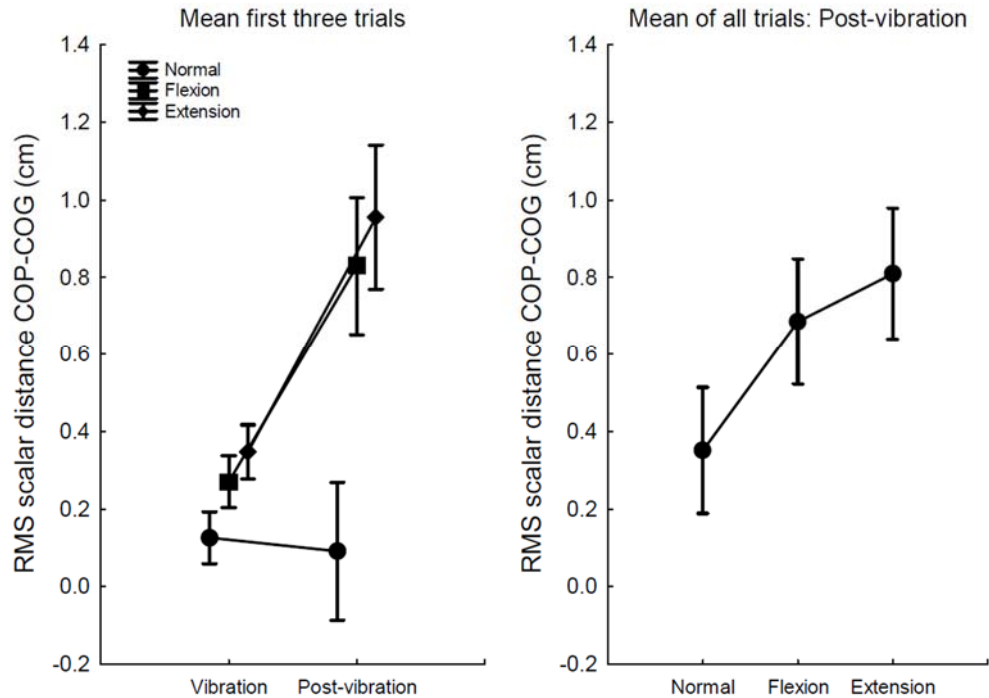


Figure 2: Left panel) Group means of the first three trials for the root mean square (RMS) value of the scalar distance between the center of pressure (COP) and the center of gravity (COG) for 2.5 s immediately following Achilles tendon vibration onset (Vibration) and immediately following vibration offset (Post-vibration). Right panel) Group means (i.e., mean of all trials) of the root mean square (RMS) value of the scalar distance between the center of pressure (COP) and center of gravity (COG) for 2.5 s immediately following Achilles tendon vibration offset for the three groups.

DISCUSSION

The aim of this study was to assess if changes in head-neck orientation would influence the balance control during sudden change in the sensory condition (i.e., sensory transition). It is acknowledged that proper balance control requires accurate perception of body sways. Because altering the orientation of the head-neck, during Achilles tendon vibration, could influence the internal representation of the earth vertical and the subjective perception of body sways, it was hypothesized that immediately following

Achilles tendon vibration onset or offset, impaired balance control should be observed. During these sensory transition epochs, altering the natural alignment of the head-neck orientation could add uncertainty about the alignment of the head-centric and the body-centric reference frame and hinder the sensorimotor control processes allowing proper balance control.

Ankle proprioception senses the orientation of the legs with respect to the support surface while cutaneous receptors in the sole of the foot respond to motion of the *COP* (and thus to changes in the ground reaction force) as the body sways [37, 38]. In contrast, the vestibular and visual systems provide information about head kinematics with respect to the earth-vertical and the visual world, respectively. These signals, from different reference frames, are integrated and contribute for creating an internal representation of the earth vertical and for perceiving body sways which are used by the sensorimotor control mechanisms to control balance [39]. Consequently, uncertainty in the internal representation of the earth vertical and subjective perception of body sway would likely lead to balance control impairments. Our results reveal that only immediately following the vibration offset, the change in the alignment of the vestibular and proprioceptive reference frames altered sensorimotor control; the RMS value of the scalar distance (*COP-COG*) was greater for the head-neck extension and flexion groups compared to the normal group (i.e., head in natural orientation). This group difference was present during the first trials (i.e., mean of the first three trials) and it sustained across trials (mean of all trials). Results from several studies have reported an asymmetry in the body sway response dynamics following sensory transition [19, 40]. For instance, transition to sensory conditions presenting a greater challenge to balance control showed faster

changes in body sway responses compared with transitions to less challenging conditions. It is possible that balance control was uninfluenced by head-neck orientation immediately following vibration onset because the amount of error in the internal representation of the earth vertical was not large enough. In contrast, immediately following vibration offset (i.e., following ~35-s of Achilles tendon vibration with the head-neck either extended or flexed), the accumulation of error in the internal representation of the earth vertical was likely large enough to alter the sensorimotor control processes. Another possibility to explain this difference would be that adding sensory information (i.e., transition from vibration to post-vibration intervals) requires to reweigh the sensory information based on the reliability of each reference frame. This process would take longer time compared to when one sensory information is removed [41]. Because of sensory redundancy, removing sensory information would alter less the sensorimotor processes.

In conclusion, during sudden change in sensory information, change in head-neck orientation likely cause unreliable internal representation of the earth vertical and less accurate subjective perception of body sways resulting in suboptimal balance control.

ACKNOWLEDGEMENT

This research was supported by grants from the NSERC Discovery program to M.S. and N.T.

AUTHOR CONTRIBUTIONS

I.X., N.T. and M.S., conception and design of research; I.X. and S.L. performed experiments; I.X. and M.S. analyzed data; I.X., and M.S.; prepared figures; I.X., N.T. and

M.S. drafted manuscript; all authors edited, revised and approved final version of the manuscript.

REFERENCES

- [1] Bronstein AM. The interaction of otolith and proprioceptive information in the perception of verticality. The effects of labyrinthine and CNS disease. *Ann N Y Acad Sci* 1999;871:324-33.
- [2] Anastasopoulos D, Bronstein A, Haslwanter T, Fetter M, Dichgans J. The role of somatosensory input for the perception of verticality. *Ann N Y Acad Sci* 1999;871:379-83.
- [3] Borel L, Harlay F, Magnan J, Lacour M. How changes in vestibular and visual reference frames combine to modify body orientation in space. *Neuroreport* 2001;12:3137-41.
- [4] Peterka RJ. Sensorimotor integration in human postural control. *J Neurophysiol* 2002;88:1097-118.
- [5] Lopez C, Lacour M, Ahmadi AE, Magnan J, Borel L. Changes of visual vertical perception: a long-term sign of unilateral and bilateral vestibular loss. *Neuropsychologia* 2007;45:2025-37.
- [6] Bronstein AM, Perennou DA, Guerraz M, Playford D, Rudge P. Dissociation of visual and haptic vertical in two patients with vestibular nuclear lesions. *Neurology* 2003;61:1260-2.
- [7] Mars F, Popov K, Vercher JL. Supramodal effects of galvanic vestibular stimulation on the subjective vertical. *Neuroreport* 2001;12:2991-4.

- [8] Barbieri G, Gissot AS, Fouque F, Casillas JM, Pozzo T, Perennou D. Does proprioception contribute to the sense of verticality? *Exp Brain Res* 2008;185:545-52.
- [9] Eklund G. General features of vibration-induced effects on balance. *Ups J Med Sci* 1972;77:112-24.
- [10] Bove M, Courtine G, Schieppati M. Neck muscle vibration and spatial orientation during stepping in place in humans. *J Neurophysiol* 2002;88:2232-41.
- [11] Bove M, Nardone A, Schieppati M. Effects of leg muscle tendon vibration on group Ia and group II reflex responses to stance perturbation in humans. *J Physiol* 2003;550:617-30.
- [12] Thompson C, Belanger M, Fung J. Effects of bilateral Achilles tendon vibration on postural orientation and balance during standing. *Clin Neurophysiol* 2007;118:2456-67.
- [13] Roll JP, Vedel JP, Ribot E. Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. *Exp Brain Res* 1989;76:213-22.
- [14] Roll JP, Vedel JP, Roll R. Eye, head and skeletal muscle spindle feedback in the elaboration of body references. *Prog Brain Res* 1989;80:113-23; discussion 57-60.
- [15] Brandt T, Krafczyk S, Malsbenden I. Postural imbalance with head extension: improvement by training as a model for ataxia therapy. *Ann N Y Acad Sci* 1981;374:636-49.
- [16] Johnson MB, Van Emmerik RE. Effect of head orientation on postural control during upright stance and forward lean. *Motor Control* 2012;16:81-93.

- [17] Paloski WH, Wood SJ, Feiveson AH, Black FO, Hwang EY, Reschke MF. Destabilization of human balance control by static and dynamic head tilts. *Gait Posture* 2006;23:315-23.
- [18] Asslander L, Peterka RJ. Sensory reweighting dynamics following removal and addition of visual and proprioceptive cues. *J Neurophysiol* 2016;116:272-85.
- [19] Asslander L, Peterka RJ. Sensory reweighting dynamics in human postural control. *J Neurophysiol* 2014;111:1852-64.
- [20] Oie KS, Kiemel T, Jeka JJ. Multisensory fusion: simultaneous re-weighting of vision and touch for the control of human posture. *Brain Res Cogn Brain Res* 2002;14:164-76.
- [21] Peterka RJ, Loughlin PJ. Dynamic regulation of sensorimotor integration in human postural control. *J Neurophysiol* 2004;91:410-23.
- [22] Masani K, Vette AH, Kouzaki M, Kanehisa H, Fukunaga T, Popovic MR. Larger center of pressure minus center of gravity in the elderly induces larger body acceleration during quiet standing. *Neurosci Lett* 2007;422:202-6.
- [23] Caudron S, Langlois L, Nougier V, Guerraz M. Attenuation of the evoked responses with repeated exposure to proprioceptive disturbances is muscle specific. *Gait Posture* 2010;32:161-8.
- [24] Poulton EC, Freeman PR. Unwanted asymmetrical transfer effects with balanced experimental designs. *Psychol Bull* 1966;66:1-8.
- [25] Poulton EC, Edwards RS. Asymmetric transfer in within-subjects experiments on stress interactions. *Ergonomics* 1979;22:945-61.

- [26] Burke D, Hagbarth KE, Lofstedt L, Wallin BG. The responses of human muscle spindle endings to vibration during isometric contraction. *J Physiol* 1976;261:695-711.
- [27] Roll JP, Vedel JP. Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. *Exp Brain Res* 1982;47:177-90.
- [28] Polonyova A, Hlavacka F. Human postural responses to different frequency vibrations of lower leg muscles. *Physiol Res* 2001;50:405-10.
- [29] King DL, Zatsiorsky VM. Extracting gravity line displacement from stabilographic recordings. *Gait Posture* 1997;6:27-38.
- [30] Zatsiorsky VM, King DL. An algorithm for determining gravity line location from posturographic recordings. *J Biomech* 1998;31:161-4.
- [31] Winter DA, Patla AE, Prince F, Ishac M, Gielo-Perczak K. Stiffness control of balance in quiet standing. *J Neurophysiol* 1998;80:1211-21.
- [32] Winter DA. *Biomechanics and motor control of human movement*: John Wiley & Sons, Inc.; 2005.
- [33] Gage WH, Winter DA, Frank JS, Adkin AL. Kinematic and kinetic validity of the inverted pendulum model in quiet standing. *Gait Posture* 2004;19:124-32.
- [34] Caudron S, Nougier V, Guerraz M. Postural challenge and adaptation to vibration-induced disturbances. *Exp Brain Res* 2010;202:935-41.
- [35] Honeine JL, Crisafulli O, Sozzi S, Schieppati M. Processing time of addition or withdrawal of single or combined balance-stabilizing haptic and visual information. *J Neurophysiol* 2015;114:3097-110.

- [36] Sozzi S, Do MC, Monti A, Schieppati M. Sensorimotor integration during stance: processing time of active or passive addition or withdrawal of visual or haptic information. *Neuroscience* 2012;212:59-76.
- [37] Morasso PG, Schieppati M. Can muscle stiffness alone stabilize upright standing? *J Neurophysiol* 1999;82:1622-6.
- [38] Kavounoudias A, Roll R, Roll JP. Foot sole and ankle muscle inputs contribute jointly to human erect posture regulation. *J Physiol* 2001;532:869-78.
- [39] Massion J. Postural control system. *Curr Opin Neurobiol* 1994;4:877-87.
- [40] Jeka JJ, Oie KS, Kiemel T. Asymmetric adaptation with functional advantage in human sensorimotor control. *Exp Brain Res* 2008;191:453-63.
- [41] Sozzi S, Monti A, De Nunzio AM, Do MC, Schieppati M. Sensori-motor integration during stance: time adaptation of control mechanisms on adding or removing vision. *Hum Mov Sci* 2011;30:172-89.