Title: The contribution of vestibular and proprioceptive signals to trunk stabilization varies between postural tasks and between walking speeds.

Yiyuan C. Li[1,2], Sjoerd M. Bruijn[1], Koen K. Lemaire[1], Simon Brumagne[2], Jaap H. van Dieën[1]

1.Department of Human Movement Sciences, Faculty of Behavioural and Movement Sciences, Vrije Universiteit Amsterdam, Amsterdam Movement Sciences, Amsterdam, The Netherlands

2. Department of Rehabilitation Sciences, KU Leuven, Leuven, Belgium

Correspondence:

Jaap H. van Dieën

Department of Human Movement Sciences, Faculty of Behavioral and Movement Sciences, Vrije Universiteit Amsterdam, van der Boechorststraat 9, NL-1081 BT Amsterdam, the Netherlands

Author E-mail address:

Yiyuan C. Li, y.li2@vu.nl, or liyiyuan0413@163.com, ORCID: 0000-0001-9470-6132

Sjoerd M. Bruijn, s.m.bruijn@vu.nl, ORCID: 0000-0003-0290-2131

Koen K. Lemaire, k.k.lemaire2@vu.nl

Simon Brumagne, simon.brumagne@kuleuven.be, ORCID : 0000-0002-0251-9338

Jaap H. van Dieën, j.van.dieen@vu.nl, ORCID: 0000-0002-7719-5585

Abstract

Stabilizing the upright posture of the trunk relies on vestibular and proprioceptive afference. Previous studies found that the feedback responses to sensory afference vary between postures and tasks. We investigated whether and how vestibular and proprioceptive afference contribute to trunk stabilization during different postural tasks, and during walking at different speeds. Twelve healthy adults performed tasks in a random order: sitting, standing on the right foot or both feet, and treadmill walking at five speeds: 0.8, 2.0, 3.2, 4.3 and 5.5 km/h, while exposed to unilateral muscle vibration on the right paraspinal muscles at the level of the second lumbar vertebra, or to a step-like electrical vestibular stimulation (EVS) with the anode behind the left ear. The mediolateral displacements of markers at the sixth thoracic level and sacrum in the global coordinate system were used to evaluate the responses to sensory stimulation. No significant responses to EVS at T6 and sacrum level were found in sitting and standing. Responses to muscle vibration were significant and differed between unipedal standing compared to sitting and bipedal standing. The latter suggests a different interpretation of the sensation of muscle lengthening in these postures. The magnitude of the responses to both stimuli increased from very slow speeds to moderate speeds. This may indicate that a different control strategy is adopted in walking at slow speeds compared to walking at faster speeds. From moderate to high speeds, the responses decreased, suggesting a decreased demand for feedback control at higher speeds.

Keywords: Trunk stabilization, Walking, Standing, Vestibular afference, Proprioception

Introduction

The trunk represents approximately 50% of the total body mass (de Leva, 1996). With its location high above the base of support, a small deviation from the upright position can produce a substantial destabilizing moment. Trunk muscles have an active role in maintaining the upright posture of the trunk and head (Hof, 2007; Wu *et al.*, 2019; Li *et al.*, 2024), which supports the use of visual and vestibular information for postural control.

Feedback information for the stabilization of upright posture against gravity is provided by different sensory modalities (Peterka, 2002; Peterka & Loughlin, 2004; Maurer *et al.*, 2006; Asslander & Peterka, 2014). For example, vestibular signals contribute to perception of the head orientation in space (Cullen, 2012), signals from muscle spindles provide a sense of trunk orientation and movement (Prochazka, 2021), and
visual information is used to assess the direction and speed of self-motion (Gibson, 1958). These signals need to be integrated to obtain estimates relevant for stabilization of upright posture but are also to some extent redundant. It is believed that redundant sensory signals are integrated based on their relative reliability, in a process called 'sensory reweighting' (Oie *et al.*, 2002; Peterka & Loughlin, 2004; Asslander & Peterka, 2014; Goar *et al.*, 2025). This reweighting process allows to compensate for imprecision, loss, or interruption of input from one or more sensory modalities.

The contribution of each sensory modality to stability control is commonly investigated with sensory perturbations (Day, 1999; Courtine *et al.*, 2007; Anson *et al.*, 2014; Duclos *et al.*, 2014; Alberts *et al.*, 2019; Li *et al.*, 2024). For instance, the contribution of vestibular information has been investigated with electrical vestibular stimulation (EVS) (Day, 1999; Alberts *et al.*, 2019; Li *et al.*, 2024). The contribution of proprioceptive signals has been investigated with muscle vibration, causing an illusion of muscle lengthening (Goodwin *et al.*, 1972; Inglis *et al.*, 1991; Vizirgianakis *et al.*, 2021).

Previous studies suggest that the gain of feedback responses to sensory afference may depend on the task performed or posture adopted. It is likely that this task- or posture-specific effect of sensory feedback relates to the difficulty of stabilizing these postures (Ali et al., 2003; Britton et al., 1993; Day et al., 1997; Fitzpatrick et al., 1994; Grangeon et al. 2015; Vizirgianakis et al., 2021). For example, in sitting, with a larger base of support, responses to visual, vestibular and proprioceptive perturbations are significantly smaller than in standing (Ali *et al.*, 2003; Grangeon *et al.*, 2015; Vizirgianakis *et al.*, 2021). Additionally, electrical vestibular stimulation induced responses were found to decrease with increased stance width and with the presence of external support (Britton *et al.*, 1993; Fitzpatrick *et al.*, 1994; Day *et al.*, 1997). In bipedal standing, responses to visual perturbations were significantly smaller compared to unipedal standing, a more challenging posture (Hazime *et al.*, 2012). However, Hazime et al. (2012) reported that ankle vibration had less effect in unipedal standing than in bipedal standing. They assumed that the vestibular signal compensates for the decreased use of proprioception through sensory integration (Hazime et al., 2012). This suggests that posture or task-dependent effects may

reflect in part reweighting instead of an overall change in feedback gain. From this perspective, the decreased effect of ankle vibration could also be attributed to decreased proprioceptive input from the ankle being compensated by an increased input from the hip and trunk, since corrective actions from the hip and trunk are required to maintain upright posture during unipedal standing (Riemann *et al.*, 2003).

Unlike in standing, which need continuous stabilization, the contribution of sensory signals to stabilization of walking is phasic, as reflected by phase-dependent gains of feedback responses (Ivanenko *et al.*, 2000; O'Connor & Kuo, 2009; Blouin *et al.*, 2011; Li *et al.*, 2024). The use of sensory signals in stabilization of walking is affected by walking speed; smaller effects of vestibular stimuli were found at higher compared to lower walking speeds (Brandt *et al.*, 1999; Jahn *et al.*, 2000; Schniepp *et al.*, 2012; Dakin *et al.*, 2013; Fabre-Adinolfi *et al.*, 2018). Visual perturbation by means of optic flow was found to have smaller effects in running than in walking, also suggesting a lower contribution of visual signals at higher speeds (Jahn *et al.*, 2001). Based on sensory reweighting, signals from one or more alternative modalities may compensate for the decreased contributions of vestibular and visual signals to stability control during faster walking. Proprioceptive signals could be a potential source of compensation in fast walking, as it has been shown that after removal of proprioceptive feedback, mice maintained the ability to walk at slower speeds, but failed to walk at higher speeds (Takeoka *et al.*, 2014; Mayer *et al.*, 2018). However, to the best of our knowledge, similar findings have not yet been reported in humans. Additionally, these studies only included limited speed ranges, i.e. comparing walking at a selected speed to running, or walking at a higher speed.

Here, we studied if, and how, proprioceptive and vestibular signals contribute to trunk stabilization during sitting, unipedal standing, bipedal standing and during walking at different speeds, by using muscle vibration on lumbar paraspinal muscles and electrical vestibular stimulation. We extended the range of walking speeds tested in previous studies to very slow speeds. We focused on the initial responses to step-like sensory stimulation, as later responses will be more affected by the gravitational perturbation that may follow from compensatory movements, and this effect varies between postures. We hypothesized that compared to bipedal standing, during unipedal standing, which poses a greater challenge to stability, both EVS and muscle vibration would lead to larger responses. Similarly, during sitting, which is inherently more robust with a larger base of support, the responses to EVS and muscle vibration would be smaller than during bipedal standing. During walking, EVS was expected to elicit larger responses at slower speeds as reported previously, whereas muscle vibration was expected to elicit larger responses at faster walking speeds because of sensory reweighting.

Methods

Participants

Nineteen healthy adults were recruited. Seven participants did not complete all measurements due to a damaged muscle vibrator. In total, data from twelve participants were used in this study (N = 12, age: 19.9 ± 2.1 years, weight: 65.7 ± 7.5 kg, height: 174.2 ± 8.9 metres). Exclusion criteria for participation were any diagnosed orthopaedic or neurological disorders, or the use of medications that can cause dizziness. All participants provided informed consent. Procedures were approved by the VU Amsterdam Research Ethics Committee (VCWE-2023-136).

Electrical vestibular stimulation

Electrical vestibular stimulation (EVS) was applied as an analogue signal through a digital-to-analogue converter (National Instruments Corp., Austin, USA) to an isolated constant-current stimulator (BIOPAC System Inc., Goleta, USA). The current was delivered via two carbon rubber electrodes (9 cm^2), which were coated with electrode gel (SonoGel, Bad Camberg, Germany) and placed over the mastoid processes with the anode on the left and cathode on the right. In this configuration, a step-like EVS signal, with an amplitude of 1 mA, induces an body sway to the anodal side, i.e. to the left, in bipedal standing (Lund & Broberg, 1983; Day, 1999).

Unilateral muscle vibration

Two muscle vibrators, consisting of DC motors (Maxon International AG, Sachseln, Switzerland) driving an eccentric mass in a PVC case, were placed 2 cm lateral to the L3 spinous processes on both the left and right paraspinal muscles. Vibrators were fixed tightly with double sided tape and an elastic band. Only the right vibrator was activated (80 Hz, with an amplitude of approximately 2 mm), which induces an illusion of right paraspinal muscle lengthening (Courtine *et al.*, 2007) .

Kinematics and ground reaction force

Whole-body kinematics were recorded using a 3D motion capture system (Optotrak, Northern Digital Inc., Waterloo, Ontario, Canada) sampling at 50 samples/s with cluster markers on the feet, shanks, thighs, pelvis, trunk, head, upper arms and forearms. Corresponding anatomical landmarks were digitized with a six-marker probe based on the model described by Kingma et al. (1996). Ground reaction forces were measured at 1000 samples/s by force plates embedded in the split-belt treadmill (ForceLink b.v., Culemborg, the Netherlands).

Protocol

For familiarization, participants were exposed to 5-second step-like EVS and muscle vibration during unipedal standing, with three repetitions of each stimulation. Participants then walked on the dual-belt treadmill at the fastest (5.0 km/h) and slowest selected speed (0.8 km/h) for 2 minutes at each speed without any stimulation. The subsequent conditions were defined by the stimulation received

(EVS or muscle vibration) and by postural tasks (unipedal standing, bipedal standing, sitting, and walking at five different speeds). The order of conditions was randomized. All conditions were performed with eyes open.

During unipedal standing, participants stood on their right foot with arms relaxed at their sides. Trials were repeated if the non-stance leg touched the ground. For bipedal standing, participants stood with their feet shoulder-width apart and arms relaxed at their sides, while for sitting, participants sat upright on a stool with arms crossed at shoulder height, feet on the ground, and knees flexed at 90 degrees. In all postural conditions, participants were instructed to minimize the movement. The 5-second stimulation (muscle vibration or EVS) in standing and sitting trials was manually triggered by the researcher with approximately 10-second intervals between stimuli, which aimed to ensure that the participant could not anticipate the stimulus. Each postural task included 10 repetitions of each stimulation. Each repetition lasted 25 seconds.

For the walking conditions, participants walked on the dual-belt treadmill at speeds of 0.8, 2.0, 3.2, 4.3 and 5.5 km/h for 4 minutes at each speed. For both EVS and muscle vibration, the stimulation was automatically triggered at right heel strikes and lasted 5 seconds, with approximately 10-second intervals between stimulations.

Data analysis

Ground reaction forces were down-sampled to 50 Hz. Gait events were identified based on the combined centre of pressure (Roerdink *et al.*, 2008). The mediolateral displacement of markers placed on the T6 spinal process and sacrum were analysed to assess the response to stimulations. A negative mediolateral displacement indicated a leftward movement.

To calculate marker displacement, the trajectories of the T6 and sacrum markers were filtered using a bi-directional 4th order, 10 Hz Butterworth low pass filter. For the walking conditions, the marker trajectories were normalized to the gait cycle starting from right heel strikes. To remove the offset, the baseline, defined as the mean marker position over 2 seconds before the onset of perturbation in standing and sitting, and over one stride before the onset of perturbation in walking, was subtracted from the marker trajectory for each repetition, trial and participant. Marker displacement was then calculated as the mean position during the first 2 seconds after the trigger in standing and sitting tasks, and the first two strides after the trigger in walking. The average displacement was calculated across repetitions for each participant, and then across participants (Figure 1).

Statistical analysis

To evaluate whether there were effects of EVS and muscle vibration on trunk stabilization, one sample t-tests were performed to compare the mediolateral displacements for each condition to zero. To assess whether the effect of EVS and muscle vibration varied across postures in standing and sitting or speed in walking tasks, we used one-way repeated measures ANOVAs with factors Postural task and Walking speed. Mauchly's test was used to check the assumption of sphericity, and Greenhouse Geisser corrections were applied when the assumption was rejected. A

Bonferroni correction was applied for the post hoc tests when appropriate. A p-value less than 0.05 was defined as significant. Statistical analyses were performed in MATLAB (2019a, The MathWorks, Natick, US).

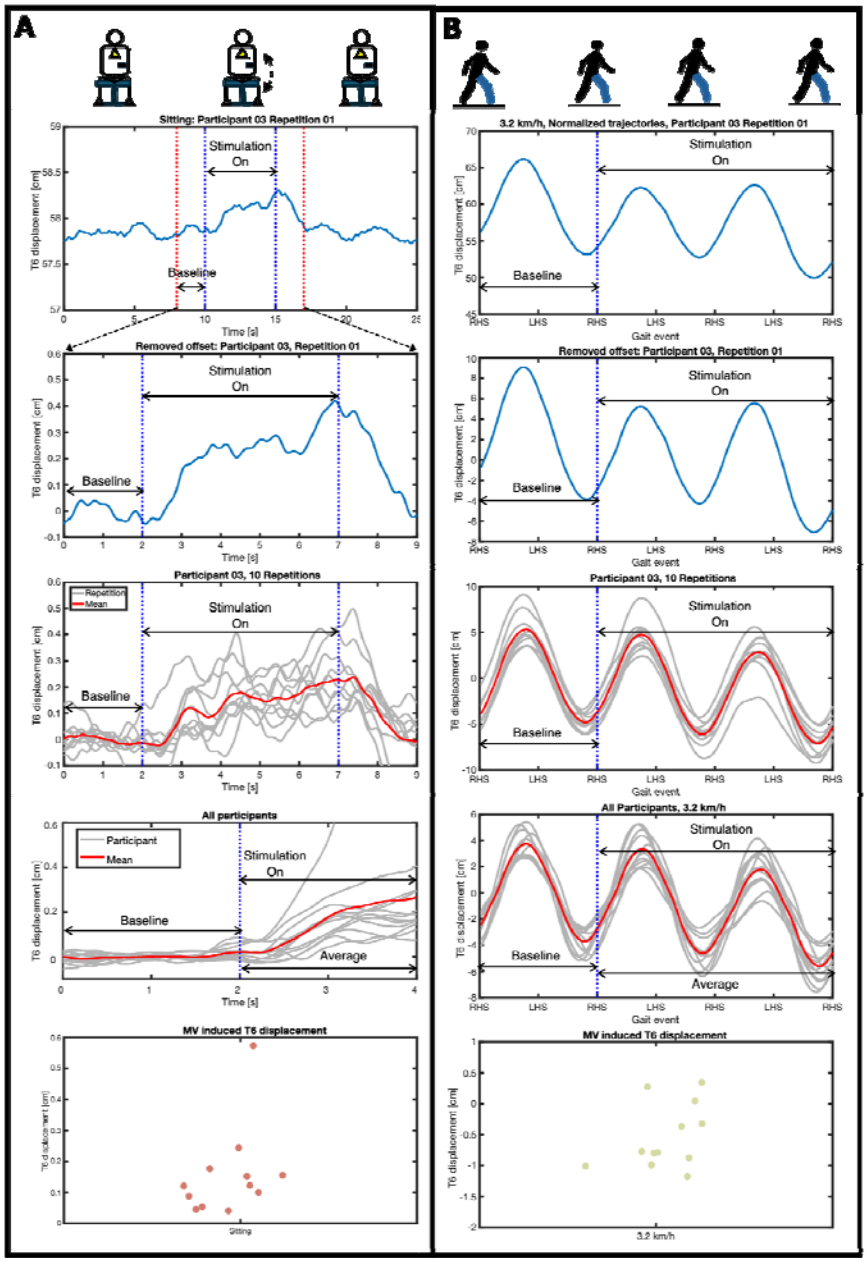

Figure 1. Example of signal analysis of data collected in sitting (A) and walking (B). From the top to bottom panel, illustrating: 1) The definition of the baseline and stimulation period during sitting and walking. 2) Removal of the offset for each participant and repetition. 3) Averaging the stimulation induced displacement over ten repetitions for one participant. Grey lines represent one trajectory for each repetition. The red line represents the mean of trajectory over ten repetitions for one participant. 4) Averaging the first two seconds after stimulation onset in static postures, and the first two strides after stimulation onset in walking for each participant. Each grey line represents the average of ten repetitions for one participant. The red line represents the mean of T6 displacement over participants. 5) The mean of T6 displacements of all participants used for statistical testing. Each dot represents the displacement of one participant.

Results

Standing and Sitting

EVS induced no significant mediolateral displacement of T6 during unipedal standing (mean ± standard deviation: -0.05 ± 0.24 cm, $p = 0.469$), bipedal standing (-0.05 ± 0.15 cm, $p = 0.281$), or sitting (-0.01 ± 0.36 cm, $p = 0.467$). There was no significant effect of Postural task on EVS induced displacement of T6 ($F(2,22) = 0.242$, $p_{task} = 0.787$) (Figure 2A). Also, no significant mediolateral displacement of the sacrum was induced by EVS during unipedal standing (-0.05 ± 0.16 cm, $p = 0.249$), bipedal standing (-0.01 ± 0.14 cm, $p = 0.820$), and sitting (-0.00 ± 0.00 cm, $p = 0.061$). There was no significant effect of Postural task on EVS induced displacement of the sacrum ($F(2,22) = 0.600$, $p_{task} = 0.588$) (Figure 2B).

Muscle vibration induced a non-significant leftward displacement of T6 during unipedal standing (-0.15 ± 0.25 cm, $p = 0.056$) and a significant rightward displacement of T6 in bipedal standing (0.10 ± 0.11 cm, $p = 0.008$) and sitting (0.16 ± 0.14 cm, $p < 0.001$). The repeated measured ANOVA test confirmed a significant effect of Postural task on the muscle vibration induced displacement of T6 ($F(1.686,18.546) = 10.655$, $p < 0.001$) (Figure 2A). For the sacrum, muscle vibration induced a significant leftward displacement in unipedal standing (-0.20 ± 0.26 cm, $p = 0.023$), but no significant displacement in bipedal standing (0.03 ± 0.07 cm, $p = 0.136$), or sitting (0.00 ± 0.01 cm, $p = 0.069$). There was a significant effect of Postural task on the muscle vibration induced displacement of the sacrum ($F(2,22) = 8.063$, $p = 0.002$) (Figure 2B).

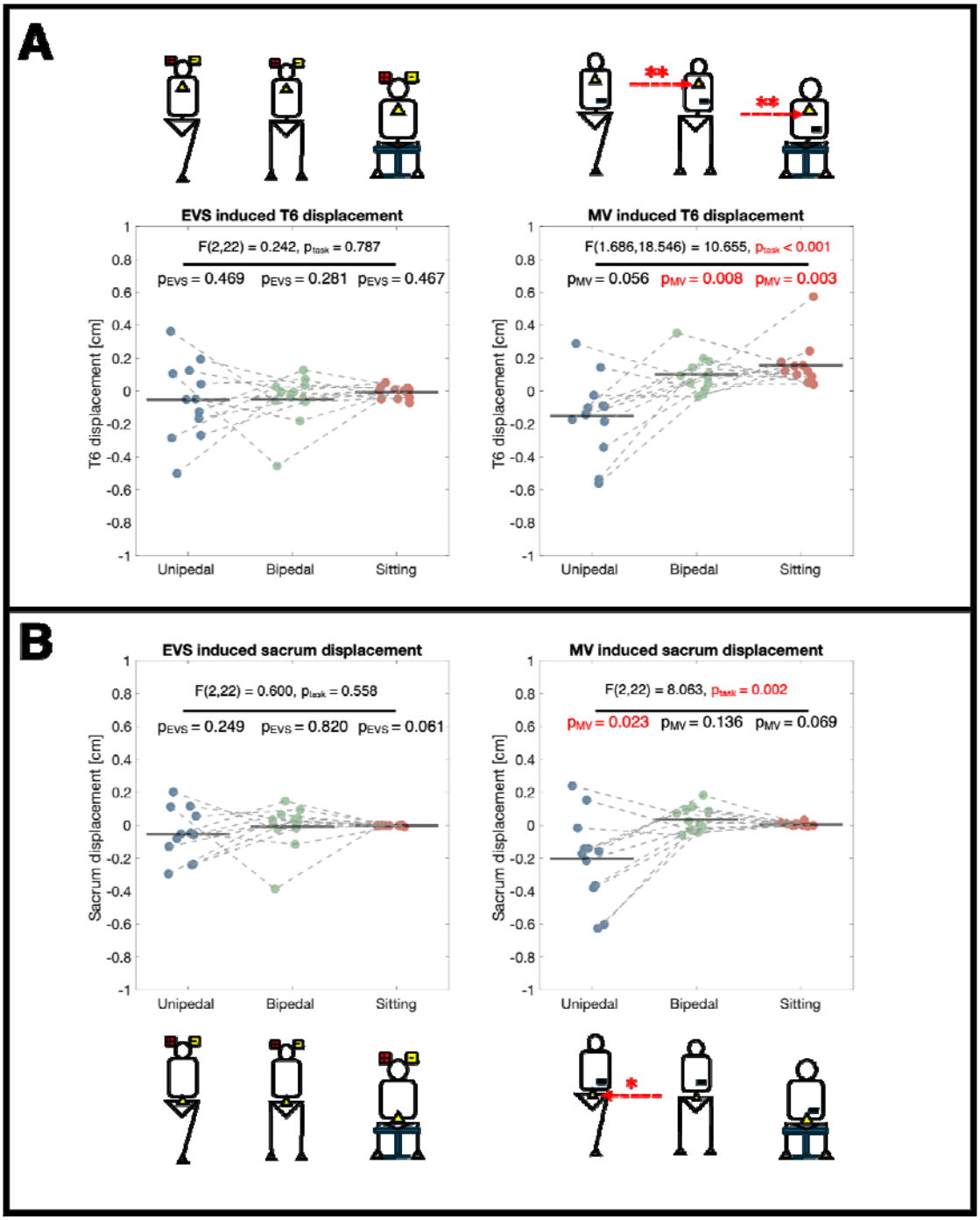

Figure 2. Averaged (bar) and individual (dots) mediolateral displacements of T6 (A) and sacrum (B) in response to electrical vestibular stimulation (EVS) and muscle vibration (MV) during unipedal standing (blue dots), bipedal standing (green dots) and sitting (red dots). In the diagrams, the red and yellow squares represent the EVS electrodes, black rectangles represent the muscle vibrator, the yellow triangles represent the cluster marker on T6 and sacrum, and the red arrows indicate the direction of the displacement.

Walking

During walking, EVS and muscle vibration (MV) induced significant leftward T6 and sacrum displacements at all walking speeds (Table 1). Speed significantly influenced the displacement at both levels, in both stimulation conditions (EVS-T6: F (3.052, 33.572) = 5.707, $p_{speed} < 0.001$; EVS-Sacrum: F (2.976, 32.736) = 4.551, $p_{speed} = 0.004$; MV-T6: F (3.068, 33.748) = 6.304, $p_{speed} = 0.002$; MV-Sacrum: F (3.412, 37.532) = 4.870, $p_{speed} = 0.002$).

The speed-dependent responses to stimulations (EVS and MV) at both T6 and sacrum levels exhibited a “U-shaped” pattern. Specifically, the induced mediolateral displacement increased from slow speeds (e.g. from 0.8 to 2.0 km/h), peaked at a moderate speed (around 4.3 km/h), and then decreased at higher speeds (approximately from 4.3 to 5.5 km/h) (Figure 3).

Table 1. Summary of the one sample t-tests on stimulation induced mediolateral displacements during walking

Speed (km/h)	T6 displacement				Sacrum displacement			
	EVS		MV		EVS		MV	
	Mean ± SD	p-value	Mean ± SD	p-value	Mean ± SD	p-value	Mean ± SD	p-value
0.8	-0.41 ± 0.49 cm	p = 0.016	-0.41 ± 0.56 cm	p = 0.030	-0.28 ± 0.38 cm	p = 0.024	-0.37 ± 0.49 cm	p = 0.023
2.0	-1.56 ± 1.37cm	p = 0.002	-0.89 ± 0.46 cm	p < 0.001	-1.07 ± 1.09 cm	p = 0.006	-0.72 ± 0.39 cm	p < 0.001
3.2	-1.16 ± 1.30cm	p = 0.010	-1.61 ± 0.56cm	p < 0.001	-0.92 ± 1.12 cm	p= 0.015	-1.00 ± 0.63 cm	p < 0.001
4.3	-1.38 ± 0.90 cm	p < 0.001	-0.98 ± 0.57 cm	p < 0.001	-1.12 ± 0.81 cm	p < 0.001	-0.84 ± 0.57 cm	p < 0.001
5.5	-1.09 ± 0.92 cm	p = 0.001	-0.44 ± 0.53 cm	p = 0.016	-0.77 ± 0.71 cm	p = 0.003	-0.34 ± 0.55 cm	p = 0.050

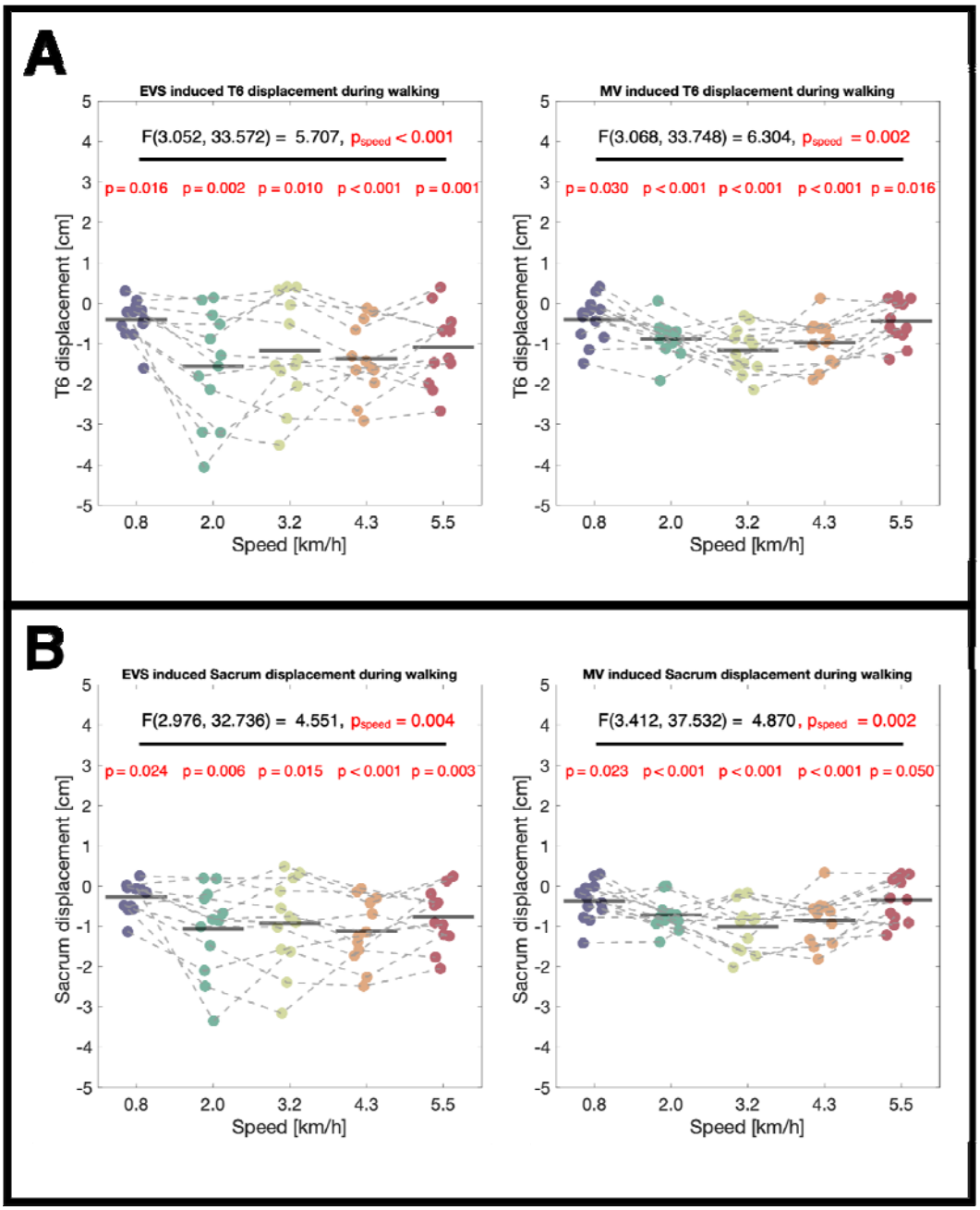

Figure 3. Averaged (bar) and individual (dot) mediolateral displacement of T6 (A) and sacrum (B) in response to electrical vestibular stimulation (EVS) and muscle vibration (MV) during walking at five different speeds.

Discussion

We investigated the task specific contribution of the vestibular and lumbar proprioceptive systems to trunk stabilization during sitting, unipedal and bipedal standing, and walking at five different speeds. Larger responses to both EVS and muscle vibration were expected during unipedal standing than during bipedal standing and during sitting. However, no significant effects of EVS on the mediolateral displacement of either T6 or sacrum during standing and sitting were found. Muscle vibration of the right lumbar paraspinal muscles induced a significant leftward displacement of the sacrum, but no significant displacement at the T6 level during unipedal standing. During bipedal standing and sitting, vibration elicited a significant rightward T6 displacement, but no effect was observed at the sacrum level. During walking at all selected speeds, both muscle vibration and EVS (with the anode on the left side) induced significant leftward displacements at T6 and sacrum levels. The response magnitudes to both EVS and muscle vibration were significantly affected by walking speed, exhibiting a “U-shaped” pattern, i.e. response magnitude increased from slow speeds, peaked at a moderate speed to decrease again at higher speeds. Below, we discuss how these findings advance our understanding of the task specific contribution of the vestibular and lumbar proprioceptive systems to the trunk stabilization.

EVS induced responses during standing and sitting

No significant responses to EVS at T6 and sacrum levels were found during sitting, uni- and bipedal standing. This is in contrast to previous studies, which observed a significant displacement of centre of pressure, head, torso and pelvis towards the anodal side in response to EVS during bipedal standing (Lund & Broberg, 1983; Day *et al.*, 1997; Fitzpatrick *et al.*, 1999). Excluding the effect of sample size and stimulation intensity, which were comparable to these studies, our null effect could be explained by the availability of visual information. Previous studies were performed with eyes closed. Hence, in those studies vestibular information was likely upweighted, increasing the effect of EVS. During bipedal standing, it has been reported that EVS-induced motor responses are smaller with eyes open compared to closed (Britton *et al.*, 1993; Fitzpatrick & Day, 2004). However, another study reported that the presence of vision did not significantly modulate the EVS induced lumbar muscle responses during sitting (Amélie *et al.*, 2021). The authors attributed this to the strong tactile input from the thighs and buttocks during sitting. Reweighting between vestibular and tactile information has been confirmed by a reduced coupling between EVS and the centre of pressure trajectory during bipedal standing when providing fingertip contact (Goar *et al.*, 2025). From a biomechanical point of view, the large contact of the thighs and pelvis with the seat provides a larger base of support, and the height of the centre of mass relative to the base of support is lower during sitting compared to standing. These factors reduce the demand for sensory feedback for posture control (Kantor *et al.*, 2001). Consequently, the gain of responses to EVS induced illusions is likely to be smaller during sitting than during uni- and bipedal standing.

EVS induced responses during walking

During walking, we found that at both T6 and sacrum level, EVS induced a significant displacement to the left, i.e. the anodal side, in line with previous literature (Bent *et al.*, 2004; Fitzpatrick *et al.*, 1999; Jahn *et al.*, 2000; Iles *et al.*, 2007). The vestibular signal encodes the head orientation in space (Cullen, 2012), and this perceived vestibular signal needs to be integrated with neck proprioception to distinguish whether the whole body is moving or only the head is moving on the stationary trunk (Pettorossi & Schieppati, 2014). In our case, participants were walking facing forward, thus head orientation was on average aligned with the trunk. Consequently, EVS induced an illusion of whole body movement to the right. A compensatory response to the left was induced to stabilize the trunk in the upright orientation.

The differences in the effects of EVS between standing and walking were partly supported by Fitzpatrick et al. (1999), who reported that EVS induced body sway during standing was smaller and more variable than during walking. During walking, a stereotyped and symmetric locomotion, the contribution of vestibular signals is phasic (Blouin et al., 2011; Ivanenko et al., 2000; Li et al., 2024; O'Connor & Kuo, 2009). As such, the phase-locked step-like EVS induced perturbation is likely to be consistent over strides. However, during standing and sitting the responses to EVS can superimpose negatively or positively on the ongoing body sway, which would increase the variability in measured responses.

Muscle vibration induced responses during standing and sitting

Muscle vibration causes an illusion of lengthening of the vibrated muscle (Goodwin *et al.*, 1972). Consistent with literature, during bipedal standing and sitting, a significant rightward T6 displacement was found (Courtine *et al.*, 2007). No significant sacrum displacement was found in these tasks. In contrast, during unipedal standing a sacrum displacement, but no trunk displacement, was observed. We therefore analysed the relative position of T6 to sacrum (Figure 4A). A rightward displacement of T6 relative to the sacrum during unipedal standing was found in all three postures. Thus, the different response during unipedal standing versus sitting and bipedal standing could be caused by a difference in the interpretation of the postural change related to trunk muscle lengthening. during bipedal standing and sitting, the sacrum is likely to maintain stable, given the wide and symmetrical support. Thus, muscle lengthening is likely to be interpreted as a leftward trunk movement relative to the sacrum, inducing a compensatory rightward trunk movement. However, in unipedal standing with a less stable and asymmetric support of the pelvis, this perceived lengthening is possibly to be interpreted as a rightward displacement of the pelvis, inducing a leftward sacrum displacement to re-align the segments.

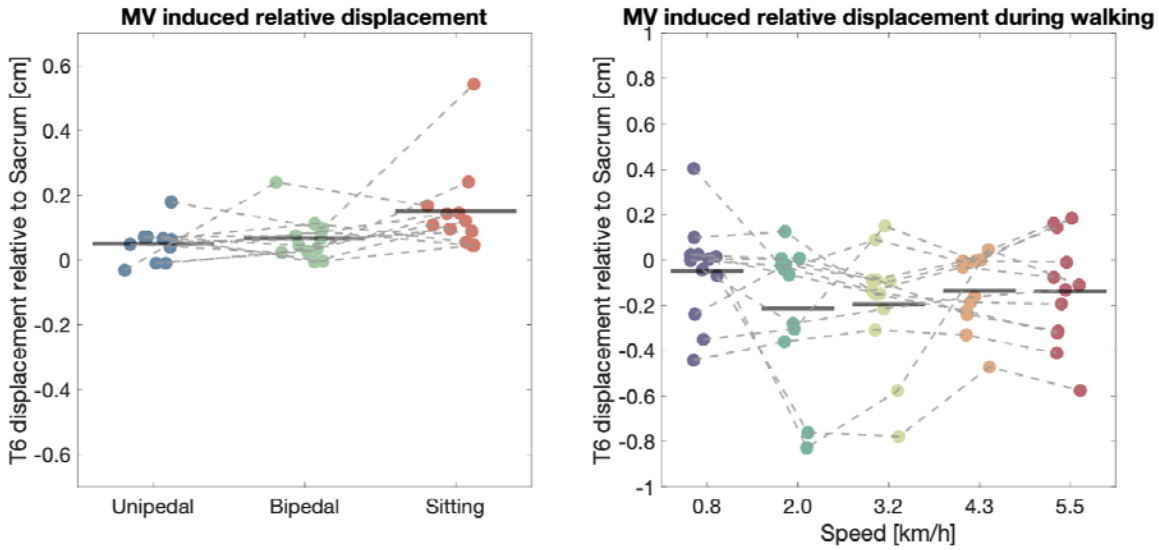

Figure 4. Averaged (bar) and individual (dots) mediolateral displacements (in centimetres, cm) of T6 relative to sacrum in response to muscle vibration (MV): A) during unipedal standing (blue dots), bipedal standing (green dots) and sitting (red dots); and B) during walking at five difference speeds. Positive value indicates a rightward displacement of T6 relative to sacrum.

Muscle vibration induced responses during walking

Similar to unipedal-standing, during walking, the vibration induced perception of paraspinal muscle lengthening may be interpreted as a pelvis movement. With vibration on the hip abductor muscle of the stance leg, an inward placement of the contralateral foot was reported, which suggests that this vibration similarly induced an illusion of pelvis displacement towards the stance side, (Arvin *et al.*, 2018). In line with this, we found that lumbar muscle vibration induced a significant leftward displacement at T6 and sacrum levels opposite to the vibrated side, also consistent with previous studies using trunk muscle vibration (Schmid *et al.*, 2005; Courtine *et al.*, 2007). Unlike during unipedal standing, the T6 displacement was more to the left relative to the sacrum during walking (Figure 5B). Thus, this response seems not to be the result of balance control. In contrast with the hip abductor muscles, lengthening of the paraspinal muscles may result from movement in different planes. Unilateral lengthening of paraspinal muscles can result not only from trunk or pelvis displacement in the frontal plane, but also from a change in orientation in the transverse plane. Schmid et al. (2005) found that during overground walking with either eyes opened or closed, lumbar paraspinal muscle vibration evoked a deviation in walking trajectory. Additionally, deviations in walking direction were evoked by vibration applied to abdominal muscles and paraspinal muscles at thoracic and lumbar levels, but not with vibrations on lower limb muscles, such as hip abductors and adductors (Courtine *et al.*, 2007). Therefore, trunk proprioceptive information

appears to play a major role in the control of balance as well as the control the heading direction during walking.

Effects of walking speed

Previously, it has been reported that vestibular stimulation has less effect during walking at higher locomotion speeds (Brandt *et al.*, 1999; Jahn *et al.*, 2000; Schniepp *et al.*, 2012; Dakin *et al.*, 2013; Fabre-Adinolfi *et al.*, 2018). Combined with the previous finding that optical flow is less effective at high locomotion speed (Jahn *et al.*, 2001), we expected that the proprioceptive signal would compensate during fast walking. Consequently, a larger muscle vibration induced response was expected with increased walking speed. However, in the selected range of speeds from 0.8 to 5.5 km/h, we found that the responses peaked at a moderate speed for both EVS and muscle vibration.

It is believed that stable walking is achieved by the interaction of multisensory feedback control, automated central pattern generators, and modulation of intrinsic mechanical properties of the body (MacKay-Lyons, 2002; Wuehr *et al.*, 2013; Grillner & El Manira, 2020). The decrease in effects of sensory stimulation from the moderate to higher walking speeds is in line with previous literature (Brandt *et al.*, 1999; Jahn *et al.*, 2000; Schniepp *et al.*, 2012; Dakin *et al.*, 2013; Fabre-Adinolfi *et al.*, 2018). Also, changes in visual information may have smaller effects at higher speeds (Jahn *et al.*, 2001). This suggests that feedback control is less required at higher speeds, which is partly in line with the reduced activity of the vestibular and somatosensory cortex during imagined running compared to imagined slow speed walking and standing (Jahn *et al.*, 2004). In animal models without movement-related sensory feedback, automated central pattern generators can generate the rhythmic muscle activity for locomotion (Grillner *et al.*, 1976; Dubuc *et al.*, 1986; Lambert *et al.*, 2012). In human participant, Dietrich et al. (2020) found the modulation of the centre of pressure to be less strongly coupled to vestibular afference when head movements became more predictable. They suggested that with a more stereotyped locomotion pattern, a CPG-derived locomotor efference copy plays a more significant role in balance control. Finally, the decreased effects of EVS and muscle vibration at higher speeds may also be explained by biomechanical factors. At faster walking speeds, trunk muscle activity is increased (Anders *et al.*, 2007), which would result in increased muscle stiffness and consequently increased trunk stiffness.

Below moderate walking speed, the sensory stimulations had less effect on trunk stabilization. This may be in line with the phenomenon that specific patient groups with sensory loss or dysfunction tend to walk slower (Menz *et al.*, 2004; Wuehr *et al.*, 2014; Hicks *et al.*, 2017). Some studies suggested that slow walking is more stable than fast walking (Dingwell & Marin, 2006; England & Granata, 2007). However, this conclusion has been debated (Bruijn *et al.*, 2009; Hak *et al.*, 2012; Best & Wu, 2020). As argued above, slow walking may increase variability and reduce predictability of walking and thus be more dependent on feedback control (Dietrich *et al.*, 2020; Best & Wu, 2020), suggesting that a larger response to sensory stimulation should be found at slower walking speeds.

Smaller feedback responses at very low speeds may be a result of the increased duration of the stance phases, especially of the double support phases, both in

absolute sense and as a percentage of the gait cycle (Wuehr *et al.*, 2014; Wu *et al.*, 2019). Given the long duration of the double support phases in very slow walking (e.g. 0.8 km/h), the control strategy may resemble that during standing, where we found smaller or no effects of sensory stimulation. However, previously we found that trunk muscle modulation in response to vestibular afference mainly took place during the double support phase (Li *et al.*, 2024).

Another possible explanation for the smaller feedback responses at very low speeds is that walking at such slow speed is controlled as a repeated transition between standing and walking. The optimal feedback control theory suggests that to enable the transition from one posture or task to another, the control set for the preceding needs to be disengaged before setting sensory feedback gains for the subsequent task (Cluff & Scott, 2016). This prediction was supported by findings from Tisserand *et al.* (2018),who reported absence of coupling between EVS and ground reaction force during the transition between standing and walking. Hence, when very slow walking is regarded as a repeated transition between standing and walking, the overall feedback gains should be low.

Limitations

We did not statistically compare the contribution of vestibular and proprioceptive information between the static and dynamic tasks in this study for several reasons. Dependent on the task, sensory information may be used not only for balance control. As we argue above, trunk proprioceptive information also contributes to the control of walking direction. Moreover, the responses to stimulation were analysed differently between walking and static conditions. Together, these factors could confound the comparison of response magnitudes to stimulation, i.e. the gain of feedback response, between static and dynamic tasks.

Another limitation is that we cannot investigate whether the relative weights of the vestibular and proprioceptive signals differed between tasks and postures for trunk stabilization. We found parallel trends in the task and speed-related modulation of responses evoked by electrical vestibular stimulation and muscle vibration, which possibly indicates an overall modification of the feedback control gain. Reweighting between sensory signals could exist for optimal feedback control in different task and postures.

We performed two separate repeated-measures ANOVAs for the T6 and sacrum markers to evaluate the effects of EVS or muscle vibration across postural tasks. This may increase the risk of Type I errors by testing the dataset from T6 and sacrum independently, as biomechanically, the motions of T6 and sacrum are not independent. Considering the Marker Position as a factor in the MANOVA test could be a reasonable solution. However, if a significant effect of marker position would be found, ANOVAs for each marker should be performed as post-hoc tests. In this case, the main finding should remain the same as current findings, i.e. the contribution of vestibular and proprioceptive information in trunk stabilization differs between postural tasks and walking speeds.

Conclusion

In conclusion, the present findings confirm that the contribution of vestibular and proprioceptive afference to the trunk stabilization varies between postures and walking speeds. Muscle vibration induced different response at the T6 and sacrum level comparing unipedal standing to sitting and bipedal standing. This suggests a different interpretation of the sensation of muscle lengthening in these postures. Similar to previous studies, decreased responses to both stimulations were found from a moderate speed to higher speeds, which suggests that stabilization of faster walking relies less on feedback control. By extending the range of selected walking speeds compared to previous studies, we found decreased responses to stimulation at very slow speeds. This suggests that a different control strategy is used during slow walking, possibly due to the long double stance duration, or perhaps because very slow walking reflects a repeated initiation of walking rather than a steady-state process.

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Additional information

Data Availability Statement

The original data are available from the corresponding author upon reasonable request.

Competing Interests

The authors declare that there are no conflicts of interest.

Author Contributions

Experiments were performed at the Dual Belt Lab in the Vrije Universiteit Amsterdam. Conception and design: Y.C.L., K.K.L., S.M.B., S.B., and J.H.D. Data acquisition: Y.C.L. Analysis and interpretation: Y.C.L., K.K.L., S.M.B., S.B. and J.H.D. Drafting and revising manuscript: Y.C.L., K.K.L., S.M.B., S.B. and J.H.D. All authors have read and approved the final version of this manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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