

Directional postural responses induced by vibrotactile stimulations applied to the torso

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Received: 3 April 2012 / Accepted: 15 August 2012 / Published online: 12 September 2012
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Abstract It has been shown that torso-based vibrotactile feedback significantly reduces postural sway in balance-compromised adults during quiet standing and in response to perturbations. This study aimed to determine whether vibrotactile stimulations applied to different torso locations induced directional postural responses and whether torso cutaneous information contributes to body representation. Eleven healthy young adults equipped with an inertial measurement unit (IMU) placed on the torso were asked to maintain an upright posture with closed eyes. Six vibrators (tactors) were placed on the torso in contact with the skin over the left and right external oblique, internal oblique, and erector spinae muscles at the L4/L5 level. Each tactor was randomly activated four times per location at a frequency of 250 Hz for a period of 5 s. The IMU results indicated that vibration applied individually over the internal oblique and erector spinae muscles induced a postural shift of about one degree oriented in the direction of the stimulation, while simultaneous activation of all tactors and activation of tactors over external oblique

muscles produced insignificant postural effects. The root mean square of the sway signal was significantly higher during vibration than before or after. However, the center of pressure displacement, measured by a force plate, was uninfluenced by any vibration. These results suggest a multi-joint postural response including a torso inclination associated with vibration-induced changes in cutaneous information. The directional aspect of vibration-induced postural shifts suggests that cutaneous information from the stimulated areas contributes to proprioception and upper body spatial representation.

Keywords Vibration · Proprioception · Body representation · Balance · Sensory augmentation · Compensatory response

Abbreviations

ANOVA	Analysis of variance
A/P	Anterior–posterior
COG	Center of gravity
COP	Center of pressure
DFT	Discrete Fourier transform
HSD	Honestly significant difference
IMU	Inertial measurement unit
M/L	Medial–lateral
PSD	Power spectral density
RMS	Root mean square

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Introduction

Vestibular, visual, cutaneous, and muscle proprioceptive information are known to contribute to postural control and

body orientation (Horak and MacPherson 1996; Horak and Shupert 1994; Lackner 1988; Lackner et al. 2000). Cutaneous information from the sole of the foot has also been shown to contribute to postural regulation (Kavounoudias et al. 1999, 2001). Vibrotactile biofeedback has been used to provide additional cues of body motion in order to reduce postural sway in healthy young adults (Davis et al. 2010; Janssen et al. 2009; Wall et al. 2001; Vuillerme et al. 2008; Lee et al. 2012b), older adults (Haggerty et al. 2012; Verhoeff et al. 2009), and individuals affected by vestibular disorders (Kentala et al. 2003; Lee et al. 2012b; Sienko et al. 2008, 2010, 2012; Wall et al. 2004). However, these applications considered vibrotactile stimulation only as an alert mechanism rather than one that induces a non-volitional postural response.

To date, the most commonly used vibrotactile display arrangement and location for upright stance applications is an array of vibrating actuators (tactors) distributed along a belt placed around the torso, co-located with an inertial motion sensing system that measures body angular and linear accelerations (Wall et al. 2001; Sienko et al. 2008). Directional cues that serve as “alarm” signals to indicate body movement in a particular direction may be assigned to correspond to either attractive or repulsive volitional postural responses. Attractive cues, that is, instructing an individual to move in the direction of a vibration, have previously been used to provide turning guidance during walking (Ross and Blasch 2000), driving, and flying tasks, and to provide pilots with information about the aircraft attitude with respect to gravity (Van Veen and Van Erp 2001). Wall et al. (2001) used repulsive cues, that is, instructing an individual to move away from a vibration, in the first vibrotactile feedback balance device to be based on the concept that an aversion/avoidance response similar to bumping into an obstacle is prompted by a vibration. Subsequent studies have employed a similar scheme. However, a postural adjustment considered a volitional response to an alarm signal may in fact be incongruous with the kinesthetic message from the tactile receptors stimulated. Although cutaneous mechanoreceptors from joint areas (e.g., finger, elbow, knee, ankle) are known to provide kinesthetic information (Aimonetti et al. 2007; Collins and Prochazka 1996; Collins et al. 2005; Edin 1992; Edin and Abbs 1991; Edin and Vallbo 1990) and contribute to spatial coding of joint movements for multi-articular joints such as the ankle (Aimonetti et al. 2007), the contribution of these receptors around the torso to a spatial representation of the upper body and postural control is unknown. It is hypothesized that if tactile receptors of the torso contribute to a directional coding of postural movements, stimulating them as the individual maintains an upright posture should induce a directional postural shift.

Hence, the present study investigates the motor and perceptual effects on standing posture of vibrotactile stimulations applied to various locations around the torso in the absence of instructions. Based on our hypothesis, a primary goal was to determine how the cutaneous information is integrated, that is, whether vibrotactile stimulation induces directional adjustments/responses away from or toward the stimulation. Postural responses show that tactile information at the level of the iliac crest contributes to spatial representation of the upper body, and their direction toward the stimulation provides understanding that is critical to the design of cuing alarms for torso-based vibrotactile displays used in balance control applications. An earlier version of the results has appeared in abstract form (Lee et al. 2012a).

Materials and methods

Participants

Eleven young healthy adults (7 males, 4 females, mean age 22.9 ± 4.8 years) naïve to the purpose of the experiment participated in this study. Exclusion criteria included any self-reported neurological or functionally significant musculoskeletal dysfunction, or a body mass index greater than 30 kg/m^2 . All participants were instructed to refrain from taking medications that might cause drowsiness or dizziness within 48 h of the experimental session. In addition, all participants were asked not to consume alcoholic beverages within 24 h of the experimental session. Informed consent was obtained from each participant prior to the start of the experimental procedures. The University of Michigan Institutional Review Board approved the study, which conformed to the Helsinki Declaration.

Instrumentation

A six degree-of-freedom inertial measurement unit (IMU; Xsens Technologies, NL), a laptop computer driving the vibrotactile control circuit, and tactors (C2; Engineering Acoustics Inc., USA) were used. An elastic belt fastened around the torso used Velcro to attach the IMU and tactors. The IMU was placed at about the L3 vertebra level of the participant's back, and the six tactors were placed on the skin over the left and right internal oblique, external oblique, and erector spinae muscles at about the level of the L4/L5 joint (Fig. 1). The angular displacements (static accuracy better than 0.5° and an angular resolution equaling 0.05°), velocities, and accelerations measured by the IMU in the anterior–posterior (A/P) and medial–lateral (M/L) directions were sampled at a rate of 100 Hz. The control circuit generated the sinusoidal signals driving the tactors

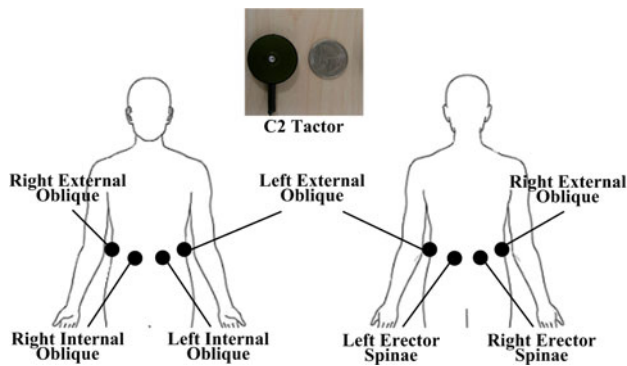


Fig. 1 Tactor and the locations where the tactors were applied to the torso

at a frequency of 250 Hz and peak-to-peak displacement amplitude of 200 μm . The C2 tactor is a linear actuator with a cylindrical moving probe at the center with a cross-sectional area of 58.6 mm^2 . The vibration frequency was selected to fit within the one-to-one frequency response of fast-adapting cutaneous receptors (Johansson et al. 1982; Knibestol and Vallbo 1970; Ribot-Ciscar et al. 1989; Vedel and Roll 1982) and largely beyond the frequency response of muscle spindles (Burke et al. 1976a, b; Roll et al. 1989). Hence, given its small displacement amplitude and high frequency, it is assumed that this stimulation activated exclusively the cutaneous receptors.

A force platform (ORG6, Advanced Mechanical Technology Inc., USA) quantified the displacements of the center of pressure (COP). The COP signals were sampled at a rate of 100 Hz and synchronized with the IMU data.

Procedure

Participants were asked to stand on the force plate with eyes closed, arms held at their sides, and feet hip-width apart with a 15° lateral rotation. Foam ear plugs and ear muffs were worn to eliminate environmental noise. Experimental trials were composed of consecutive measurement periods that included an initial period of 5 s without vibrotactile stimulation followed by 5 s with vibrotactile stimulation. A post-vibrotactile stimulation 5-s period was recorded for a subset ($n = 5$) of the participants. Either only one or all tactors were activated during the vibration period, henceforth referred to as “single location” and “all locations”, respectively. Two trials for each stimulation condition were performed in random order for a total of 14 trials per participant (i.e., two measurements each of six “single location” trials and one “all locations” trial). The duration of each trial was 15 s (maximum), and consecutive trials were separated by a 5-s rest period during which the participants were instructed to open their eyes and move their torso. No information

regarding the application and duration of vibration was provided to the participants. Following the completion of the experimental trials, participants were asked to report if the vibrotactile stimulation affected their body sway using a simple Likert scale (1 = strongly disagree, 2 = disagree, 3 = neither disagree nor agree, 4 = agree, and 5 = strongly agree).

Data analysis

The processing of recorded signals from both the IMU and force plate was performed using MATLAB (MathWorks, Natick, MA). The frequency range of the COP signals is below 10 Hz for quiet standing posture in healthy populations (Winter 1995); hence, the corresponding data were low-pass filtered with a zero phase, second order Butterworth filter with a 10 Hz cutoff frequency. The IMU data were automatically filtered with a Kalman filter embedded in the Xsens controller. For data analysis, the “pre-vibration” and “post-vibration” periods were defined as the 5 s preceding and following the vibrotactile stimulation, respectively. Three metrics were defined to quantify postural responses to vibrotactile stimulations: postural shift vector, root-mean-square (RMS) sway, and power spectral density (PSD) of sway.

As illustrated in Fig. 2 for data acquired with the IMU, a two-step process determined the magnitude and direction of the postural responses between consecutive periods of interest (pre-/per- and per-/post-vibration periods). First, Fig. 2a shows how the 2D postural trajectories corresponding to each period were separately fit with 95 % confidence interval ellipses. The center of each ellipse was used to calculate the 2D postural shift vector that quantified the magnitude and direction of the postural displacement. The coordinates of the center of the pre-vibration ellipse were subtracted from the centers of the pre-, per-, and post-vibration ellipses in order to shift the origin of the coordinate system to the center of the pre-vibration ellipse [i.e., (A/P, M/L) = (0,0)], as shown in Fig. 2b. A per-vibration postural shift vector was computed from the center of the pre-vibration ellipse to the center of the per-vibration ellipse in order to quantify vibration-induced postural changes (Fig. 2b). Similarly, a post-vibration postural shift vector was computed from the center of the per-vibration ellipse to the center of the post-vibration ellipse in order to quantify post-effects (also Fig. 2b). The same procedure was used for the COP data.

RMS and PSD values of M/L and A/P angular displacements (sway) of body posture as a function of pre-, per-, and post-vibration periods were separately computed to evaluate response amplitude and characterize the frequency distribution and power magnitude of postural sway within specific bandwidths (0.0–2.0 Hz). Average values of

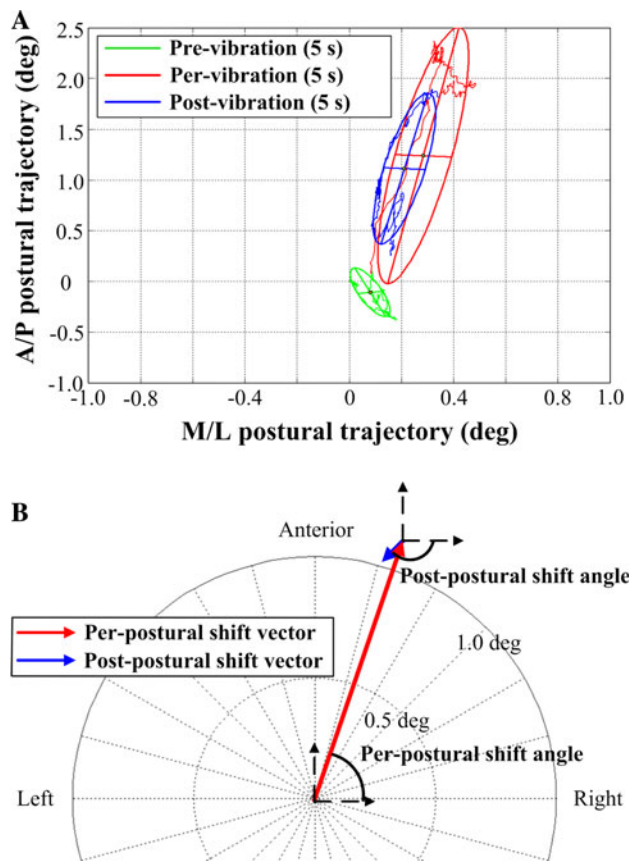


Fig. 2 **a** Illustrative postural trajectories and 95 % confidence interval elliptical fits for each vibration period when the factor was placed over the right internal oblique. Positive values are defined as movement in the anterior and lateral (*right*) directions, respectively. *Green, red, and blue lines* represent pre-, per-, and post-vibration periods, respectively. **b** Two-axis postural shift vectors quantifying the magnitude and direction of postural changes. *Red and blue vectors* represent per- and post-postural shift vectors, respectively (color figure online)

these metrics were computed for each participant and each period as a function of the stimulation location/condition. A similar procedure was used for the COP data.

A two-way analysis of variance (ANOVA) was conducted to determine the main effects of vibration location (six “single location” and the “all locations” conditions) and vibration period (number of periods used in the model varied based on the metric as described in the results section) as well as their interactions for each dependent variable (i.e., analysis metric). Hypotheses for the main effects of the vibration location and period as well as their interactions were tested using an *F* test. To determine which factors influenced the main and interaction effects, post hoc tests (Tukey Honestly Significant Differences (HSD)—for multiple comparisons) were conducted. The level of significance was set at $P < 0.05$. To assure the assumptions of normality, both A/P and M/L RMS values were transformed to a logarithmic scale.

Results

Figure 3 shows typical results from the IMU data for one participant corresponding to vibration applied to the skin over the internal oblique (Fig. 3a, b) and erector spinae (Fig. 3c, d) locations. The posture shifted in the direction of the vibrotactile stimulation during the per-vibration period. A post-effect, indicated by a shift in the direction opposite the vibration application direction, was also observed when vibrotactile stimulation ceased. Figure 4 shows the mean postural trajectories across all participants in both A/P and M/L directions during the pre- and per-vibration periods when vibration was applied to the skin over the right internal oblique muscle. The average latency of vibration-induced postural shifts was 800 ms after the onset of vibration. For each trial, the latency was calculated using a 10-sample moving average (i.e., 0.1-s interval) and a threshold. The latency was defined as the interval when the filtered IMU position signal first crossed the 10.31 deg threshold, which corresponds to the average of the IMU position signal for pre-vibration periods across all participants. This latency was similar (not statistically different, $P > 0.05$) between the conditions inducing a postural shift (right and left internal oblique and erector spinae locations).

There were no significant differences ($P > 0.45$) observed for the COP metrics based on vibration location and vibration period. In other words, the COP did not exhibit vibration-induced changes. Subsequent results detail only the IMU data analysis, and therefore, the term “postural shift” is associated with torso directional inclination.

Postural shift vector

Magnitude

Figure 5 presents per- and post-vibration postural shift vectors relative to the pre-vibration period as a function of the vibration location. ANOVA indicated that the main effects of location [$F(6,140) = 27.70$, $P < 0.0001$] and period [$F(1,140) = 113.82$, $P < 0.0001$] as well as the location \times period interaction [$F(6,140) = 20.91$, $P < 0.0001$] were significant. Post hoc analysis showed that vibration induced a significant shift of posture ($P < 0.02$, Tukey HSD) when applied over the internal oblique and erector spinae locations, but that the magnitude of this shift was not significantly different ($P > 0.26$, Tukey HSD) across these four locations. However, the postural shifts were negligible when vibration was applied over the external oblique locations ($P > 0.27$, Tukey HSD), or at all locations simultaneously ($P > 0.11$, Tukey HSD).

The magnitude of the postural shift vector when stimulation was applied over the internal oblique and erector spinae locations was on the order of 1.2° . The average

Fig. 3 Illustrative postural trajectories and elliptical fits (95 % confidence interval) when vibrotactile stimulation was applied over the internal oblique and erector spinae locations. *Green, red, and blue lines* represent pre-, per-, and post-vibration periods, respectively. Positive values are defined as movement in the anterior and lateral (*right*) directions, respectively (color figure online)

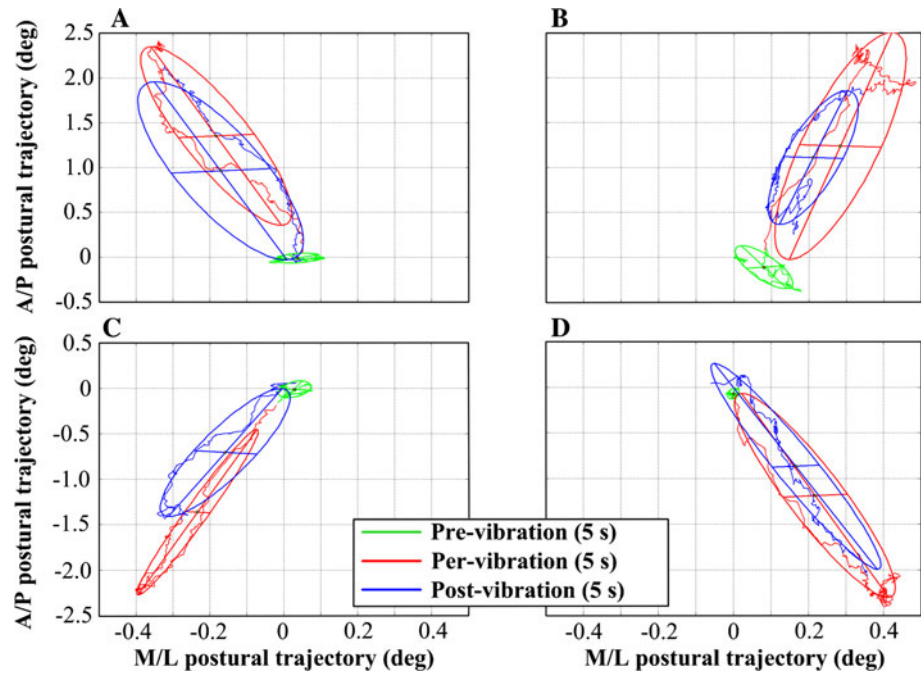
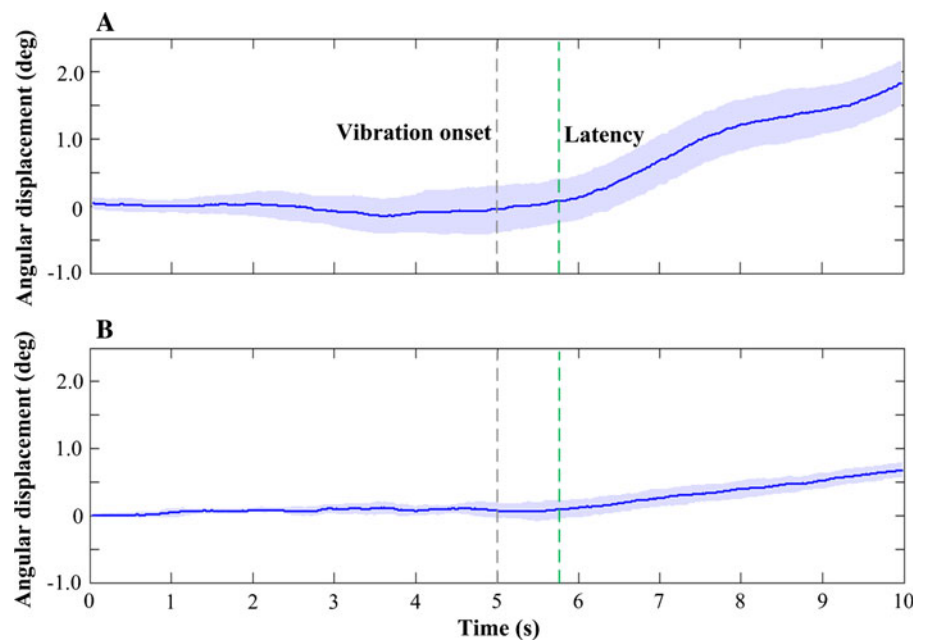


Fig. 4 **a** Average A/P postural trajectories. Positive values correspond to motions in the anterior direction. **b** Average M/L postural trajectories. Positive values correspond to motions in the lateral direction. *Solid blue lines* represent average postural trajectories. *Shaded areas* indicate standard error of the corresponding average postural trajectories (color figure online)



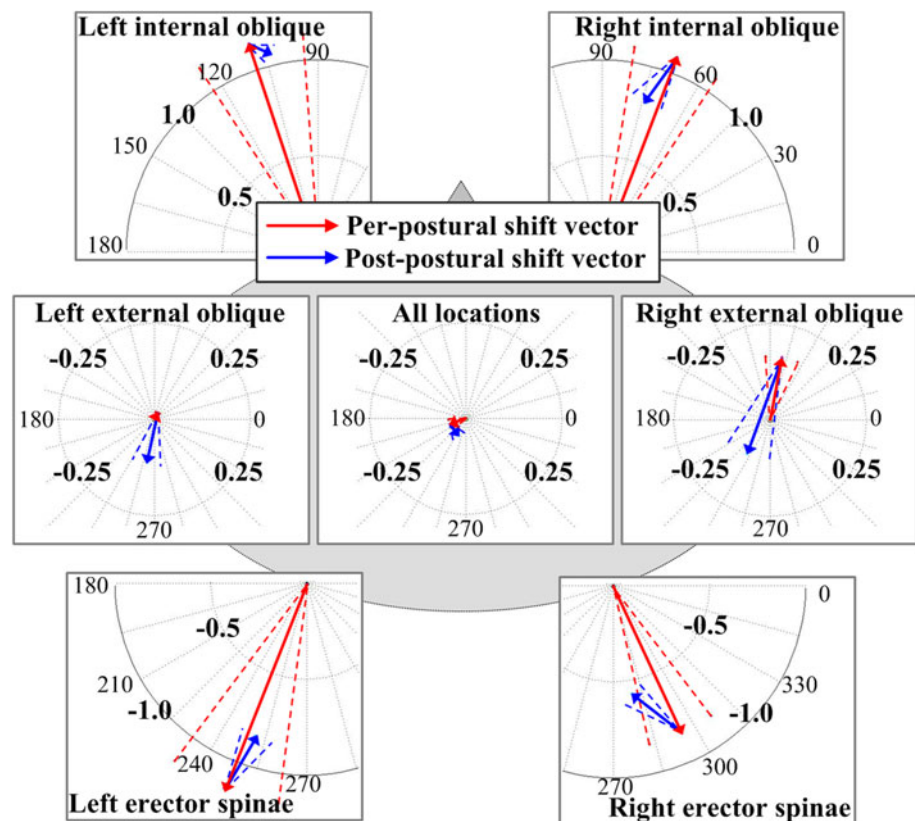
maximum angular displacement in the A/P direction was approximately 2.2° when vibrotactile stimulation was applied over the internal oblique and erector spinae locations.

Direction

ANOVA applied to the directional angle of the postural shift vector showed a significant main effect of location [$F(6,140) = 7.56$, $P < 0.0001$] and period [$F(1,140) =$

71.18 , $P < 0.0001$] as well as a significant location \times period interaction [$F(6,140) = 5.99$, $P < 0.0001$]. Post hoc analysis showed that when vibration was applied over the internal oblique and erector spinae locations, posture significantly shifted ($P < 0.006$, Tukey HSD) in the direction of the corresponding locations during the vibration period and reversed ($P < 0.038$, Tukey HSD) during the post-vibration period, as shown in Fig. 5. However, the directional angle of the postural shifts was not significant when vibration was applied at all locations

Fig. 5 Average postural shift vectors during per- and post-vibration periods, respectively, as a function of tactor location. Red and blue vectors indicate per- and post-postural shift vectors, respectively. Dashed lines indicate standard error of the mean (color figure online)



simultaneously ($P > 0.71$, Tukey HSD), or over the external oblique locations ($P > 0.11$, Tukey HSD). Note that shift magnitudes were negligible for these stimulation conditions.

RMS sway and PSD

Tables 1 and 2 summarize the results of the ANOVA and post hoc tests for the RMS and PSD variables in the M/L and A/P directions. Pair-wise comparisons include the pre-per-, per-post-, and pre-post-vibration periods as a function of location.

Figure 6a, b depicts the average M/L and A/P RMS sway values, respectively. The post hoc analysis showed that M/L and A/P RMS sway values were significantly higher during the per- and post-vibration periods than during the pre-vibration period when vibration was applied over the internal oblique and erector spinae locations. This analysis also showed that the M/L and A/P RMS sway values were not statistically different for the pre-vibration periods preceding all stimulation conditions (six single location and all tactor conditions). Furthermore, the vibration-induced increase in M/L and A/P RMS sway values was not statistically different for the internal oblique and erector spinae locations. However, changes in M/L and A/P RMS sway values were not significant when vibration was applied at all locations simultaneously, or over the external oblique locations.

The PSD in both M/L and A/P directions was computed in the 0.0–2.0 Hz frequency range for each vibration period. Significant main effects of the per-vibration period were observed in the frequency range below 0.5 Hz. Hence, the following results correspond to changes in the PSD magnitude below 0.5 Hz.

Figure 7a, b shows the average PSD magnitude of sway in the M/L and A/P directions as a function of the vibration location for each vibration period, respectively. Post hoc analysis showed that the M/L and A/P PSD magnitudes were significantly larger during the per-vibration period than during the pre- or post-vibration periods when vibration was applied over the internal oblique and erector spinae locations. This analysis also showed that the magnitudes of the M/L and A/P PSD were not significantly different between the pre- and post-vibration periods for any tactor location. The magnitudes of the M/L and A/P PSD were similar when vibration was applied over the internal oblique and erector spinae locations. Furthermore, changes in M/L and A/P PSD magnitudes were not significant when vibration was applied at all locations simultaneously, or over the external oblique locations.

Subjective responses

The majority of participants (9/11) did not perceive vibration-induced postural changes (avg. 2.7/5).

Table 1 Statistically significant results of the dependent variables [i.e., location (L) and period (P)] and their interactions for M/L and A/P RMS sway

M/L RMS				A/P RMS			
Effects	<i>df</i>	<i>F</i> value	Pr > <i>F</i>	Effects	<i>df</i>	<i>F</i> value	Pr > <i>F</i>
L	6, 210	30.44	<0.0001*	L	6, 210	13.70	<0.0001*
P	2, 210	56.44	<0.0001*	P	2, 210	47.03	<0.0001*
L × P	12, 210	6.05	<0.0001*	L × P	12, 210	2.99	<0.0001*
Location	Effects	Pr > <i>F</i>		Location	Effects	Pr > <i>F</i>	
RIO	Pre versus per	0.001*		RIO	Pre versus per	<0.0001*	
	Pre versus post	<0.0001*			Pre versus post	<0.0001*	
	Per versus post	0.853			Per versus post	0.770	
REO	Pre versus per	1.000		REO	Pre versus per	0.983	
	Pre versus post	0.971			Pre versus post	0.964	
	Per versus post	0.967			Per versus post	0.996	
RES	Pre versus per	<0.0001*		RES	Pre versus per	<0.0001*	
	Pre versus post	<0.0001*			Pre versus post	<0.0001*	
	Per versus post	0.682			Per versus post	0.989	
LES	Pre versus Per	0.005*		LES	Pre versus per	<0.0001*	
	Pre versus post	0.002*			Pre versus post	<0.0001*	
	Per versus post	0.931			Per versus post	0.954	
LEO	Pre versus per	0.754		LEO	Pre versus per	0.361	
	Pre versus post	0.656			Pre versus post	0.214	
	Per versus post	0.986			Per versus post	0.940	
LIO	Pre versus per	0.002*		LIO	Pre versus per	<0.0001*	
	Pre versus post	0.001*			Pre versus post	<0.0001*	
	Per versus post	0.857			Per versus post	0.428	
ALL	Pre versus per	0.725		ALL	Pre versus per	0.920	
	Pre versus post	0.779			Pre versus post	0.448	
	Per versus post	0.995			Per versus post	0.683	

RIO right internal oblique, REO right external oblique, RES right erector spinae, LES left erector spinae, LEO left external oblique, LIO left internal oblique, ALL all locations

* Statistical significance

Discussion

The results show that vibrations applied to the skin over the internal oblique and erector spinae muscles induce postural shifts in the direction of the vibration location; in these conditions, the average vibration-induced postural shift indicated by the IMU is 1.2°. This directional effect is not observed for vibrations applied over the external oblique locations or applied simultaneously at all locations around the torso.

The apparent paradox between vibration-induced body inclinations, measured at the torso level, concomitant to no COP changes, measured under the feet, suggests two major inferences. First, postural shifts measured by the IMU correspond primarily to torso inclinations, and second, posture is reorganized to maintain/preserve the location of

the center of gravity (COG) and, as a consequence, the COP location. This is in agreement with the global control of COG position when standing (Dietz 1992) and is also in agreement with a postural strategy based on available sensory information (Nashner et al. 1989) and a mixed hip-ankle/multi-joint strategy that minimizes the “neural effort” to preserve balance (Kuo 1995; Kuo and Zajac 1993). A detailed analysis of postural control or posture reorganization following a change in sensory information is beyond the scope of this study, which focuses on the contribution of cutaneous information to body representation and the sensory feedback component of posture control. Furthermore, torso axial rotation concomitant to flexion/extension or lateral bending cannot be excluded when considering the muscle lines of action. However, such rotation is rather small/negligible for small torso

Table 2 Statistically significant results of the dependent variables [i.e., location (L) and period (P)] and their interactions for M/L and A/P PSD

M/L PSD				A/P PSD			
Effects	<i>df</i>	<i>F</i> value	Pr > <i>F</i>	Effects	<i>df</i>	<i>F</i> value	Pr > <i>F</i>
L	6, 210	46.67	<0.0001*	L	6, 210	40.87	<0.0001*
P	2, 210	83.31	<0.0001*	P	2, 210	107.62	<0.0001*
L × P	12, 210	16.88	<0.0001*	L × P	12, 210	10.03	<0.0001*
Location	Effects	Pr > <i>F</i>		Location	Effects	Pr > <i>F</i>	
RIO	Pre versus per	<0.0001*		RIO	Pre versus per	<0.0001*	
	Pre versus post	0.149			Pre versus post	0.980	
	Per versus post	<0.0001*			Per versus post	<0.0001*	
REO	Pre versus per	0.159		REO	Pre versus per	0.728	
	Pre versus post	0.105			Pre versus post	0.598	
	Per versus post	0.974			Per versus post	0.207	
RES	Pre versus per	<0.0001*		RES	Pre versus per	<0.0001*	
	Pre versus post	0.194			Pre versus post	0.760	
	Per versus post	<0.0001*			Per versus post	<0.0001*	
LES	Pre versus per	<0.0001*		LES	Pre versus per	<0.0001*	
	Pre versus post	0.956			Pre versus post	0.406	
	Per versus post	<0.0001*			Per versus post	<0.0001*	
LEO	Pre versus per	0.310		LEO	Pre versus per	0.051	
	Pre versus post	0.198			Pre versus post	0.085	
	Per versus post	0.959			Per versus post	0.894	
LIO	Pre versus per	<0.0001*		LIO	Pre versus per	<0.0001*	
	Pre versus post	0.055			Pre versus post	0.873	
	Per versus post	<0.0001*			Per versus post	<0.0001*	
ALL	Pre versus per	0.797		ALL	Pre versus per	0.566	
	Pre versus post	0.685			Pre versus post	0.425	
	Per versus post	0.315			Per versus post	0.969	

RIO right internal oblique, *REO* right external oblique, *RES* right erector spinae, *LES* left erector spinae, *LEO* left external oblique, *LIO* left internal oblique, *ALL* all locations)

* Statistical significance

flexion/extension since, for example, the twist moment generated by the internal oblique is only 1/3 of the flexion moment in a maximal exertion (Gatton et al. 2001).

The vibration-induced postural responses strongly support the contribution of cutaneous afferents to an internal representation of the upper body and to body representation. Previous results have shown that cutaneous receptors located in the skin around the finger (Collins and Prochazka 1996; Collins et al. 2005; Edin and Vallbo 1990), elbow (Collins et al. 2005; Goodwin et al. 1972), ankle (Aimonetti et al. 2007; Collins and Prochazka 1996), and knee (Collins et al. 2005; Edin 2001) joints provide proprioceptive information. Cutaneous receptors encode movement kinematics much like muscle spindles do (Edin 1992; Edin and Abbs 1991; Hulliger et al. 1979; Grill and Hallett 1995) and show directional sensitivity around the ankle (Aimonetti et al. 2007; Kavounoudias et al. 1999) and wrist joints (Edin 1992). The present results show that

vibrotactile stimulation induces directional compensatory postural shifts similar to the results of muscle vibration (Lackner et al. 2000; Eklund 1972; Gregoric et al. 1978; Kasai et al. 2002; Kavounoudias et al. 2001; Martin et al. 1980; Lackner and Levine 1979; Wierzbicka et al. 1998; Hayashi et al. 1981; Eklund 1969; Magnusson and Johansson 1989; Slijper and Latash 2004). The direction of the shift for stimulations applied to the skin over the internal oblique and erector spinae locations was congruent with the postural response to skin stretch attendant to muscle lengthening. This stimulus-directional response congruence is similar to that observed when muscle spindles are stimulated by vibrations (Burke et al. 1976a, b; Lackner et al. 2000; Eklund 1972; Martin et al. 1980; Lackner and Levine 1979; Wierzbicka et al. 1998). The 800-ms latency of vibration-induced postural shifts and slow drifts (Fig. 4) when vibration was applied over the right and left internal oblique as well as right and left

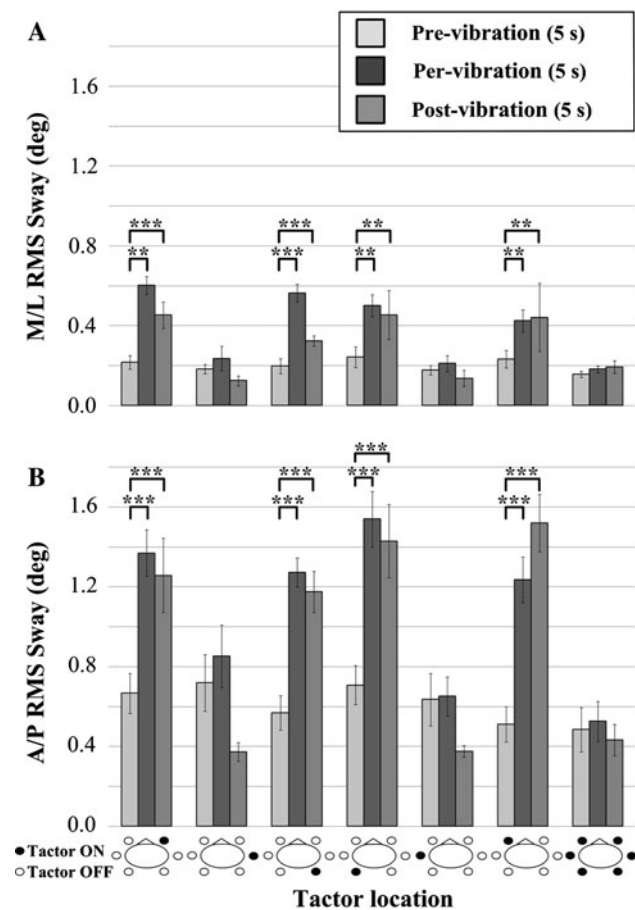


Fig. 6 Average RMS sway as a function of tactor location. **a** M/L RMS sway. **b** A/P RMS sway. Light, dark, and intermediate gray bars represent pre-, per-, and post-vibration periods, respectively. Error bars indicate standard error of the mean. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$

erector spinae locations is substantially greater than that of a reflex response, which is known to be less than 100 ms (Kugelberg and Hagbarth 1958; Martin et al. 1990). Therefore, the latency and slow settling of these responses are not compatible with a cutaneous reflex contribution. Furthermore, vibration applied to the skin over the external oblique locations did not induce a significant shift, as will be discussed below, which also does not favor a cutaneous reflex response. A “tickle” reflex response may be also excluded for the same reasons, and additionally, vibration applied to all locations simultaneously did not induce significant movements.

Presumably, the postural responses observed are involuntary postural adjustments associated with a change in sensory (cutaneous) information, as is the case when muscle proprioceptive information is disrupted by vibrations. Indeed, powerful muscle stimulations can induce falling before the participant realizes the loss of balance (Martin et al. 1980), that is, all postural adjustments in response to muscle stimulation are not perceived

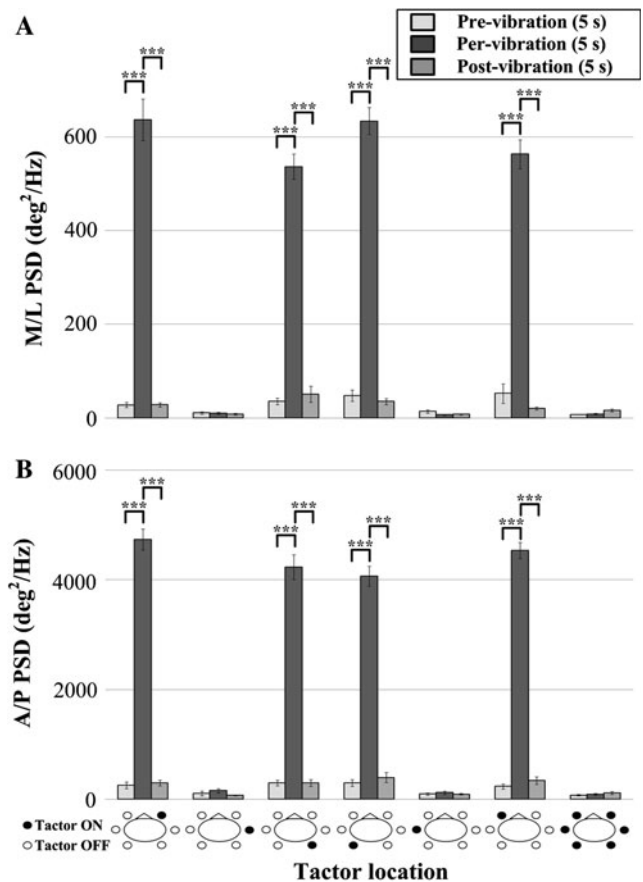


Fig. 7 Average PSD magnitude as a function of tactor location. **a** M/L PSD. **b** A/P PSD. Light, dark, and intermediate gray bars indicate pre-, per- and post-vibration periods, respectively. Error bars indicate standard error of the mean. *** $P < 0.0001$. Note that the scale is ten times greater in **b** than in **a**

consciously (e.g., Lackner et al. 2000; Kavounoudias et al. 2001; Martin et al. 1980). The absence of postural shift perception by a large majority of the participants (9/11), the slow drift of postural shifts, and the absence of drift for the “all” external oblique conditions also preclude the alternative of conscious voluntary responses. The dissociation between perceptual and motor effects may result from the relatively small shift and thus is an automatic motor response that does not require a cognitive intervention, which is common in limb position control and postural regulation, since the displacement is not sufficient to seriously compromise stability. Alternatively, attention may have been diverted by the stimulus, which was perceived, and thus, the small postural change was missed at the conscious level.

Hence, the directional involuntary compensatory response indicates that in the absence of vision, the CNS relies on proprioceptive information from peripheral sensory receptors (Lackner 1988; Massion 1992) during upright stance. In the present context, it should be considered that the frequency response of muscle

proprioceptive receptors is typically limited to approximately 120 Hz (Burke et al. 1976a, b; Martin and Park 1997; Roll and Vedel 1982), but may rise to 220 Hz for the most sensitive receptors (Burke et al. 1976a, b; Roll et al. 1989). However, the frequency response of cutaneous receptors can be as high as 280 Hz (Ribot-Ciscar et al. 1989). Therefore, it is postulated that the 250 Hz vibration was largely ineffective in stimulating the spindle primary endings while activating cutaneous receptors. Our results suggest that the role of cutaneous information in postural stabilization and orientation is significant in the absence of vision and that cutaneous receptors in the skin over the torso's primary mover muscles supply proprioceptive information. This hypothesis is confirmed by the absence of postural shift when all locations around the torso are stimulated simultaneously. This parallels the results obtained during simultaneous vibration at the same frequency of antagonist muscle pairs (Roll et al. 1989; Gilhodes et al. 1986; Calvin-Figuere et al. 1999), which did not produce movement illusions, and co-vibration of the tibialis anterior and soleus muscles (Kavounoudias et al. 1999) and whole trunk vibration (Martin et al. 1980), which did not induce postural effects. In these conditions, homogeneous stimulation of all receptors contributing to body representation produced a neutral effect.

The present vibrotactile-induced shifts are smaller than the movements induced by muscle vibration activating Ia afferents (Calvin-Figuere et al. 1999; Kavounoudias et al. 2001; Roll and Roll 1988). Although postural responses of proprioceptive or tactile origins are frequency dependent (Kavounoudias et al. 2001), they are also limited by the frequency response of each type of receptor, number of receptors stimulated, and weight of each sensory input. Hence, considering that frequency may not be a major factor when stimulations correspond to the upper limit for each receptor category, the difference between vibration-induced postural shifts of cutaneous and muscle proprioceptive origin is likely to reflect the difference in the number of receptors stimulated (Penfield and Rasmussen 1950; Purves et al. 1997), as well as the interaction/incongruence between muscle and cutaneous information, since in the present case, only information from tactile receptors was altered by vibration. Due to the magnitude of stimulation used in most experiments, it is usually assumed that proprioceptive receptors are typically stimulated by tendon vibration (Roll and Vedel 1982); however, in the present case, the amplitude of the tactile vibration was very small ($<200\ \mu\text{m}$) and focused onto a small area ($180\ \text{mm}^2$). Accordingly, the cutaneous vibration-induced afferent flow was relatively small. Therefore, despite these two limitations (cutaneous afferent flow and incongruence between the two modalities), the observed postural shifts support a significant contribution of cutaneous information

to proprioception in the tested areas and the integration of information from the two sensory modalities as suggested previously (Gurfinkel et al. 1988; Horak and MacPherson 1996; Massion 1992).

The lack of significant effects resulting from the external oblique locations is not surprising, since postural stability is greater in the M/L direction than the A/P direction during normal stance (Martin et al. 1980; Winter et al. 1998; Kirby et al. 1987). This effect is commonly associated with the mechanical limitation of bipedal posture, which constrains torso lateral flexion (Huffman et al. 2010; Winter et al. 1998; Kirby et al. 1987). Moreover, the hip-width separation of the feet used in this study likely contributes to a high lateral stability, meaning that small vibration-induced changes in sensory information about the lateral direction may not require a postural shift to avoid instability.

The sway frequency analysis shows that the PSD magnitude in both the M/L and A/P directions increases only in the low-frequency range ($<0.5\ \text{Hz}$) when vibration is applied over the internal oblique and erector spinae locations. Since the postural sway frequency is within the normal range of less than 1.0 Hz (Sienko et al. 2010; Peterka 2002), vibrotactile stimulation does not appear to induce disruptive higher frequency behavior.

To conclude, our findings emphasize the importance of cutaneous information supplied by the receptors over the torso's primary mover muscles in posture regulation and internal representation of the "postural body scheme" that previous research has attributed primarily to muscle proprioception (Lackner 1988; Massion 1992; Roll et al. 1989). The compensatory motor response associated with vibrotactile stimulation of these receptors corresponds to a movement in the direction of the stimulated location, indicating that proprioceptive information from cutaneous receptors in this area obeys the vector rule observed for other locations (Aimonetti et al. 2007). These results may have implications for the design of vibrotactile displays for balance-related applications, since vibrotactile stimulation can be used as an alarm to indicate the direction in which an individual affected by a vestibular disorder has to move to maintain a stable standing posture. Vibrotactile stimulation associated with the instruction, "Move away from the vibration" (Haggerty et al. 2012; Lee et al. 2012b; Sienko et al. 2008, 2012; Wall et al. 2004; Wall et al. 2001), appears incompatible with the "natural" tendency revealed here. Vibrotactile biofeedback techniques leveraging this "natural" tendency may facilitate postural adjustments by reducing the reaction time (response delay) for tactile cues.

Acknowledgments This research was supported by the National Science Foundation's CAREER program (RAPD-0846471, funded under the American Recovery and Reinvestment Act of 2009). The authors acknowledge Jongwha Chang and the Center for Statistical Consultation and Research at University of Michigan for their

consultation regarding statistical analysis and Seunghun Baek for assistance with figure presentation.

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