Postural responses to various frequencies of vibration of the triceps surae and forefoot sole during quiet standing

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Abstract. The purpose of this study was to determine the role of somatosensory input to the sensory reference system in quiet standing. We applied vibration (0.5 mm amplitude, 1–60 Hz) to the triceps surae and the forefoot sole to stimulate the muscle spindles and the mechanoreceptors, respectively, and evaluated postural responses. Thirteen young healthy adults who showed backward-lean and forward-lean responses to vibration at high and low frequencies, respectively, participated in the full experiment. The lowest vibration frequencies inducing backward-lean responses (B-LF) were 15–55 Hz for the triceps surae and 16–60 Hz for the forefoot sole. The highest frequencies inducing forward-lean responses (F-HF) were 3–18 Hz for the triceps surae and 1–20 Hz for the forefoot sole. When vibration was simultaneously applied to the triceps surae and forefoot sole at F-HF, no response was induced in 70% of trials. A forward-lean response was induced in the remaining 30% of trials. Simultaneous vibration of the triceps surae and forefoot sole at B-LF induced backward-lean responses in all trials. All postural responses occurred 0.5–4.3 s after vibration onset. Postural responses to high-frequency vibration conceivably occur as a compensatory movement to the illusionary perception that standing position is deviating forward from quiet standing, which must be a reference position. Postural responses to low-frequency vibration possibly occur to equalize the positional information that is received from the triceps surae and the forefoot sole. Both postural responses are likely to involve the sensory reference system, which is located in the supraspinal nervous system.

Keywords: vibration stimulation, sensory reference frame, postural response, positional perception, triceps surae, forefoot sole

1 Introduction

Sensory information from the muscle spindles of the lower-leg muscles and the mechanoreceptors of the soles of the feet is important for the perception of standing position with eyes closed. This has been demonstrated using vibration stimulation (Eklund, 1972; Fujiwara, Maeda, & Toyama, 2003; Kavounoudias, Roll, & Roll, 1998). During vibration of the triceps surae muscle, information about muscle length and the change in muscle length is transmitted along sensory nerves (the secondary and primary endings, respectively) to the central nervous system (Gardner & Johnson, 2013). The distribution of the muscle spindles (Motobe, 1967) and the neural impulses that are generated by vibration (Ribot-Ciscar, Vedel, & Roll, 1989) suggest that vibration to the forefoot sole is likely to stimulate the skin rather than the planter foot muscles. During vibration of the forefoot sole, information about pressure and the change in pressure is transmitted along sensory nerves from Merkel discs and Ruffini endings, and Meissner corpuscles and Pacini corpuscles, respectively, to the central nervous system (Gardner & Johnson, 2013). Optimal vibration frequencies for the former (the secondary ending and the Merkel discs and Ruffini endings) are lower than that for the latter (Ribot-Ciscar et al., 1989; Roll, Vedel, & Ribot, 1989; Vedel & Roll, 1982).

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When a subject is standing with eyes closed, vibration of the triceps surae or forefoot soles at 20–150 Hz induces backward-lean of the body for most subjects, with a longer response latency than spinal reflexes (Eklund, 1972; Kavounoudias, Roll, & Roll, 2001; Kavounoudias, Roll, & Roll, 1999b). When the standing subject is prevented from moving, an illusionary perception of forward leaning is induced by the vibration (Fujiwara et al., 2003; Roll, Kavounoudias, & Roll, 2002). Therefore, the postural response to vibration is thought to occur as a compensatory response to the illusionary perception created via the sensory reference system, which is located in the supraspinal nervous system (Gurfinkel & Levick, 1991; Lackner & Levine, 1979).

The postural response to high-frequency vibration indicates that the sensory information that results from vibration of the lower-leg muscles or the foot sole is perceived as a deviation from the quiet standing position. In quiet standing the center of pressure in the anteroposterior direction (CoP_{ap}) sways within ±1 cm (Goshima, 1986) at very low frequencies, mainly <2 Hz (Fujiwara, Koyama, Ikegami, & Okada, 1982; Njiokiktjien & Rijke, 1972). With the slow CoP_{ap} sway, the soft tissue in the feet, the skeletal structure of the feet, and the bone of the lower leg are slightly compressed, changed, and inclined, respectively (Burke & Eklund, 1977; Gurfinkel, Ivanenko, & Levik, 1994; Wright, Ivanenko, & Gurfinkel, 2012). It may be assumed that the resulting low-frequency oscillations in sensory information from the lower-leg muscles and foot soles are involved in the organization of the sensory reference frame in quiet standing (Lackner & Levine, 1979; Popov, Kozhina, Smetanin, & Shlikov, 1999). Therefore, it may be worthy to investigate postural responses during simultaneous vibration of a lower-leg muscle and the foot sole.

Postural response to simultaneous vibration of two body parts that induce postural responses to the opposite direction could be explained by vector operation, but the response latency did not differ from that to the single part (Kavounoudias, Gilhodes, Roll, & Roll, 1999a; Kavounoudias et al., 2001). These results suggest that common brain regions are involved in processing the single and simultaneous vibrations (Kavounoudias et al., 2008). However, the postural response to simultaneous vibration of two body parts that induce postural responses to the same direction has not been investigated. It is expected that simultaneous high-frequency vibration of the triceps surae and forefoot sole will induce a backward-leaning response with same latency as that induced by vibration at only one of these locations.

The postural response to low-frequency vibration in the same conditions has not previously been investigated. In a preliminary experiment we found that relatively low-frequency vibration of the triceps surae or forefoot sole induced a forward-lean response, which is the opposite direction to the above-mentioned compensatory response to high-frequency vibration. In the biceps brachii muscle vibration at frequencies ≤20 Hz generates the illusion of muscle shortening, whereas vibration at frequencies >20 Hz generates the illusion of muscle lengthening (Cordo, Gurfinkel, Bevan, & Kerr, 1995; Sittig, Denier van der Gon, & Gielen, 1987). The different illusionary perceptions are thought to occur due to the difference of firing rates by the vibration stimulation to those generated naturally (Cordo et al., 1995). In the forefoot sole pressure information with standing position and sensory information with the vibration are generated during standing (Ribot-Ciscar et al., 1989; Vedel & Roll, 1982). Thus, a similar hypothesis could be applied to the forward-lean response induced by low-frequency vibration. Combining with the vectors theory, simultaneous low-frequency vibration of the triceps surae and forefoot sole would be expected to induce a forward-lean response.
In this study we investigated the postural responses induced by vibration of the triceps surae and forefoot sole at various frequencies. The working hypotheses were as follows: (1) a forward-lean response would be induced when low-frequency vibration was applied to the triceps surae or the forefoot sole, (2) a forward-lean response would be induced when low-frequency vibration was simultaneously applied to these two locations, and (3) the latency of these postural responses would be longer than the latency of a spinal reflex.

2 Methods

2.1 Preliminary experiment for selection of subjects
Sixty-eight healthy young adults (thirty-two men, thirty-six women), selected randomly from students of Kanazawa University, received vibration (60 Hz) for 5 s to both the triceps surae (left and right) or both forefoot soles (left and right) while they were standing with their eyes closed. Sixty-one adults (90%) leaned backward in response to vibration of the triceps surae, and twenty-five (37%) leaned backward in response to vibration of the forefoot sole (figure 1). Twenty-three adults (eleven men, twelve women) showed backward-lean responses to both vibratory stimuli and participated in a further experiment, where they received relatively low-frequency vibration (1–20 Hz) for 5 s to both the triceps surae (left and right) or both forefoot soles (left and right) while they were standing with their eyes closed. Twenty (87%) of these adults leaned forward in response to low-frequency vibration of the triceps surae, and fourteen (61%) leaned forward in response to low-frequency vibration of the forefoot sole. Thirteen participants showed forward-lean responses to both vibratory stimuli and participated in the full experiment.

![Figure 1. The subject selection process. Thirteen adults who showed backward-lean responses to high-frequency vibration of the triceps surae and the forefoot sole and forward-lean responses to low-frequency vibration of the triceps surae and forefoot sole participated in the full experiment.](image)

2.2 Subjects
Subjects were thirteen adults (six men, seven women) who showed backward-lean responses to high-frequency vibration of the triceps surae and the forefoot sole and forward-lean responses to low-frequency vibration of the triceps surae and forefoot sole and participated in the full experiment. The mean ± standard deviation (SD) of age, height, weight, and foot...
length of the subjects was 24.4 ± 5.0 years, 163.5 ± 7.8 cm, 56.5 ± 8.6 kg, and 24.1 ± 1.2 cm, respectively. None of the subjects had a history of neurological or orthopedic impairment. Informed consent was obtained from all subjects after they had received an explanation of the experimental protocol, which was in accordance with the Declaration of Helsinki and approved by our institutional ethics committee.

2.3 Apparatus and data recording
Mechanical vibration was applied to the triceps surae and/or the forefoot sole bilaterally through the skin using four vibrators (FS102, Electro-design, Japan; figure 2). The vibrators had actuators with piezoelectric devices whose displacement could be magnified (MTA05S400F9, Mechano Transformer Corporation, Japan). The pressure capacity of each device was 8 N. Vibration frequency (1–60 Hz) and peak-to-peak amplitude (0.5 mm) were controlled by the change in sinusoidal waveform from a signal generator (WF1966, NF, Japan). The two vibrators for the triceps surae were fixed to a handmade frame located posterior to the subject. The vibrators could be moved freely in three dimensions on the frame. The head of each vibrator (14 × 20 × 13 mm) was oriented along the sagittal plane and set perpendicularly against the Achilles tendon at the level of the medial malleolus. The vibrators were pressed up against the tendons with a force of about 2 N so that they moderately extended the triceps surae during vibration. The two vibrators for the forefoot sole were fixed to the anterior part of a plate with a hard surface (length × width, 50 × 50 cm). The vibrators could be positioned freely in the mediolateral direction on the plate. The head of each vibrator (12 mm diameter) was attached to the metatarsal head area of the foot sole at the point of maximum pressure during quiet standing (figure 2). This part of the sole has many mechanoreceptors (Motobe, 1976). The initial height of the vibrator heads was the same as that of the plate surface. In a subject with average weight (56 kg), foot length (24 cm), CoP\textsubscript{ap} position during quiet standing (46% of the foot length from the heel), and point of maximum pressure (near the 2nd metatarsal head; figure 2), the pressure loaded on each foot-sole vibrator was approximately 4 N during quiet standing. We confirmed that the vibration frequency did not change with a change in the pressure loaded on the vibrator.

A force platform (WA1001, WAMI, Japan) composed of three load cells was set under the plate that contained the vibrators for the forefoot sole to determine CoP\textsubscript{ap}. A pressure distribution measurement system (RSscan International, Belgium) with a spatial resolution of 5.0 mm in the anteroposterior direction and 7.0 mm in the mediolateral direction was used to identify the point of maximum pressure in the metatarsal head area.

Electromyographic (EMG) activity of the tibialis anterior, medial head of the gastrocnemius, and soleus muscles was recorded bilaterally using surface electrodes (P-00-S, Ambu, Denmark). After shaving and cleaning the skin with alcohol, electrodes were aligned along the long axis of each muscle with an interelectrode distance of about 3 cm. The input impedance for all electrodes was reduced to ≤5 kΩ. Signals from electrodes were amplified (×4000) and band-pass filtered (5–500 Hz) using an amplifier (Biotop 6R12, NEC-Sanei, Japan; common mode rejection ratio: 86 dB, input impedance: >10 MΩ).

All electrical signals were sent to a computer (EX/522CME3, TOSHIBA, Japan) for subsequent analyses via an A/D converter [ADA16-32/2(CB)F, CONTEC, Japan] with a sampling frequency of 1000 Hz and 16-bit resolution. The CoP\textsubscript{ap} electrical signal was also sent to two other devices: a buzzer generator (HIRUTA, F-H6408) to inform subjects when they were within a range of ±1 cm from CoP\textsubscript{ap} during quiet standing (Goshima, 1986), and a digital oscilloscope (DS6612, IWATSU, Japan) to enable an investigator to inform subjects of CoP\textsubscript{ap} deviation during the trials.
All measurements were taken while the subjects stood barefoot with the feet parallel and 10 cm apart and the arms relaxed at the sides. Prior to the experiment, subjects stood on the plate for 10 s to enable measurement of pressure distribution and identification of the point of maximum pressure during quiet standing (c), which was determined based on the foot pressure distribution recorded prior to the experiment (d).

Figure 2. Experimental setup. Vibrators for the triceps surae were set perpendicularly against the Achilles tendon at the level of the medial malleolus (a, b). Vibrators for the forefoot sole were fixed to the anterior part of a plate with a hard surface and positioned near the metatarsal head under the point of maximum pressure during quiet standing (c), which was determined based on the foot pressure distribution recorded prior to the experiment (d).

2.4 Procedures
All measurements were taken while the subjects stood barefoot with the feet parallel and 10 cm apart and the arms relaxed at the sides. Prior to the experiment, subjects stood on the plate for 10 s to enable measurement of pressure distribution and identification of the point of maximal pressure in the metatarsal head area. This position was adopted as the stimulation position for the forefoot sole, and its mean ± SD was 71.0 ± 4.4% of the foot length from the heel and 49.4 ± 17.6% of the foot width from the medial side of the foot.

CoP ap fluctuation while maintaining a quiet standing posture with eyes closed was measured for 10 s, and the mean and SD CoP ap position were calculated. The mean and the mean SD of the five measurements were adopted as quiet standing position (QSP) and SDQSP, respectively.

The experiment consisted of two sessions: (1) single vibration and (2) simultaneous vibration. In the single vibration session vibration was bilaterally applied to the triceps surae or the forefoot sole at various frequencies. The large interindividual differences in the vibration frequencies that induced backward-lean responses have been reported (Eklund, 1972;
Kavounoudias et al., 1999b, 2001). Therefore, in each subject the lowest frequency that induced a backward-lean response (B-LF) and the highest frequency that induced a forward-lean response (F-HF) were determined as follows. First, we confirmed that vibration at 60 Hz induced a backward-lean response for three consecutive trials. Next, the vibration was applied three times at each frequency beginning at 30 Hz and changing in steps of 10 Hz, and then in steps of 1 Hz. B-LF was defined as the lowest frequency that induced a backward-lean response in three consecutive trials and was determined for each location. In the same manner, frequencies lower than B-LF were searched to identify F-HF in each location. In the simultaneous session vibration was performed five times at B-LF and five times at F-HF. However, if same response was observed in the first three consecutive trials, no further trials were performed at that frequency. The order of stimulus location (triceps surae and forefoot sole) in the single session and of stimulus frequency (B-LF and F-HF) in the simultaneous session was randomized across subjects.

In each trial vibration was applied as follows (figure 3). First, subjects maintained a QSP within a range of ±1 cm, which was indicated by a buzzer sound, with eyes open for at least 10 s (eyes-open period). Next, they closed their eyes and kept maintaining a QSP for at least 5 s. Then, vibration was applied 5–10 s after cessation of the buzzer sound. For the trials in which vibration was applied to the triceps surae, the head of the vibrators was placed against the Achilles tendon in the eyes-open period. The subjects were instructed to relax and not to resist any postural responses, and were supported by an investigator either at the manubrium or at the superior angle of the scapula when the CoP<sub>ap</sub> exceeded ±4 SD<sub>QSP</sub>. The vibration was stopped once the subjects were supported, or if a response did not appear within 5 s. All subjects rested with eyes open while standing for 30 s between trials and while seated for 3 min when the vibration at a given frequency finished. Before each trial, voluntary forward and backward leaning of the body with pivoting at the ankles and eyes closed was repeated a few times to reset the influence of vibration on postural control and prevent habituation to the vibration (Thompson, Bélanger, & Fung, 2007).

![Figure 3. Protocol of a vibration trial.](image)

2.5 Data analysis
CoP<sub>ap</sub> and EMG data were analyzed using signal-processing software (BIMUTAS II, Kissei Comtec, Japan) by investigators who were blinded to the vibration condition. A CoP<sub>ap</sub> deviation of more than 4 SD<sub>QSP</sub> in the anterior direction was taken as a forward-lean response, and a CoP<sub>ap</sub> deviation of more than 4 SD<sub>QSP</sub> in the posterior direction was taken as a backward-lean response (figure 4). The inflection point of the CoP<sub>ap</sub> deviation was defined as the onset of the postural response. In all backward-lean response trials the CoP<sub>ap</sub> shifted slightly forward just before leaning backward, and the start point of the forward deflection was regarded as the onset of the postural response (Fujiwara, Kiyota, & Maeda, 2011). The amount of time that elapsed from the start of the vibratory stimulus to postural response onset was defined as postural response onset time.
The EMG data were passed through a 40 Hz high-pass Butterworth filter using the seventh-order method and were then full-wave rectified to exclude electrocardiographic and movement artifacts. Backward-lean responses were preceded by an activation of a triceps surae muscle (gastrocnemius or soleus), and forward-lean responses were preceded by an activation of tibialis anterior and/or a deactivation of soleus (figure 2), as in previous studies (Fujiwara et al., 2011; Kiyota & Fujiwara, 2008; Kurokawa, Fujiwara, & Kiyota, 2013). For each trial, activation or deactivation onset was identified as the point in which amplitude increased or decreased more than mean amplitude ± 2 SDs of background activity for at least 50 ms, respectively (Fujiwara et al., 2011; Kiyota & Fujiwara, 2008). The amount of time that elapsed from the start of the vibratory stimulus to the onset of EMG change was defined as EMG onset time. The time between the EMG onset and the postural response onset was measured (Kurokawa et al., 2013).

2.6 Statistical analysis

All data were statistically analyzed using SPSS 14.0J (SPSS Japan, Japan). The data were tested for normality using the Shapiro–Wilks test and for equality of variance using Levine’s test. Nonparametric statistics were used when assumptions of parametric statistics were violated. The postural response onset time in the single vibration session (triceps surae only, forefoot sole only) was compared across response directions (backward-lean, forward-lean) using Wilcoxon’s signed-rank test and a paired t-test, respectively. In the subjects who showed forward-lean and backward-lean responses to the simultaneous vibration at F-HF and B-LF, respectively, the postural response onset time in the simultaneous vibration session was compared across response directions using a paired t-test. The backward-lean response onset time was compared across vibration conditions (triceps surae only, forefoot sole only, simultaneous vibration of the triceps surae and forefoot sole) using the Friedman test. EMG onset time was compared across response directions (backward-lean, forward-lean) using Student’s t-test, and the time difference between the EMG onset and the postural response onset was compared across response directions (backward-lean, forward-lean) using the Mann–Whitney U-test. The α-level was set at $p < 0.05$. 

![Figure 4](image)

**Figure 4.** Representative waveforms of electromyogram (EMG) and the center of pressure in the antero-posterior direction (CoP$_{ap}$) before and during vibration of the triceps surae. (a) Vibration at the lowest vibration frequency that induced a backward-lean response (B-LF). (b) Vibration at the highest vibration frequency that induced a forward-lean response (F-HF). TA = tibialis anterior; GCM = medial head of the gastrocnemius; Sol = soleus.
3 Results
In the single vibration session the B-LF was 29.1 ± 10.2 Hz (range = 15–55 Hz) for vibration of the triceps surae and 31.2 ± 14.2 Hz (16–60 Hz) for vibration of the forefoot sole. The F-HF was 10.4 ± 4.1 Hz (3–18 Hz) for vibration of the triceps surae and 4.3 ± 5.2 Hz (1–20 Hz) for vibration of the forefoot sole. There were large interindividual differences in B-LF and F-HF, as shown in figure 5. Simultaneous vibration of the triceps surae and forefoot sole at F-HF did not induce any postural response in 68.9% trials (N = 11, table 1). In the other trials (31.1%, N = 5) a forward-lean response was induced. Simultaneous vibration of the triceps surae and forefoot sole at B-LF induced a backward-lean response in all trials (N = 13).

Figure 5. The lowest vibration frequency that induced a backward-lean response (B-LF; filled circles) and the highest vibration frequency that induced a forward-lean response (F-LF; open circles) when applied to the triceps surae (left) and forefoot sole (right). Large circles and error bars indicate mean and standard deviation, respectively. Small circles indicate individual data.

Table 1. Percentage of trials with a postural response in the simultaneous vibration session.

| Postural response          | Simultaneous vibration |
|----------------------------|-------------------------|
|                            | at F-HF | at B-LF |
| No response                | 68.9% (11) | 0.0% (0) |
| Forward-lean response      | 31.1% (5)  | 0.0% (0) |
| Backward-lean response     | 0.0% (0)   | 100.0% (13) |

F-HF, the highest vibration frequency that induced a forward-lean response; B-LF, the lowest vibration frequency that induced a backward-lean response. The total number of trials was 45 at F-HF and 39 at B-LF. Numbers shown in parentheses indicate the number of subjects.
Figure 6 shows the postural response onset times. In the single vibration session the onset time of forward-lean responses was significantly later than that of backward-lean responses [2.1 ± 0.8 s (0.9–3.6 s) vs 1.4 ± 0.8 s (0.6–3.4 s) for vibration of the triceps surae, \( p < 0.05 \); 2.5 ± 0.9 s (1.2–4.3 s) vs 1.4 ± 0.7 s (0.5–2.5 s) for vibration of the forefoot sole: \( t_{12} = 5.184, p < 0.001 \). The onset time of backward-lean responses in the simultaneous vibration session was not significantly different from that in the single vibration session.

In the five subjects who showed forward-lean responses to the simultaneous vibration at F-HF, no significant difference in the onset time was found between the forward-lean responses (1.7 ± 0.3 s) at F-HF and backward-lean responses (1.3 ± 0.5 s) at B-LF in the simultaneous vibration session.

Activation of gastrocnemius and/or soleus occurred just before the onset of backward-lean responses in 75.2% of trials (88/117). Activation of tibialis anterior or transient deactivation of soleus occurred just before the onset of forward-lean responses in 53.3% of trials (49/92). The EMG onset time was 1.3 ± 0.9 s for backward-lean responses and 2.0 ± 1.0 s for forward-lean responses (\( t_{135} = 4.49, p < 0.001 \); figure 7). The time between the EMG onset and the postural response onset was 88 ± 26 ms for backward-lean responses and 152 ± 60 ms for forward-lean responses (\( U = 728, p < 0.001 \); figure 8).
Vibration of a relatively high frequency applied to the triceps surae or forefoot sole clearly induced a backward-lean response, as reported in previous studies (Eklund, 1972; Fujiwara et al., 2003; Kavounoudias et al., 1998; Roll et al., 1993). As mentioned in section 1, this backward-lean response is regarded as a compensatory response to the illusionary perception of a forward-lean, which occurs via the sensory reference frame (Fujiwara et al., 2003; Gurpinski & Levick, 1991; Lackner & Levine, 1979; Roll et al., 2002). Simultaneous vibration of the triceps surae and forefoot sole at this high frequency also induced a backward-lean response. The latency of this response was similar to that of the response to vibration at a single location, suggesting that the sensory processing of high-frequency vibration was similar for the single-location and simultaneous sessions.

A previous study that applied vibration to the soles of the feet at 20, 40, and 60 Hz reported that the compensatory backward-lean response reduced or disappeared at the lower frequencies (Kavounoudias et al., 1999b), but vibration frequencies lower than 20 Hz have not been previously investigated. The present study is the first to demonstrate that a forward-lean response is induced by low-frequency (1–20 Hz) vibration applied to the triceps surae or forefoot sole. The latency of this response was similar to that of the response to vibration at a single location, suggesting that the sensory processing of high-frequency vibration was similar for the single-location and simultaneous sessions.

A previous study that applied vibration to the soles of the feet at 20, 40, and 60 Hz reported that the compensatory backward-lean response reduced or disappeared at the lower frequencies (Kavounoudias et al., 1999b), but vibration frequencies lower than 20 Hz have not been previously investigated. The present study is the first to demonstrate that a forward-lean response is induced by low-frequency (1–20 Hz) vibration applied to the triceps surae or forefoot sole. The difference in the direction of the postural response induced by high-frequency and low-frequency vibration might partly be due to differences in the response of the peripheral organs, such as the sensory receptors or primary afferent fibers, to the different vibration frequencies (Ribot-Ciscar et al., 1989; Roll et al., 1989). It is possible that the forward response is caused by the negative difference of sensory information by the vibration stimulation from that with standing (Cordo et al., 1995; Ribot-Ciscar et al., 1989; Vedel & Roll, 1982). It is considered that, from this viewpoint, simultaneous low-frequency vibration of the triceps surae and forefoot sole should induce a forward-lean response. In the present study, however, no postural responses were recognized in 70% of simultaneous low-frequency vibration sessions. We therefore propose the following hypothesis to explain our results.
Postural responses to low-frequency vibration to the single location possibly occur to equalize the positional information that is received from the triceps surae and the forefoot sole. Therefore, when low-frequency vibration is applied simultaneously to the triceps surae and the forefoot sole, positional information from both parts may become equivalent, resulting in no postural response. However, in 30% of simultaneous low-frequency vibration trials, forward-lean responses were induced. In these trials there may have been a small difference in the sensory information generated from the above-mentioned two sources (Collins, Refshauge, Todd, & Gandevia, 2005; Kluzik, Horak, & Peterka, 2005), resulting in a forward-lean response to match the resultant positional sensory information, as in the single-location low-frequency vibration. In quiet standing the CoP\textsubscript{ap} sways within about 2 cm at very low frequencies, mainly ≤2 Hz, and the mean position is distributed from 30% to 60% of foot length from the heel (Fujiwara et al., 1982; Goshima, 1986; Njokiktjien & Rijke, 1972). The low-frequency sensory information generated within the range of quiet standing may play a role in the organization of the sensory reference frame (Fujiwara et al., 2003; Gurfinkel & Levick, 1991) and may be integrated in the same manner as our hypothesis.

The backward-lean responses occurred 0.5–3.4 s after the vibration onset, as in previous studies (Eklund, 1972; Kavounoudias et al., 1998; Roll et al., 1993). The latency of the primary component of somatosensory-cortical-evoked potentials is about 40 ms (Dumitru, Kalantri, & Dierschke, 1991). The latency of the stretch reflex in the lower leg muscles is <50 ms for the short component, <100 ms for the middle component, and about 120 ms for the long component (Andersen, Sonnenborg, & Arendt-Nielsen, 1999; Diener & Dichgans, 1986). Thus, the backward-lean responses might not be reflex responses, but instead might occur via the sensory reference system located in the supraspinal nervous system. The brain regions associated with the vibration-induced illusionary perception are the secondary somatosensory area, parietal lobe, superior temporal sulcus, insula, and cingulate gyrus (Casini et al., 2006; Kavounoudias et al., 2008; Radovanovic et al., 2002).

The onset time of the forward-lean response to low-frequency vibration (0.9–4.3 s) was later than that of backward-lean response to high-frequency vibration in the single-location session. Also, in the simultaneous session the onset time of the forward-lean response was likely to be later than that of the backward-lean response (N = 5), but there was no significant difference, possibly due to the small subject numbers. The difference in the onset time between forward-lean and backward-lean responses may be related to differences in the receptors and primary afferent fibers, as described above, and may also be influenced by biomechanics. The forward-lean response was preceded by activation of the tibialis anterior and/or deactivation of the soleus, and the backward-lean response was preceded by activation of the triceps surae. The EMG onset times were later, and the time from the EMG onset to the postural response onset was also later in forward-lean responses than in backward-lean responses. The time required for the integration of sensory information in the compensatory (backward-lean) and matching (forward-lean) responses may be related to these results. Brain regions involved in the integration of sensory information during vibration of the brachial muscle were similar for low-frequency and high-frequency vibration (Radovanovic et al., 2002). The forward-lean response is also likely to involve the sensory reference system located in the supraspinal nervous system.

In the present study we proposed a new hypothesis about the role of sensory information in the organization of the sensory reference frame in quiet standing, based on the disappearance of postural response to simultaneous low-frequency vibration. Further research about this hypothesis will be required. The range of vibration frequencies that induced forward-lean and backward-lean responses could not be identified, suggesting large individual differences. In order to investigate the cause of the forward-lean response to simultaneous low-frequency vibration of the triceps surae and forefoot sole, we should slightly change the vibration
frequency during the response and demonstrate the combination of vibration frequencies at which the postural response disappears. The timing of the sensory input could be identified using electrical stimulation. The effect of attention to the sensory stimulation on the postural responses should also be investigated in future studies.

5 Conclusions
When vibration was bilaterally applied to only the triceps surae or forefoot sole, a backward-lean response occurred for high-frequency vibration and forward-lean response occurred for low-frequency vibration. However, when the low-frequency vibration was simultaneously applied to both locations, the forward-lean response disappeared in many trials. It is likely that all postural responses involved the sensory reference system in the supraspinal nervous system.

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