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THIS study investigated the role of the plantar cutaneous information in controlling human balance. We hypothesized that the cutaneous afferent messages from the main supporting zones of the feet have sufficient spatial relevance to inform the CNS about the body position with respect to the vertical reference and consequently to induce adapted regulative postural responses. Skin mechanoreceptors of anterior and/or posterior areas of one or both soles of 10 standing subjects were activated by superficial mechanical vibration with high frequency and low amplitude. Variations of the subject's center of pressure (CoP) were recorded. Spatially oriented whole-body tilts were observed for every subject. Their direction depended on the foot areas stimulated and was always opposite to the vibrationsimulated pressure increase. These responses are found to subserve a postural regulative function and we suggest that co-processing of the various cutaneous messages followed a vector addition mode. NeuroReport 9: 3247-3252 © 1998 Lippincott Williams & Wilkins.

Key words: Center of pressure (CoP); Human posture; Soles; Tactile afferents; Vibration

The plantar sole is a 'dynamometric map' for human balance control

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Introduction

In addition to the central postural program, multiple sensory modalities are involved in the organization and control of human erect posture. Numerous studies have focused on the specific role of vestibular,^{1,2} visual^{3,4} or muscular^{5,6} sensory information, but little is known about the role of cutaneous information from the soles. Because they are at the boundary between the body and the ground, the cutaneous mechanoreceptors of the soles might play an important role in controlling balance.

Data supporting this view were obtained through two experimental approaches. A first method consisted of transiently eliminating the exteroceptive afferents by cooling⁷ or anesthetizing^{8,9} the plantar soles. In all cases, suppressing these inputs increased the postural instability. The body sways induced by sinusoidal low frequency (0.3 Hz) displacement of the supporting surface were also increased when an ischemic block of afferent fibers was applied above the ankles. 10,11 In addition, this loss of foot sensitivity resulted in a new strategy to compensate the body disequilibrium, that is, an increased hip strategy instead of the ankle strategy generally used under normal conditions.¹² The ischemic blocking method, however, does not selectively exclude the tactile afferences since it also eliminates all the

somatosensory inputs from the feet, including the proprioceptive ones.

The second method generally used to study the role of plantar cutaneous messages in postural control consisted of changing the characteristics of the supporting surface on which the subject is standing. In fact, by recording the pressure distribution under the soles, Wu and Chiang¹³ demonstrated that standing on a soft (foam) surface reduced the amplitude of the maximal plantar pressures and increased the contact area between the sole and the support. The resulting ankle muscle responses induced by a sudden toes-up rotation of this supporting surface were then delayed. Conversely, standing on a shotgun ball platform¹⁴ resulted in a decrease in the postural body sways.

The contribution of plantar cutaneous afferents to balance control is largely evidenced by these protocols excluding or stimulating all of these afferents. However, how the plantar mechanoreceptors are functionally involved in balance control remains unclear. Studies focusing on the mechanoreceptors of the glabrous skin of the rat foot¹⁵ and of the human hand¹⁶ and foot¹⁷ have shown there are different types of mechanoreceptors, whose distribution and density vary according to the skin areas considered. Because of their specific functional properties, the mechanoreceptors are able to code together the spatial origin,

the amplitude, and the rate of changes in amplitude of a pressure exerted on the skin. Therefore, one can expect that tactile inputs from the main foot supporting areas tell the CNS continuously and precisely how the mechanical pressures are spatially and sequentially distributed on the skin.

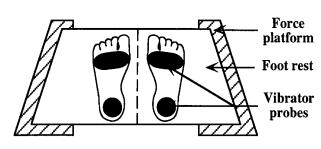
To study the specific role of the cutaneous plantar information in the control of the erect posture, we selectively stimulated the mechanoreceptors of different areas of the sole skin. Superficial, low amplitude and high-frequency vibrations were applied to the anterior and posterior supporting areas of the soles of standing subjects in order to induce cutaneous sensory messages simulating the pressure changes usually associated with oriented body displacements.

Materials and Methods

Subjects: The experiment was performed in 10 healthy subjects (four men and six women, age range 22–55 years). They gave their informed consent to the experimental procedure as required by the Helsinki declaration (1964) and the local Ethics Committee.

Experimental set-up: To selectively stimulate the plantar mechanoreceptors, we used mechanical vibrations with a high frequency and a very low amplitude. Mechanical vibrations were delivered by four electromagnetic vibrators (Ling Dynamic Systems, type 201). The vibrators were driven by rectangular pulses (5 ms) coupled to power amplifiers. The amplitude of the vibrations, measured using a photocell system mounted in the vibrator probes, ranged between 0.2 and 0.5 mm. Because the vibration driving the cutaneous receptors¹⁷ partially differs from that driving the muscle spindles, we set vibration frequency to 100 Hz, i.e. 20 Hz higher than the mean limit for one-to-one driving of muscle spindle endings.¹⁸ The vibrator probes were differently shaped according to the mean shapes of the anterior and posterior supporting zones of the feet of a healthy subject standing upright. The probes of the posterior vibrators were circle shaped (40 mm diameter) to stimulate the heels, and the probes of the anterior vibrators had an ellipse shape (30 mm and 75 mm axis lengths) overlapping the region of the five metatarsal heads of the soles (Fig. 1). The four vibrators were fixed independently on the ground under an elevated rest. They were arranged so that each vibrator probe passed through a hole in the foot rest. In addition, the height of each vibrator could be adjusted until the standing subject perceived only a tactile superficial sensation so that the probes were flush with the subject's soles.

Forward



Backward

FIG. 1. Top view of the experimental device. Subjects stood erect on an elevated foot-rest on a force platform including two pairs of transducers. The vibrators were under the foot-rest and level with the soles. The posterior vibrators were equipped with circular probes to stimulate the plantar skin of the heels; the ellipse shape of the anterior vibrator probes served to stimulate the plantar skin overlapping the region of the five metatarsal heads.

Antero-posterior and lateral displacements of the CoP exerted by the subject's feet were recorded by four strain gauges in the force platform.

Procedure: Subjects were asked to stand barefoot on the foot rest with their hands at their sides, and their eyes closed. They were instructed to relax and not to resist any vibration-induced body tilts. They were promised that if need be, the experimenter would prevent them from falling during the experiments.

Subjects were tested under nine conditions of stimulation, each consisting of 10 trials automatically averaged, except for the control condition, in which no vibration was applied. Under four conditions of single stimulation, vibration occurred either at the anterior or posterior zone of either the left or right sole. Under four other experimental conditions, covibration was applied to two plantar zones as follows: (1) the two anterior zones of both soles, (2) the two posterior zones of both soles, (3) the anterior and posterior zones of the left or (4) the right sole. Under the ninth experimental condition, co-vibration was applied to the four zones of both soles.

Data analysis: In each trial, CoP coordinates were recorded at a sampling rate of 500 Hz for a period of 5 s. The vibration started 500 ms after the beginning of the trial and lasted for 3 s. Under all experimental conditions, every subject's CoP displacement in the plane was analysed during the first 3 s of recording, i.e. before the experimenter had to sometimes prevent the subject from falling. The direction and amplitude of the CoP displacement were defined by a vector whose polar coordinates were obtained by fitting a linear regression of the antero-posterior vs lateral CoP sway recorded for up to 3 s.



To analyse the possible additive effects of covibrating two parts of the soles, we compared the mean experimental vector with the expected one resulting from the vectorial sum of the mean vectors obtained upon vibrating each of these cutaneous regions separately. Under each co-stimulation condition, we tested by the v-test¹⁹ whether the direction of the experimental vectors (α_i) for all subjects (i = 1, ..., n) was randomly distributed over a circle or had a significant tendency to cluster around the theoretical values (α'_i). For this purpose, we calculated every subject's angular deviation (ϕ_i) with respect to the direction defined by the theoretical vector. The distribution of angular deviations ϕ_i (around a unit circle) was first statistically summarized by a mean vector whose direction ϕ_m expressed the angular mean of the distribution, and the length R_m (between 0 and 1) expressed the concentration of the distribution around the angular mean:

$$\begin{split} &\varphi_i = \alpha_i - \alpha_i'; \\ &C = 1/n^* \sum cos\varphi_i; \\ &S = 1/n^* \sum sin\varphi_i; \\ &R_m = \surd(C^2 + S^2); \\ &\varphi_m = \arctan\left(S/C\right) + k^*180^\circ \\ &\text{with } k = 0 \text{ if } C > 0 \text{ and } 1 \text{ otherwise} \end{split} \tag{1}$$

The v value was obtained by multiplying the length of the mean vector by the cosine of the angular mean: $v = R_m \times \cos(\phi_m)$. So, if the directions of the experimental vectors (\alpha_i) did not differ much from the expected values (α'_i) , v was close to 1. Otherwise, v was considerably less than 1 when the angular deviations (ϕ_i) were either uniformly distributed over the circle or clustered in a direction different from that of the theoretical vectors.

For all the subjects (i = 1, ...10) the length of the experimental vectors (l_i) was normalized by assigning the length of the theoretical vectors (l'_i) a value of 1. Using Student's paired t-test, we then compared the normalized data $(L_i = l_i/l'_i)$ with the reference value of 1.

Finally, because co-vibration of the four areas of the two soles induced only small postural body instability without preferred direction, the mean amplitudes of the CoP displacement in the antero-posterior (Y) and lateral (X) planes were respectively compared by Student's paired t-test with those recorded under the control condition.

Results

Applying low amplitude and high-frequency vibration to one or both soles induced involuntary wholebody tilt in all the subjects. The tilt direction depended on how the pattern of stimulation was spatially applied to the foot skin.

Directional body tilts are induced by single or combined tactile stimulations of the soles: Under the four experimental conditions in which the anterior or posterior part of one sole was stimulated, the resulting body tilts were roughly oriented in an oblique direction and in the sense opposite to the vibrated region. In fact, the postural body tilts were oriented backwards and to the left (mean direction (\pm s.d.) $\alpha_{\rm m} = 245 \pm 11^{\circ}$) in response to stimulation of the anterior part of the right sole, and backwards and to the right $(\alpha_m = 286 \pm 19^\circ)$ in response to stimulation of the anterior part of the left sole. Likewise, the postural responses were directed forwards and to the left ($\alpha_m = 118 \pm 18^\circ$) when the right heel was stimulated and, conversely, forwards and to the right ($\alpha_m = 57 \pm 17^\circ$) after left heel stimulation (Fig. 2A).

When vibration was simultaneously applied to two skin areas of either the same sole or the two soles, the whole-body tilts were always orthogonally oriented and contralateral with respect to the vibrated plantar sites, i.e. rightwards ($\alpha_m = 358 \pm 33^\circ$) for left sole stimulation and leftwards ($\alpha_m = 201 \pm$ 25°) for right sole stimulation. Likewise, co-vibration of the anterior or the posterior zones of both feet gave rise to backward ($\alpha_m = 265 \pm 4^\circ$) and forward $(\alpha_{\rm m} = 87 \pm 5^{\circ})$ body tilts, respectively (Fig. 2B).

Lastly, simultaneous vibration of the four plantar areas of both feet never induced clearly oriented displacement of the body; only the postural instability slightly increased (Fig. 2C). In this case, the mean X and Y amplitudes of the CoP displacement did not differ significantly (t-test, p > 0.05) from those recorded during the control condition (Fig. 2D), in which no vibration was delivered.

Experimental vs theoretical combined postural responses: To determine whether the postural response induced by co-vibrating two regions of the soles was the directional and amplitude sum of the singly induced effects, we compared for all the subjects the experimental vectors with the theoretical ones.

Figure 3 gives the mean experimental vectors whose angular direction (ϕ_m) and length (L_m) were normalized with the theoretical ones. Under the four experimental conditions in which the anterior and posterior regions of the soles were stimulated by pairs, the mean experimental vectors were in the close vicinity of the theoretical ones. The direction of the experimental responses had a significant tendency (v-test, p < 0.001) to cluster around the directions of

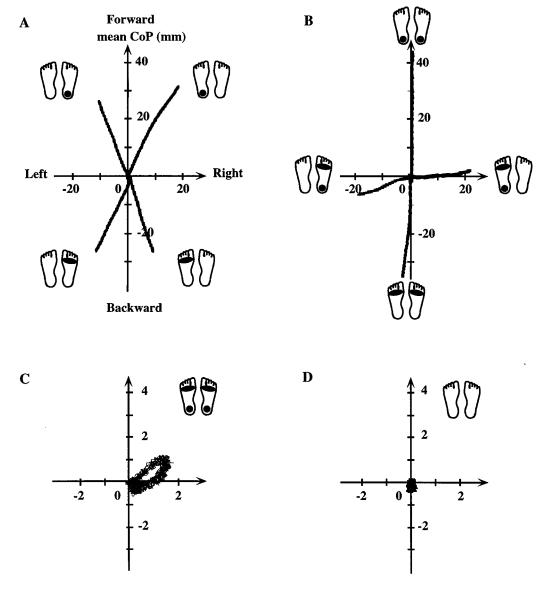


FIG. 2. Mean oriented postural responses induced by applying vibratory stimulation to the anterior and posterior areas of the soles. (A) Single vibration of the anterior or posterior area of the right or the left sole; (B) Combined vibration of two areas of one or both soles; (C) Combined vibration of the four areas of both soles; (D) No vibration, control condition. Traces are the mean trajectories (mm) of the CoP during the first 3 s of recording. The pictograms indicate the vibration sites. Because the subjects' displacements were very small under both control and four vibration conditions, a larger scale was used in (C) and (D).

the theoretical ones, and the lengths of the mean experimental vectors did not differ from theoretical ones (t-test, p > 0.05).

Discussion

Tactile messages from various foot areas contribute to balance control: The noteworthy finding is that oriented whole-body tilts are observed when high-frequency vibration is applied to the skin covering the main foot supporting areas of a standing subject. This clearly demonstrates that cutaneous afferents contribute to human balance control.

That vibration with high-frequency and low amplitude is a particularly relevant stimulation to evoke tactile sensory messages has been proven by many experiments in humans and animals. Microneurographic recordings have shown that both slowly and rapidly adapting cutaneous receptors of the glabrous skin of the human hand as well as those of the foot dorsal part could be activated by applying mechanical vibrations on their receptive fields; most of them are driven with a one-to-one mode up to 200–300 Hz.¹⁷ Those authors also reported that slow adapting pressure receptors are able to code the static pressures applied to their receptive fields as well as their dynamic changes.²⁰ Therefore, the application

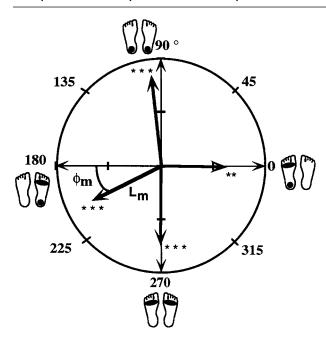


FIG. 3. Comparison between the theoretical and the mean experimental responses induced by the co-vibration of two areas of one or both soles. Bold arrows: mean experimental vectors of the CoP displacements during the first 3 s of recording. The angular direction (ϕ_m) and length (L_m) were normalized with respect to those of the theoretical vectors. Thin arrows: theoretical vectors corresponding to the vectorial sum of the two mean experimental vectors obtained when the plantar areas were stimulated separately. Theoretical vectors are taken as the orthonormed coordinate system of the figure. Note that the direction of the experimental vectors had a significant tendency to cluster around that of the theoretical ones (v-test: ***p < 0.0001, **p < 0.001).

of vibration to a given skin area of the sole probably simulates a local pressure increase, as when the body is actually tilted in the direction of this area. Then, whole-body tilt is triggered in the opposite direction to compensate the virtual disequilibrium. For instance, right heel stimulation gives rise to a sensory message indicating that the body is inclined backwards and to the right; consequently, a compensatory postural response is observed forwards and to the left. This response is forwards when a backward whole-body tilt is simulated by vibrating the two heels. Wu and Chiang¹³ proposed a similar interpretation of the postural responses induced by a sudden toes-up rotation of the supporting platform. In fact, they showed that the pressure variations under the various supporting points of the soles correlate with the direction and amplitude of the compensatory postural responses.

These results should be conflated with those obtained by specifically handling the proprioceptive inputs from ankle muscle groups. Indeed, previous studies have shown that vibratory stimulation of various ankle muscles also induces oriented postural responses. However, that the vibration would spread from the soles up to the leg muscles fails to explain the specific direction of the postural responses obtained upon stimulating the soles. Stimulating the two heels induced a forward body tilt whereas stimulating the Triceps surae proprioceptors induced a postural response in the opposite direction.^{6,21} Moreover, the subjects were all submitted to long vibration (20 s) of the soles before the experiment and never reported kinesthetic illusion whereas such a long vibration applied to different ankle muscles evoked an illusory movement corresponding to the lengthening of the stimulated muscle.¹⁸

Taken together, these results show that the vibration-induced sensory messages from cutaneous or muscle proprioceptive receptors are able to provoke a compensatory whole-body motor response to regulate upright body posture. This is functionally consistent with the fact that every inclination of the body in a given direction causes a lengthening of some specific muscles, which is coupled with a pressure increase in one or various particular sole

The foot sole as a 'dynamometric map'22: Since the postural response induced by co-stimulating two plantar areas of the soles was the vectorial sum of the responses when each of these areas was stimulated separately, the tactile information from various plantar regions is probably permanently coprocessed and integrated by the CNS. Such a vector addition law has been reported for muscle23 and vestibular²⁴ proprioception in order to describe the perceptual and sensorimotor integration of these sensory messages. Thus, in this context, the overall sensory modalities involved in balance control could obey the same integration rules following a vector addition law.

By co-processing the multiple tactile messages from the various plantar areas stimulated, the CNS probably extracts a spatial distribution cue of the pressures in the plane of the feet that is transformed into a body position cue indicating the direction and the amplitude of whole-body inclination. Furthermore, a spatially relevant cue could emerge from the contrast between the pressure levels exerted on each foot or between the anterior and posterior areas of the same foot. Indeed, no oriented body tilts were observed when vibrations were applied simultaneously to the anterior and posterior areas of both soles. In this case, as the pressures are evenly distributed within each foot as well as between the two feet, the tactile sensory messages indicated that the body remained upright and that no compensatory response had to occur. Conversely, any asymmetrical distribution of the pressures under either one sole or between both soles becomes spatially relevant by indicating that the body has deviated from its

equilibrium position, and this gives rise to a compensatory postural reaction to cancel the pressure difference, thus again setting up the body stance.

This interpretation is consistent with the finding that subjects with one sole anesthetized perceived their body as being inclined in the direction opposite to the anesthetized foot.8 Likewise, the EMG activity of the leg muscles of a standing subject whose anterior and posterior parts of the soles rested on different rigidity supports varied according to the pressure difference between the forefoot and rearfoot regions.25

Finally, Wu and Chiang, 13 focusing on the response latencies of two ankle muscles to a sudden toes-up rotation of a platform, also found that both medium and long latency responses in the leg muscles varied according to the dynamic changes of the pressures between the anterior and posterior areas of the soles.

To conclude, these findings led us to consider the sole as a 'dynamometric map' equipped with numerous sensors able to spatially code every pressure exerted against the sole. The processing of the cutaneous messages from the sole along with the other sensory messages must allow the CNS to constantly extract body position information and trigger appropriate responses to reduce the gap between the body position and the equilibrium position.

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