Cutaneous afferents from human plantar sole contribute to body posture awareness

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We investigated whether the tactile information from the main supporting areas of the foot are used by the brain for perceptual purposes, namely body posture awareness and body representation in space. We applied various patterns of tactile stimulation to one or both soles of unmoving and blindfolded subjects by a 60 micro-vibrator tactile matrix set in a force platform. The perceptual effects of the stimulation were assessed through a 3D joystick handled by the subjects. All subjects reported illusory perceptions of whole-body leaning. Both orientation and amplitude of these perceptions depended on the stimulation pattern. Additional kinesthetic illusions sometimes occurred along the longitudinal axis of the body. We conclude that foot sole input contributes to the coding and the spatial representation of body posture. *NeuroReport* 13:1957–1961 © 2002 Lippincott Williams & Wilkins.

Key words: Cutaneous afferents; Foot soles; Human; Postural Illusion; Tactile matrix

INTRODUCTION

Every human sensory system is equipped with sensors giving rise to specific signals that contribute to the awareness of whole-body posture [1]. These signals are integrated to provide the CNS with information about the body geometry necessary for spatially oriented behavior and planning of movements. The nervous mechanisms and brain structures involved in the sensory integration for postural purposes remains a topical question for the neurosciences, usually studied by investigating the effect of vestibular, visual, proprioceptive, and tactile inputs on the upright stance [2–6]. The various sensory modalities may operate in a complementary rather than redundant way [7], and their relative weights may change according to various contextual factors related to body or environment [8,9].

The postural function of cutaneous afferents from the plantar sole has been studied through ankle ischemia and anesthesia of foot sole [10,11]. By inducing oriented postural responses from localized vibration of the foot skin of standing subjects [4], we later showed that the tactile afferents from the feet provide the CNS with information about the body position with respect to the vertical axis. Moreover, plantar inputs may be co-processed with ankle proprioceptive inputs for complementary postural functions [7]. Maurer *et al*. [12] suggested that these cutaneous signals may play a double role: determine body orientation in space and specify the support on which the feet are resting. Various studies have shown the stabilizing influence of tactile information from any body part on human stance. For instance, posture equilibrium is improved by only a light active touch of a finger on an external support [13] or even when the leg or shoulder is passively touched [14]. These studies, however, focused only on the regulative aspects of stance. We thus investigated whether the cutaneous afferents from the foot sole serve in body posture awareness by attempting to evoke, in stabilized subjects, perceptual rather than motor responses to plantar stimulation. Kinesthetic illusions of body tilts occur in standing subjects after manipulating muscle proprioception at various body levels [15], central and peripheral vision [16], and the vestibular apparatus [17]. Analogous effects have never been described after stimulation of the plantar sole. Whole-body kinesthetic illusions were reported only when a support was rotating under the unloaded plantar soles of seated subjects [18]. Most often, tactile illusions resulted from skin stretching or tangential stimulation applied superficially to the skin, and they concerned only a body segment [19–21].

To evaluate whether plantar cutaneous afferents contribute to posture representation and how far they subserve specific functions, plantar areas of either one or both foot soles of unmoving standing subjects were stimulated, and their kinesthetic perceptions were recorded.

We expected that illusory body tilts would be induced by stimulation of the foot soles and that these body tilts would be differently oriented according to the pattern of stimulation.

MATERIALS AND METHODS

Subjects, stimuli, procedure: Ten healthy volunteers (five men and five women, 25–50 years of age) gave informed consent to participate in the experiment according to the recommendations of the local Ethics committee. None of them presented any postural deficit.

Experiments were performed with the subjects blindfolded and standing with the body restrained at the shoulder and hip levels. A joystick set in a small hand rest was fixed to the subject's right or left side by a large belt. Subjects stood on a matrix of tactile stimulation ($500 \times 500 \times 400$ mm), consisting of 60 micro-vibrators whose probes (1.1 cm in diameter) were flush with the foot sole. There were 30 vibrators under the main supporting areas of each foot as follows: three lines of five vibrators under the five metatarsal heads; four lines of three vibrators under the heel, and the three remaining vibrators were lined up under the external border of the foot. The tactile matrix was set on a force platform with three strain gauges to record variations of center of foot pressure (COP; Fig. 1).

Five areas of the foot soles were randomly stimulated (five times each) for 10 s: forefoot or rear-foot zones of both feet, right or left foot sole, and both feet. Under these five conditions of stimulation, subjects were tested using vibration frequency from 0 to 100 Hz with a set amplitude of 0.5 mm. A sixth condition, in which no vibration was applied, served as control.

The kinesthetic effects of the stimulation were assessed through joystick displacements. To check whether the subjects moved the joystick in a direction consistent with their actual perceptions, they described their illusory perceptions after each trial. Variations of COP were recorded for 13 s (2 s before and 1 s after vibration) to ensure no body displacements occurred during the stimulation.

Data analysis: Data were analyzed through mean angular deviations of the joystick along the lateral (X), antero-posterior (Y), and vertical (Z) axes after 8 s of vibration, for each subject in each condition. Because the joystick range was differently calibrated in x and y axes ($\pm 30°$) and in z axis ($\pm 45°$), the amplitude of the responses was expressed as a percentage of the maximal joystick range.

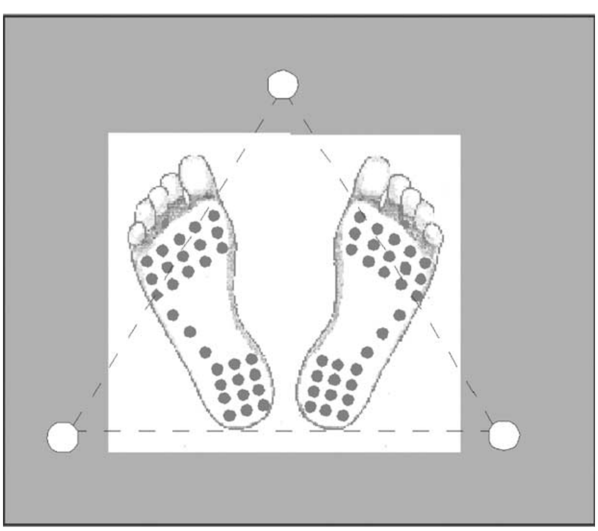

Fig. 1. Tactile matrix of foot sole stimulation: 30 vibrator probes distributed under each foot were flush with the subjects' soles; the three empty circles correspond to the strain gauges of the force platform set under the matrix.

The direction and the amplitude of the illusory postural tilts evoked in the antero-posterior and lateral axes were defined by the polar coordinates (α_i, l_i) of the vector in the plane calculated from the joystick displacements. According to our previous results, we expected vibrating plantar zones would cause postural illusions oriented to the side of the stimulation, that is forward ($\alpha' = 90°$) for the forefoot zone stimulation, and backward ($\alpha' = 270°$) for the stimulation of the heels, and left ($\alpha' = 180°$) or right ($\alpha' = 0°$) for the left or the right foot stimulation, respectively. To verify this hypothesis we used the v-test [22] to test whether the direction of the vectors (α_i) for all subjects ($i = 1 \ldots 10$) was randomly distributed over a circle or if had a significant tendency to cluster around expected values (α'_j) under each vibration condition ($j = 1 \ldots 4$). For all subjects, we calculated the angular deviation ($\theta_i = \alpha_i - \alpha'_j$) of postural illusions relative to the orthogonal direction expected (α'_j). The distribution of these angular deviations θ_i around a unit circle was first statistically summarized by a mean vector whose direction θ_m expressed the angular mean of distribution, and the length R_m (between 0 and 1) expressed the concentration of distribution around the angular mean θ_m. Finally, for each condition of stimulation we calculated $v = R_m \cos(\theta_m)$ (v-test equations are described elsewhere [4]).The v value is close to 1 if θ_i tends to zero, i.e the directions of the responses (α_i) do not differ much from the expected values (α'_j). Otherwise, v is considerably less than 1 when the angular deviations are either uniformly distributed over the circle or clustered in a direction different from that expected.

In addition, we tested the influence of the stimulated sites on the amplitude of the postural illusions evoked in the horizontal plane by one-way ANOVA (significance level $p < 0.05$) with the length of the experimental vectors (l_i) as dependent variable. A one-way ANOVA was also carried out on latency of the illusions. Because the kinesthetic illusions evoked along the vertical axis were not systematically observed in the whole group, they were analyzed separately.

RESULTS

Whatever the plantar zone stimulated, foot sole vibration gave rise to illusory perceptions of oriented body leanings. The direction of these postural illusions varied with the foot sole areas stimulated (Table 1). Subjects reported that the body tilts they perceived were always orthogonally directed and ipsilateral to the vibrated plantar site. As expected, subjects perceived their body slowly leaned forwards when the anterior part of both soles was stimulated and backward when both heels where stimulated. Likewise, illusory perception of rightward or leftward body tilt occurred after right and left foot sole vibration, respectively (Fig. 2). Table 1 shows that the directions of illusory body tilts in the horizontal plane had a significant tendency to cluster around the expected ones (v tests, $p < 0.05$).

No significant difference was found either in the mean amplitude of kinesthetic illusions evoked under these conditions ($F(3,27) = 2.44$, $p = 0.86$) or in illusion latency ($F(3,27) = 0.67$, $p = 0.42$), which was very late (Table 1).

Table 1. Mean ($\pm$ s.d.) latencies, directions (α_m), and amplitudes (L_m) of the postural illusions evoked in the horizontal plane according to the plantar site stimulated ($n = 10$). The v values in the last column show that the experimental directions α_i tended significantly to cluster around the expected orthogonal directions α'_j ($p < 0.005$).

	Latency (s)	L_m (%)	α_m (°)	α'_j (°)	*v* value
Forefoot zones	3.85 $\pm$ 1.2	22.8 $\pm$ 18.4	95.7 $\pm$ 48	90	0.642
Heels	3.53 $\pm$ 0.74	23.2 $\pm$ 19.5	264.4 $\pm$ 39	270	0.767
Right foot	4.02 $\pm$ 1.02	26.3 $\pm$ 22.8	352.2 $\pm$ 18	360	0.944
Left foot	3.89 $\pm$ 1.06	32.6 $\pm$ 19.9	176.3 $\pm$ 37	180	0.790

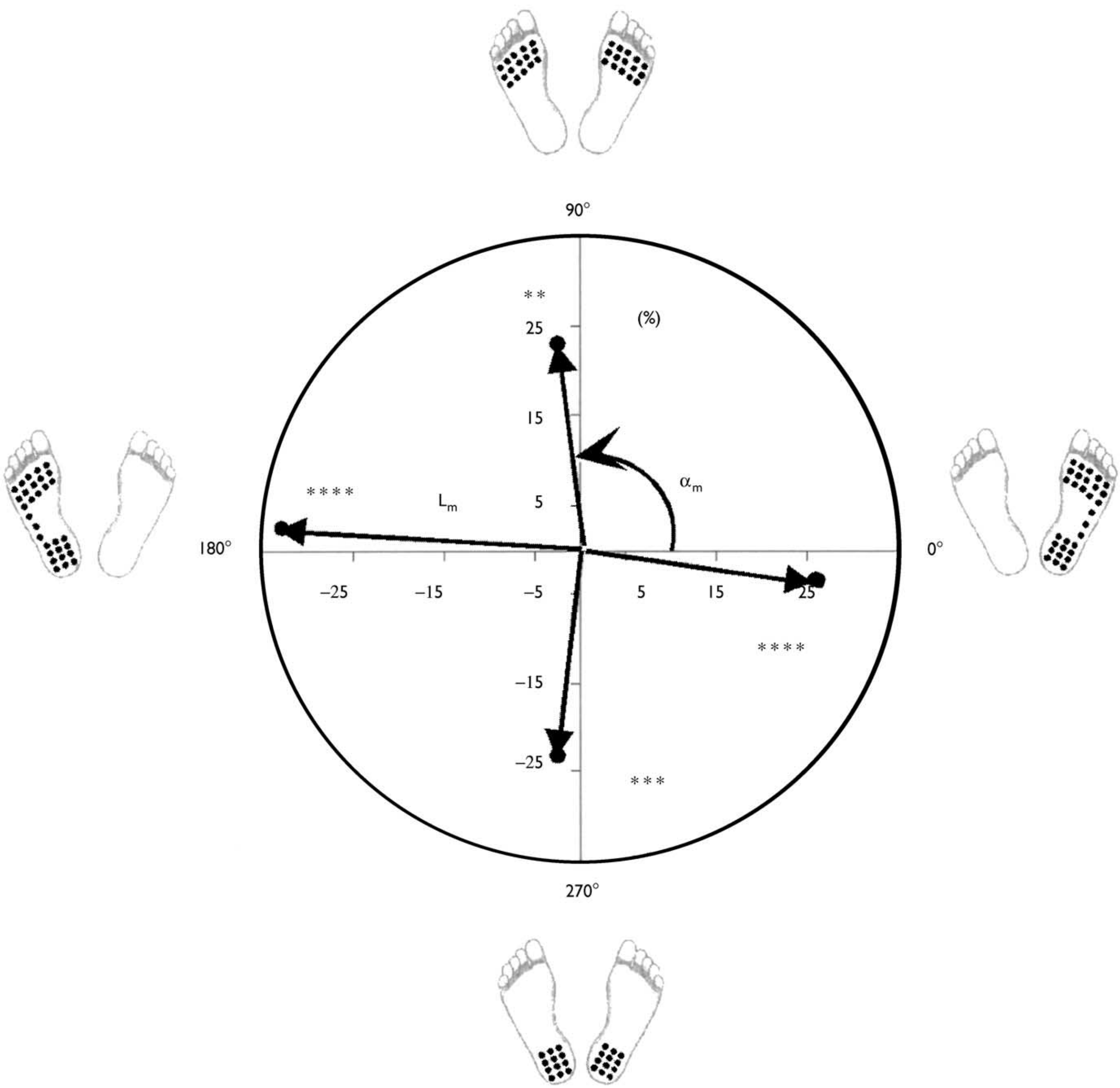

Fig. 2. Mean postural illusions evoked by vibrating various plantar zones for 8 s at 100 Hz. Each vector shows the mean angular direction (αm) and the mean amplitude (Lm) of the perceived body tilts in the horizontal plane ($n = 10$ subjects). Note that the direction of the vectors had a significant tendency to cluster around the theoretical orthogonal direction expected (v-test: ****$p < 0.0001$, ***$p < 0.001$, **$p < 0.005$).

Unlike the asymmetrical patterns of vibration, stimulations simultaneously and equally distributed on the skin of the two feet made the subjects feel only a small instability increase ($L_m = 5.7 \pm 5.0\%$); none of them perceived illusory movements clearly oriented in the horizontal plane.

Surprisingly, 3–7 of 10 subjects reported that kinesthetic illusions could occur concomitantly in the vertical (z axis) and horizontal (x,y axes) planes (Fig. 3). For example, one subject reported, 'my body was tilting backward while my heels were plunging into the ground' during vibration of his plantar rear foot zones. Depending on the subjects, however, these vertical illusions concerned either the whole body or only the lower limbs. Figure 3 shows that the maximum perceptual effect in the vertical direction occurred when the two feet were simultaneously vibrated. In this case, 7 of 10 subjects reported their whole body clearly moved along the longitudinal body axis (z) and perceived this as 'a space rocket taking off' or as 'a load plunging into the ground'.

DISCUSSION

Tactile inputs in foot skin contribute to body posture awareness: Tactile afferent messages evoked by vibration of various foot sole areas of unmoving standing subjects induced kinesthetic illusions oriented specifically in the horizontal plane and in the same sense as the plantar site stimulated. This finding further validates our methodology and corroborates our previous interpretation that plantar stimulation simulates a local pressure increase corresponding to a change of supporting points of the body [4]. When the body is free to move, change in pressure level in a given sole area endangers the subject's stance, provoking a compensatory postural response to prevent falls. Under our present conditions where the body is restrained, the virtual disequilibrium did not need to be compensated: it only gave the subjects the illusion their body leaned in the direction of the pressure increase. This assertion is based on the experimental demonstration that slowly and rapidly adapting cutaneous mechanoreceptors of the border of human foot skin code static and dynamic pressures through a one-to-one coupling between receptor responsiveness and the vibration frequency (100 Hz) [23,24]. Kennedy and Inglis, using microneurographic recordings in the tibial nerve of prone subjects during the application of pressures of 0.5–5000 mN against the foot skin, found both groups of mechanoreceptors, with a majority of rapidly adapting ones, whose receptive fields were evenly distributed in the foot sole [25].

These results support our view that the spatial coding of body verticality by plantar inputs results from the ever-changing contrast between the pressure exerted on different parts of one foot or between the two feet [6]. This view is further supported by the large number of receptors in the main areas holding up the body weight such as heels, metatarsal zones, and external border of the foot, corresponding to those we stimulated. Further evidence that these receptors play a key role in balance control comes from their lack of spontaneous activity in unloaded position and when no specific stimulation was applied to the soles

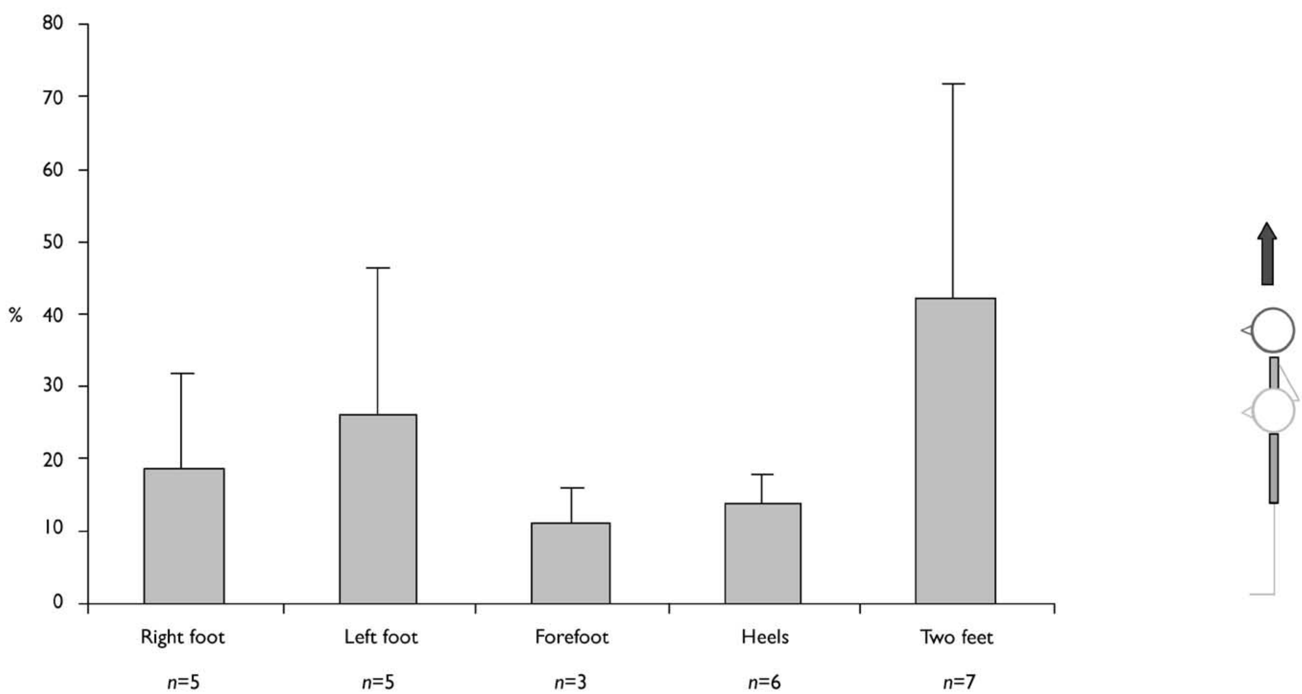

Fig. 3. Mean amplitudes and SD of the vertical illusions according to the plantar site vibrated for 8 s. The number of subjects who reported kinesthetic illusions along the z axis changed under the various conditions, with a maximum (7 subjects of 10) when both feet were simultaneously stimulated. In addition, the highest amplitude of the illusion was found in this latter condition.

[25]. Because balance is mainly dynamical, change in skin pressure under the sole signals how the foot is in contact with the ground and subsequently how far the body position has to be straightened.

It appears the cutaneous afferents from the sole are encoded in a pressure scale and decoded as spatially relevant cues about body orientation for perceptual or motor postural purposes. That notion implies a high-order transformation has occurred from the peripheral signal indicating plantar pressures are asymmetrically distributed, to a spatially oriented body representation signaling body position has changed.

The foot skin as a link between body and environment: Unexpectedly, in some subjects kinesthetic illusions in the vertical plane occurred concomitantly with the horizontal ones. That means that the conscious coding of body position resulting from the transformation of plantar cues into spatial cues also includes the third dimension of space, i.e., that it is done in 3D. Actually, we move our body vertically every time we stand on tiptoes to reach for an object or even simply to go up stairs. That the amplitude of the illusions along the vertical axis was highest when the pressure increased symmetrically under both feet can be interpreted as follows: since no body disequilibrium is expected in the horizontal plane, the body-related processing of pressure increase under the soles occurs in the most spatially relevant direction, that is vertically.

We previously found perceptual illusions that the whole body rises along the z axis in microgravity, where new motor abilities are built as whole-body propulsion inside the module [27]. Postural perceptual responses induced by muscle vibration in standing astronauts vanished after a few days in weightlessness. However, these responses could be transitorily restored by in-flight application of artificial axial forces thanks to stretchers that provided foot sole contact with the ground.

Plantar information was also decoded in terms of environment-related cues, such as nature or state of foot support. Some subjects felt their body plunged into the ground after stimulation of both feet, which is consistent with the data from Wu and Chiang [26] showing that standing on a foam surface increased the contact area between the feet and the ground and made the plantar pressures more evenly distributed throughout the soles. Other subjects in the same condition of stimulation felt their body was pushed upward by a moving support as in the case of an elevator. The pressure change could thus be differently interpreted regarding the context cues.

Foot skin receptors may be functionally involved in exteroceptive and proprioceptive processing by informing the brain about body position and support state. This interpretation differs from that of Maurer *et al.* that these receptors would be involved mainly in exteroceptive functions of evaluating properties of foot support [12]. Their assumptions are based on results that additional tactile stimulation did not improve the responses to platform tilt of normal subjects nor those of patients with vestibular loss. However, the body displacement induced by the moving support could make the tactile stimulation negligible, all the more so as those authors pointed out that small but clear postural responses occurred when identical stimulation was applied to the foot sole of normal subjects under stabilized condition.

In conclusion, although tactile sensitivity can be considered an exteroceptive modality, our results clearly speak for a proprioceptive function of tactile inputs from the foot sole that directly contribute to body representation.

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