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# Support stability influences postural responses to muscle vibration in humans

Yuri P. Ivanenko,[1,2] Vera L. Talis[1] and Oleg V. Kazennikov[1]
[1]Institute for Information Transmission Problems, Russian Academy of Sciences, Bolshoy Karetny 19, Moscow, 101447, Russia
[2]Section of Human Physiology, IRCCS Santa Lucia, via Ardeatina 306, 00179 Rome, Italy

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## Abstract

We studied the effect of support stability on postural responses to the vibration of Achilles tendons and of neck dorsal muscles in healthy humans. For this purpose we compared postural responses on a rigid floor and on 6 cm high rocking supports (see-saws) of different curvatures (different radii: 30, 60 and 120 cm). The subject stood with eyes closed, the centre of the feet coincided with the centre of the see-saw. We recorded platform tilt, horizontal displacements of the upper body, ankle joint angle and activity of ankle joint muscles. On the rocking platform subjects maintained balance in a sagittal direction by making see-saw rotations placing the support under the body's centre of gravity. Equilibrium maintenance requires that the torque in the ankle joint increases during forward body displacements, as on the rigid floor, and be accompanied by a plantar flexion (not by a dorsiflexion) in the ankle joint. The directional dependence of vibration-induced reactions on the see-saw was the same (relative to space) as on the rigid floor: backward body displacement during Achilles tendon vibration and forward body displacement during neck muscle vibration. A decrease of support stability (with a decrease of the radius from 120 to 30 cm) diminished significantly the effect of Achilles tendon vibration and to a lesser extent the effect of neck muscle vibration. In contrast, the increase of platform stability by hand contact with a stable external object gave rise to prominent body sway in response to Achilles tendon vibration. Neck muscle vibration on the movable support provoked a quick initial forward body sway. This initial quick response was absent during vibration of the Achilles tendons. We conclude that postural responses to muscle vibration reflect the participation of different muscles in posture control and depend on the support properties. Support instability changes the role of proprioceptive information and the state of the system of equilibrium maintenance.

## Introduction

The vibration of muscle tendons has become a frequent tool for studying the relative role of muscle proprioception in human posture control (Roll *et al*., 1993; Smetanin *et al*., 1993; Gurfinkel *et al*., 1995a, 1996; Wierzbicka *et al*., 1998). The mechanism of stimulation is based on a selective activation of muscle spindles, predominantly Ia afferents. In a relaxed muscle there is a one-to-one relationship with the vibratory cycles at least in the frequency range of $< 100$ Hz (Bianconi & van der Meulin, 1963; Brown *et al*., 1967; Burke *et al*., 1976; Roll & Vedel, 1982; Roll *et al*., 1989a). As a result of spindle activation, one can observe a contraction of the muscle being vibrated—the tonic vibration reflex (Eklund & Hagbarth, 1966; Lance *et al*., 1966; Matthews & Stein, 1969), or illusions of movements (Lackner & Levine, 1979; Clark *et al*., 1979; Biguer *et al*., 1988).

Intensive investigations of postural responses to muscle vibration began with the pioneering works of Eklund (1969, 1972, 1973) in which he showed that vibration-induced muscle activity influences body equilibrium. Muscle spindles have long been known to be a source of input for both spinal and supraspinal pathways. During quiet standing the spindle activity in gastrocnemius-soleus muscles (usually less than 10 Hz, Burke & Eklund, 1977) is much less relative to that during vibratory stimulation. Yet, Eklund (1972, 1973) noted that the vibration-induced postural sway is not likely explained by tension changes at the ankle joint due to a local tonic vibration reflex. Since then many studies have shown that for a vertical posture vibration induces not local but global reactions related to the change of the whole-body position. This transition from local muscle reactions to whole-body sway is observed during stimulation of different postural muscles: shin, back, hand, neck and even eye muscles (Gregoric *et al*., 1978; Lund, 1980; Pyykko *et al*., 1989; Roll *et al*., 1989b; Quoniam *et al*., 1992; Smetanin *et al*., 1993). It is possible that, in these conditions any proprioceptive signals are interpreted as signals linked to the change in whole-body orientation. Equilibrium control might have a dominant influence on reflex modulation.

The importance of the gravity field for the manifestation of vibration-induced postural reactions was shown during long-term exposure to microgravity. Roll *et al*. (1993) suggested a possible reorganization of motor and perceptual processing of muscle proprioceptive information during space flight: muscle discharges arising from the ankle gradually ceased to mediate the control of standing posture and switched over to the local reflex control of foot motor activity alone.

The directional dependence of postural reactions could indicate a functional meaning of proprioceptive feedback. For instance, during dorsal neck muscle vibration, the postural shift in a direction contralateral to the vibration side suggests motor assistance behaviour associated with whole body orientation (Roll & Roll, 1988), and may be

*Correspondence*: Dr Y. P. Ivanenko, at both above addresses.
E-mail: yi@ccr.jussieu.fr

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explained by interpreting proprioceptive signals from the neck in the context of vestibular signals of head movement (Lund, 1980, 1983; Popov *et al*., 1996).

Support stability might provide an important instrument for the investigation of the role of muscle proprioception as well as visual and vestibular information in the control of vertical human posture (Gurfinkel *et al*., 1974, 1994, 1995b; Dietz & Berger, 1982; Nashner & McCollum, 1985; Dietz *et al*., 1992, 1993; Krizkova *et al*., 1993; Fitzpatrick *et al*., 1994; Ivanenko *et al*., 1997). In the present experiments we investigated whether the reduction of support stability changes the manifestation and the direction of postural responses to the vibratory stimulation of different muscle groups (neck and shin muscles). For this purpose we used movable rocking supports (see-saws) of different curvatures, which allowed a combined rotational and translational movement of the support surface. It is well known that the effect of muscle vibration increases with the increase of frequency of vibration and that, in order to predict the afferent response to vibration, the mechanical characteristics of tendon vibration must be controlled (Cordo *et al*., 1993). The rational of our study was to compare vibration effects on different supports at the same moderate level (40 or 60 Hz) of vibratory afferent activation. The results showed that support instability has a profound influence on postural responses to muscle vibration.

## Materials and methods

### *Experimental set-up*

A group of nine normal subjects (six men, three women, age 25–45 years) participated in the study. Subjects stood on a movable support (see-saw) capable of producing translational–rotational movement (rolling) in the sagittal direction. The lower part of the see-saw was curved in the form of a circular sector and was made of metal in order to have as small a contact with a rigid floor as possible. We used platforms of different radii of the lower cylinder part (30, 60 and 120 cm) and at a height of 6 cm. The total mass of the platform equalled 3 kg. The subject stood with eyes closed, the centre of the feet coincided with the centre of the see-saw. None of the subjects presented any history of neurological disease or vestibular impairment. They gave their written informed consent to the study after the procedure had been explained.

### *Parameters of vibration*

Two identical vibrators (direct current motors VMZ, DPM-30-N1-01, Voronez, Russia, equipped with eccentric rotating masses) were fixed bilaterally by an elastic belt to the Achilles tendons at the ankle level. A moderate vibration (40 Hz, 0.8 mm) was applied.

Stimulation of neck muscle proprioceptors (60 Hz, 0.5 mm) was also carried out by means of a similar DC vibrator (VMZ, DPM-20-N1-01, Russia). The vibrator was fixed on the cervical level to the back of the neck (trapezius and splenius tendons). With this symmetrical position (relative to the cord) of the vibrator, the activation of neck muscle afferents evokes a typical forward body sway in standing humans. Using these parameters of neck vibration, the magnitude and dynamics of the body sway on the rigid surface were similar to those for Achilles tendon vibration (Fig. 3).

### *Data recording*

We recorded the angle of the ankle joint, the angle of platform rotation, horizontal displacements of the upper body (breast) and EMG activity of ankle joint muscles. Positive angular changes corresponded to forward body inclinations. The signals were fed to a PC computer for subsequent processing. Sampling rates for EMGs and angle records were 500 and 20 Hz, respectively.

EMG activity of soleus and tibialis anterior muscles was recorded (Medicor, MG42, Budapest, Hungary) by surface electrodes placed on the left leg. Platform tilt was measured by a strain gauge sensor. Ankle angle was measured as follows: a metal plate was attached to the shin, which curved in accordance with the contour of the shin cross-section. This metal groove was tightly bandaged to the shin by a rubber band so that its flattened part rested on the planum tibia. With a non-elastic string, this plate was connected to a potentiometer, placed on a metal support fixed to the platform in front of the subject's left leg. Thus, shin tilt produced a turn of the potentiometer. The returning force was provided by a weak spring (see Gurfinkel *et al*., 1995b for details on this method).

The displacement of the upper part of the body in the anterior–posterior direction was measured with a strain gauge connected by an elastic string to the 'breast point' (point on the mid-line of the sternum on the level of interaxillary line). The tension and stiffness of the elastic string were small (0.8 N and 7 N/m, respectively) and did not influence the subject's posture.

### *Data analysis*

The duration of muscle stimulation was always 20 s. To quantify the effect of vibration we compared the changes of the mean angle of platform, ankle joint angle and horizontal displacement of the upper body (breast point). For this purpose we compared the last 15 s of vibration (from 5 to 20 s) with the 10-s period prior to vibration. Thus, the transient period which usually lasted several seconds was excluded from the estimation of mean value changes.

The equilibrium was possible at any platform tilt, the only necessary condition being the coincidence of the projection of the body's centre of gravity (CG) with the point of contact between the platform and the floor (Fig. 1A,B). The relationship between the angle of platform inclination $\Delta\alpha$ and the change of the moment arm of the gravitational force $\Delta l$ follows unequivocally from the requirement of equilibrium:

$$l = AO \cdot \sin(\angle AOK),$$

where the change of the angle $\angle AOK$ is equal to $\Delta\alpha$. The distance $AO$ was estimated for each subject by measuring the position of the ankle joint relative to the platform. This distance increases with increasing radius $R$. Thus, small changes of platform inclination must give rise to larger changes in the ankle torque on see-saws of larger radius (Fig. 1C).

The relationship between platform tilt, gravity moment arm, horizontal breast point displacement, ankle angle and platform radius is illustrated on Fig. 1C–E for one subject (subject's height = 1.81 m, the distance between the ankle joint and the CG = 1.09 m, the distance between breast point and the CG = 0.15 m). The change of breast point displacement $\Delta x$ and of the ankle joint angle was estimated with the assumption that body mobility takes place only at the ankle joint. In this case $\Delta x$ is equal to the horizontal displacement of the $K$ point ($\Delta\alpha \cdot R$) plus the displacement of the breast point relative to the K point:

$$\Delta x = \Delta\alpha \cdot R + \Delta\theta \cdot \text{'distance between breast point and CG'},$$

where $\theta$ is the angle of body inclination relative to the vertical ($\Delta\theta = \Delta l/$'*distance between point A and CG*'). For small angles $\Delta l \approx AO \cdot \Delta\alpha$. Thus,

$$\Delta x \cdot \Delta l \cdot R/AO + \Delta l \cdot 0.15/1.09 = \Delta l \cdot R/AO + 0.15/1.09)$$

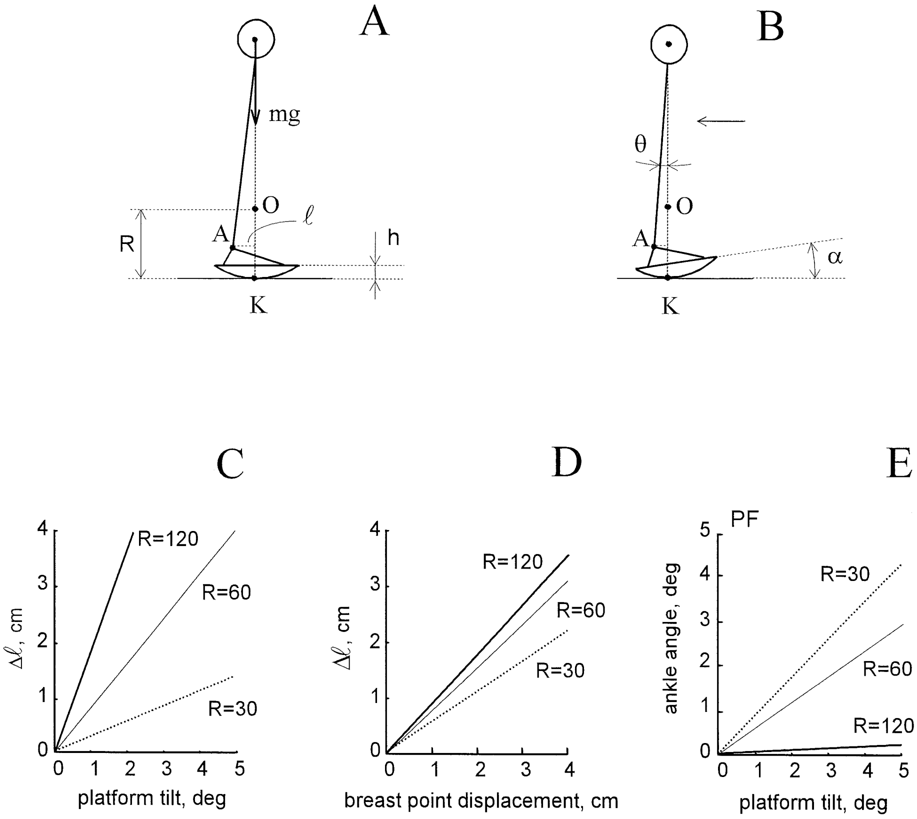


FIG. 1. Peculiarities of the maintenance of body equilibrium on the see-saw. (A) The requirement of equilibrium: the projection of body's CG should coincide with the point of contact of the see-saw with the floor. (B) The direction of ankle joint shift relative to the point 'K' during backward platform rotation: this corresponds to a decrease of the gravitational force moment arm. (C) Calculated change of the moment arm of the gravitational force $\Delta l$. (D) Calculated change of breast point displacement and of $\Delta l$. (E) Calculated change of the ankle joint angle during forward platform inclination. $\Delta l$ was calculated from $\Delta\alpha$. Changes of breast point displacement and of the ankle joint angle were calculated with the assumption that body mobility takes place only at the ankle joint. *O*, the centre of the circle of the see-saw support; *h*, see-saw height; *R*, radius; *A*, axis of the ankle joint; *l*, the moment arm of the gravitational force relative to the ankle joint axis; K, the point of contact of the platform with the floor; α, platform tilt; θ, the angle of body inclination relative to the vertical; PF, plantar flexion.

The change of the ankle joint angle β is:

$$\Delta\beta = \Delta\theta - \Delta\alpha \approx (AO/\text{'distance between point A and CG'} - 1) \cdot \Delta\alpha.$$

### Additional experiments

In an additional series of experiments, we studied the dependence of mean platform inclination on the foot position relative to the centre of the see-saw. For this purpose we used the 30 cm radius see-saw as during standing on this platform it required larger tilts to change the moment arm of the gravitational force (Fig. 1C). The feet were displaced 2 cm forward or backward from the central position. Five trials, each of 1 min duration, were recorded in each condition. Between tests the subject rested, sitting on a chair for 2–3 min with feet supported on the platform. By measuring the mean platform inclination and the geometry of the ankle joint axis relative to the platform we calculated the change in the moment arm of the gravitational force (Fig. 1C). Seven subjects participated in this experiment.

In another experiment we used a finger contact with an external immobile object as a way to increase postural stability (Jeka & Lackner, 1995). During Achilles tendon vibration on the most unstable support of $R = 30$ cm, we asked the subject whose eyes were closed to touch a rigid immobile external object (in front of him/her at a comfortable height and distance) with two fingers of the right hand. The horizontal component of the force of contact was measured by a strain gauge in order to estimate the interaction force with the external object. Five subjects participated in this experiment.

## Results

### Requirement of equilibrium on movable support

Maintaining equilibrium on the rocking platform requires that the projection of the body's CG coincides (within the precision of small oscillations) with the point of contact of the see-saw with the floor (Fig. 1A,B). The see-saw possesses an essential property that allows the subject to maintain equilibrium—the possibility of translational movement: platform rotation automatically causes a horizontal displacement. In the case studied, balance was maintained by means of horizontal displacements of the support under the feet in the direction of the body's CG shift. Horizontal support displacements in the direction of the body's CG shift were the result of active movements in the ankle joint (Ivanenko *et al*., 1997).

The relationship between the angle of platform inclination and the change in the torque in the ankle joint follows unequivocally from the requirement of equilibrium (Fig. 1B,C). One can see the main similarity and the difference between equilibrium on the rigid floor and on the movable support. The displacement of CG forward must be accompanied by the dorsiflexion in the ankle joint on the rigid floor and plantar flexion on the movable support. However, in both cases the moment arm of the gravitational force increases; therefore, the ankle torque increases too.

In the absence of vibration, oscillations in the ankle joint angle, estimated as a standard deviation from a mean value, equalled $0.2 \pm 0.1°$ (mean ± SD) on the rigid floor; $0.2 \pm 0.2°$, on the platform of $R = 120$ cm; $0.7 \pm 0.4°$, on the platform of $R = 60$ cm; and $3.4 \pm 2.6°$, on the platform of $R = 30$ cm. Thus, on the large radius platform the oscillations of the ankle joint and the platform angles were relatively small. It is worth noting that subjects could stand on the movable platform without large efforts or any preliminary practice. Yet, subjectively it was easier to stand on the 120 cm vs. 30 cm see-saw.

### Influence of feet position on the choice of convenient posture

It is known that the natural posture on a rigid floor is characterized by a certain attitude and projection of the body's CG relative to the

TABLE 1. The change of the mean angle of platform ($R = 30$ cm) inclination $\Delta\alpha$ and of the moment arm of the gravitational force $\Delta l$ after displacing feet 2 cm forward or backward from the central position ($n = 7$)

| | – 2 cm (backward) | | 2 cm (forward) | |
|---|---|---|---|---|
| Subject | $\Delta\alpha$ (°) | $\Delta l$ (cm) | $\Delta a$ (°) | $\Delta l$ (cm) |
| 1 | – 7.0 | 0.0 | 6.5 | – 0.6 |
| 2 | – 5.3 | 0.5 | 5.1 | – 0.2 |
| 3 | – 4.6 | 0.7 | 3.6 | – 1.0 |
| 4 | – 2.2 | 1.4 | 2.5 | – 1.5 |
| 5 | – 1.2 | 1.7 | 1.8 | – 1.3 |
| 6 | – 1.1 | 1.7 | 1.4 | – 1.6 |
| 7 | – 0.4 | 1.9 | 1.1 | – 1.7 |
| mean | – 3.1 | 1.1 | 3.2 | – 1.1 |

$\Delta l$ was calculated from $\Delta\alpha$. $\Delta l = 0$ means that the subject changed the platform inclination in order to keep the same torque in the ankle joint.

support area. In our experiments we aimed to find the mean platform inclination (in the absence of vibration) after displacing feet forward or backward on the platform. For this purpose we used the movable platform of 30 cm radius.

When the centre of feet coincided with the centre of the platform, the mean platform position was approximately horizontal; therefore, there was approximately the same ankle angle and ankle torque as on the rigid floor. However, this was not the case after displacing the feet on the platform. Table 1 shows the results of such an experiment. For each subject there was an identifiable mean inclination of the platform as the intrasubject variability was not large (the scatter of $\Delta l$ in five trials did not exceed 0.5 cm). However, different subjects adopted different strategies. Some subjects indeed tended to maintain the horizontal platform position, while others tended to compensate the influence of feet displacement in such a way that the change in ankle torque was minimal. Thus, it seems that both parameters (ankle joint angle and ankle torque) are important for the choice of the convenient posture on the movable support.

### Postural reactions to vibration of Achilles tendons

Vibration of the Achilles tendons on a rigid floor induced backward body sway (Fig. 2). On average, the horizontal displacement of the upper trunk was $-5.8 \pm 1.9$ cm and the change in the ankle joint angle was $-0.8 \pm 1.8°$. The small change in the ankle joint angle was due to the fact that in three of the eight subjects the backward body sway occurred mainly due to the torso backward inclination (presumably due to extension in the pelvis and hip joints, and not in the ankle joint). In these subjects the ankle angle changed often in two phases: first, there was a whole body tilt, then while the upper trunk continued to sway slowly backward, the change in the ankle angle slowed or even changed sign after the torso inclination began. Thus, despite the different behaviour of the lower part of the body, the displacement of the body's CG occurred monotonically in the backward direction. This was accompanied by a decrease in the activity of the soleus muscle.

Both on the rigid floor and on the movable support, there was a backward body displacement in response to vibration of the Achilles tendons (Fig. 3). The intensity of vibration-induced reactions depended on the curvature of the movable support. On average, the effect was rather weak on the see-saw of 30 cm radius and increased with increasing radius (Table 2). Interindividual variability in body sway was rather large even on the rigid surface. This may be explained by the large interindividual variability of the effects induced by muscle vibration (Eklund & Hagbarth, 1966). Nevertheless, all subjects showed the same behaviour when the support stability was decreased. Only one subject displayed similar horizontal displacements of the upper trunk (about 6 cm) regardless of the type of support.

The magnitude of postural responses to muscle vibration was estimated by measuring the magnitude of breast movement and platform tilt (which is directly related to the change of the gravity moment arm, Fig. 1C). We have previously demonstrated that during easy standing both on rigid floor and on movable supports the mobility takes place mainly at the ankle joint (Ivanenko *et al*., 1997). In this case the body can be considered in a first approximation as a single segment. However, during muscle vibration some subjects produced upper trunk displacements by rotating the pelvis and the hip joint (see for example Fig. 2). Therefore, the mean changes of the ankle joint angle were rather small during vibration or even opposite to the expected ones (Fig. 3, Tables 2 and 3).

### Postural responses to neck muscle vibration

Both on the rigid floor and on the movable support, the vibration of neck muscles elicited forward body sway, accompanied by an increase in the ankle torque and in the activity of the soleus muscle (Fig. 3). However, on the movable support the change in the ankle joint angle was opposite to that on the rigid floor. On the movable support the forward body displacement was accompanied by a compensatory plantar flexion in the ankle joint that displaced the support under the body's CG.

It is worth noting two peculiarities of neck muscle vibration on the movable support. First, decreases in platform stability (when we decreased the radius from 120 to 30 cm) decreased the effect of vibration, although to a lesser extent than the effect of the Achilles tendons vibration (Fig. 2, Tables 2 and 3). On the most unstable support of $R = 30$ cm the mean change of platform inclination

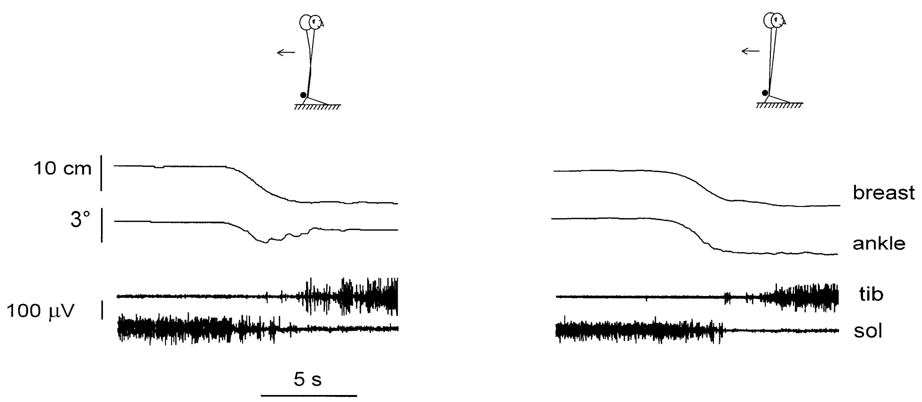


FIG. 2. Postural responses to Achilles tendon vibration on the rigid floor for two subjects.

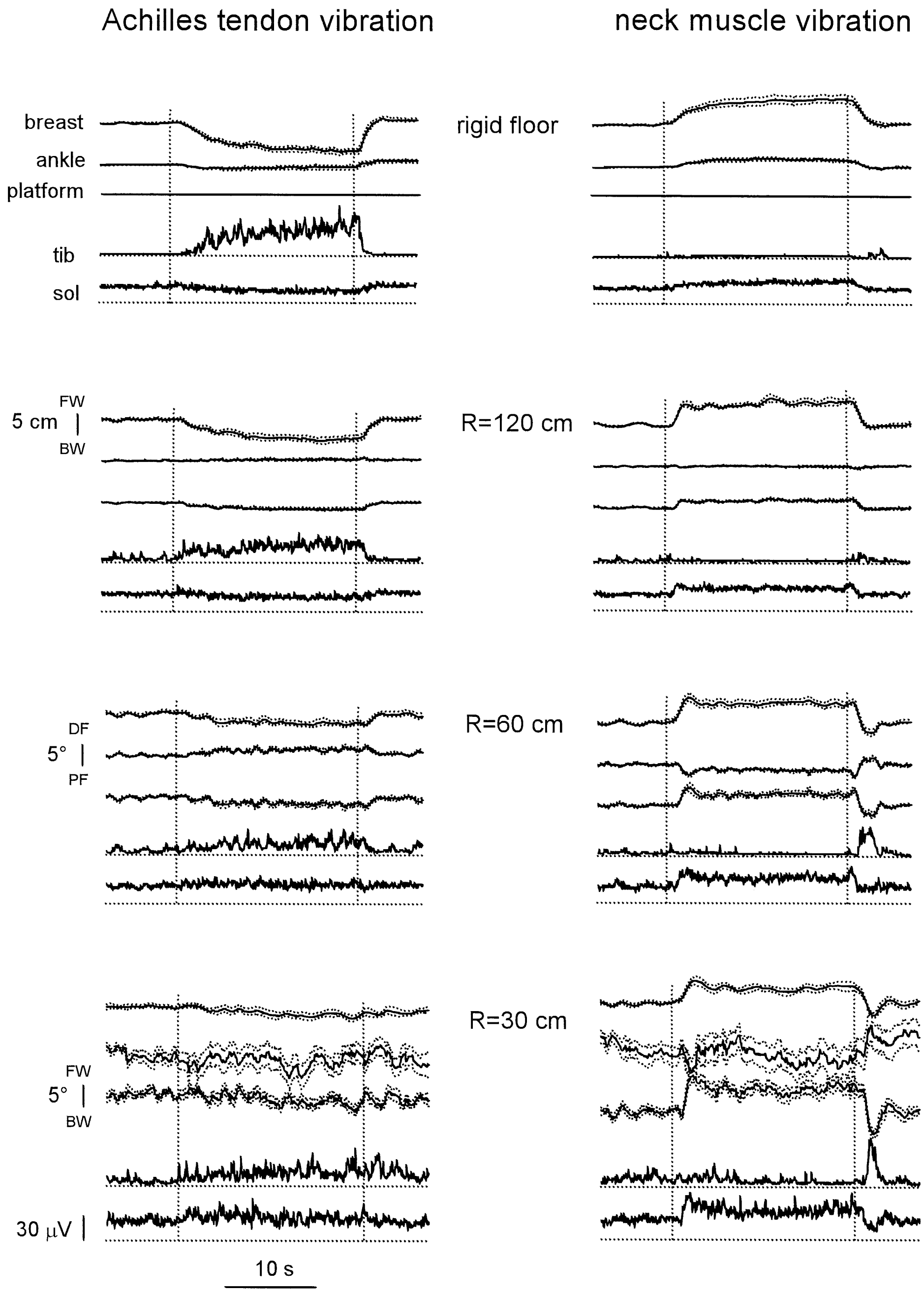


FIG. 3. Averaged (for eight subjects) postural responses to Achilles tendon (left panel) and neck muscle (right panel) vibration on the rigid floor and on the see-saws. EMGs were averaged after preliminary rectifying and filtering. Dashed lines represent ± 1 SEM. FW, forward; BW, backward; DF, dorsiflexion; PF, plantar flexion.

was significantly greater during neck muscle vibration than during vibration of the Achilles tendons (paired *t*-test, $P = 0.01$). Second, during neck muscle vibration on the movable support we observed an initial quick body sway (Fig. 3), which was usually absent during vibration of the Achilles tendons. Some 'over-correction' also occurred at the cessation of vibration on see-saws of smaller radius. Interestingly, the quick initial response was not prominent on the rigid floor but was observed even on the relatively stable movable platform of $R = 120$ cm.

### *The effect of hand contact with external immobile object on postural responses to vibration of Achilles tendons*

We used finger contact with an external immobile object as a way to increase postural stability. The hand contact decreased significantly the oscillations of the platform. On the other hand, the horizontal force of the hand contact with the external object was small (usually less than 3 N) and did not influence significantly the projection of the CG relative to the support (the requirement of equilibrium, Fig. 1A).

On average, the response to Achilles tendon vibration was very small on the unstable 30 cm radius support (Fig. 3). However, when the subject touched the external object the reaction to muscle vibration immediately appeared (Fig. 4). The direction of this reaction was rather sensitive to the feet position relative to the centre of the platform. Usually, if subject shifted the feet 1–3 cm forward, the body sway was in the forward, rather than backward direction. It is possible that hand contact with the external object changes the relative contribution of different sources of information to the control of the postural reference. Nevertheless, it is worth stressing that postural

TABLE 2. Horizontal displacement of the upper trunk, the change of the mean angle of platform inclination Δα ankle joint angle and the moment arm of the gravitational force Δ*l* during vibration of Achilles tendons ($n$ = 9)

| | Breast point displacement (cm) | Δα (°) | Δ*l* (cm) | Change in ankle joint angle (°) |
|---|---|---|---|---|
| Rigid floor | – 5.8 (1.9) | – | – | – 0.8 (1.8) |
| $R$ = 120 cm | – 4.2 (1.9) | – 1.3 (0.6) | – 2.4 (1.1) | 0.3 (0.8) |
| $R$ = 60 cm | – 2.3 (1.8) | – 1.5 (1.5) | – 1.2 (1.2) | 1.6 (0.9) |
| $R$ = 30 cm | – 1.7 (1.9) | – 1.3 (1.6) | – 0.4 (0.5) | – 0.5 (4.5) |

Δl was calculated from Δα. SD given in parentheses.

TABLE 3. Horizontal displacement of the upper trunk, the change of the mean angle of platform inclination Δ(ankle joint angle and the moment arm of the gravitational force Δl during neck muscle vibration ($n$ = 9)

| | Breast point displacement (cm) | Δα (°) | Δ*l* (cm) | Change in ankle joint angle (°) |
|---|---|---|---|---|
| Rigid floor | 6.0 (4.2) | – | – | 1.9 (1.4) |
| $R$ = 120 cm | 5.2 (1.8) | 1.7 (0.8) | 3.1 (1.5) | 0.2 (0.8) |
| $R$ = 60 cm | 4.8 (2.4) | 2.8 (1.6) | 2.3 (1.3) | – 1.2 (1.1) |
| $R$ = 30 cm | 3.7 (1.9) | 5.2 (3.2) | 1.5 (0.9) | – 1.9 (7.0) |

Δ*l* was calculated from Δα. SD given in parentheses.

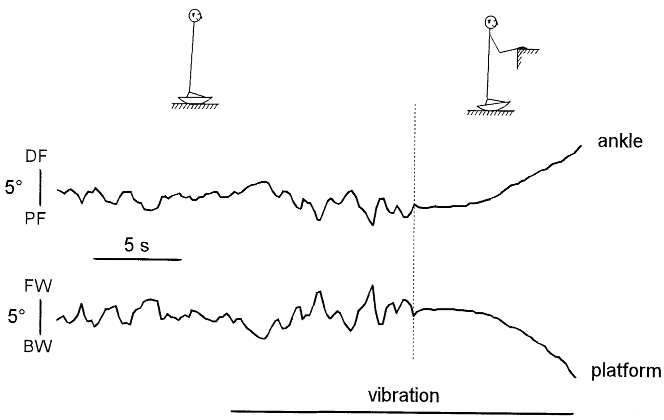


FIG. 4. The effect of hand contact with the external immobile object on postural response to Achilles tendon vibration on the see-saw of 30 cm radius. The dashed line indicates the moment of hand contact. FW, forward; BW, backward; DF, dorsiflexion; PF, plantar flexion.

responses to muscle vibration were easily observed on the movable support when the postural stability was increased due to hand contact with the external object.

## Discussion

One of the most interesting results of this study is that the effect of Achilles tendon vibration diminishes gradually with the diminishing of support stability (Fig. 3). Some data in the literature support these results. It was shown (Gurfinkel *et al.*, 1996) that decreasing postural stability in the frontal plane, by decreasing stance width, diminished significantly body sway in the frontal plane in response to vibration of tensor fascia latae muscles. The authors suggested that, during unstable posture the vibration-induced artificial afferent flow is blocked. Increasing limits of postural stability in the frontal plane increased also the lateral body sway in response to real or illusory head turns during balanced bilateral vibration of tensor fascia latae muscles (Gurfinkel *et al.*, 1995a). However, there is also an observation that, in a tandem Romberg posture, vibration of peroneus brevis and longus muscles was so destabilizing that subjects sometimes fall (DiZio *et al.*, 1997). Possibly, the tandem Romberg posture is very difficult and unstable that small perturbations can evoke falling reaction. Further investigations are needed to clear up this point. Our data are consistent with the suggestion of Gurfinkel *et al.* (1996) and show that the effect of support stability is similar for sagittal and for frontal directions and likely reflects the commonality of underlying mechanisms of equilibrium maintenance.

Instead of large disturbances of equilibrium which could be expected on an unstable support, the influence of vibration of postural muscles strikingly diminished on the movable support. The question arises as to why vibration-induced afferent flow is blocked on the unstable support. A classic definition of stability is based on the behaviour of the system during its perturbation. A stable system should either come back asymptotically to the initial position or the resulting motion should rest within small limits around a stable equilibrium point. Such a condition is true for standing on a rigid floor as the passive elasticity of active shin muscles is enough to compensate for small body perturbations (Gurfinkel *et al.*, 1974). Postural instability should cause large changes in the state of the system of equilibrium maintenance.

It is possible that the central nervous system decreases the reliance on proprioceptive information for postural control when this source of information is confounded by support surface instability. In usual conditions during easy standing on a rigid floor the posture control system elaborates the reference position using information about the relative positions of body links, muscular torques and interaction with the support, taking into account the energy cost of standing and demands for stability and security (Gurfinkel *et al.*, 1995b). This referent vertical is based to a considerable extent on proprioceptive information. It is worth noting the well-defined position (about 4–5 cm in front of the axis of the ankle joint) of the projection of the body's CG relative to the support contour that requires torque in the ankle joint. Operative control of posture occurs relative to this referent vertical. Vibration-induced muscle stimulation can create a false additional signal evoking the displacement of the referent position. As a result, the body sways forward or backward and regulation takes place relative to the new position.

The activation of muscle afferents on a rigid floor can be unequivocally interpreted as a forward body tilt. This is not the case on the movable support. It is not sufficient to use propioceptive information about relative positions of successive links of the body kinematic chain to measure the change in body position relative to vertical, as the platform inclination is not measured by proprioception. Standing on all see-saws can be considered as unstable as it can be maintained only by active reactions and by making see-saw rotations to place the support under the body's CG. From this point of view the platform of 120 cm radius was more stable as the oscillations in the ankle angle were relatively small and a slight tilt of the see-saw was enough for compensation (Fig. 1C–E). This was confirmed by subjective sensations of the participants. Thus, active movements are needed on the unstable support for compensation of the body's CG shifts. Active correcting movements are evoked by vestibular input (in the absence of visual information) and, possibly, by interaction forces with the support. The dependence of postural equilibrium on vestibular input is evident from the inability of patients with complete loss of vestibular function to maintain balance on the see-saw when denied vision (A. Sèmont, personal communication). The importance of feet–support interaction was also shown for maintaining balance on the see-saw (Dietz *et al*., 1992; Ivanenko *et al*., 1997).

It is worth emphasizing that in standing humans the sway–stabilizing reflex contraction operates in 'alpha-gamma linkage', and that these contractions are not generated by segmental stretch reflex pathways (Gurfinkel *et al*., 1974; Burke & Eklund, 1977). Owing to coactivation of fusimotor and alpha-motor units the total afferent activity of shin muscles is proportional to the muscle activity. Therefore, one might even question whether the interpretation of the increased artificial afferent flow on the rigid floor is a stretching of the soleus muscle or the increase of it's activity consistent with the forward displacement of the body's CG.

The support input might be a source of the reference for posture control. Furthermore, pressure input from the human feet contributes to postural stability and influences on galvanically or vibration-induced body sway (Magnusson *et al*., 1990a, b). Both parameters – ankle angle and ankle torque – are important for the choice of the convenient posture on the movable support (Table 1). Taking into account that on the rigid floor quasi-static body sways should be accompanied by changes in the ankle torque (or centre of foot pressure), one can suggest that load interactions with the support play an important part in subjective sensation of body displacement forward or backward in the gravity field. Possibly, this could explain the direction of postural responses on the movable support: vibration of the Achilles tendons always evoked backward body displacement and the decrease of the ankle torque despite a different behaviour in the ankle joint angle (Fig. 3). Vibration responses were also more prominent on see-saws of larger radius on which the platform tilt was accompanied by larger load changes for shin muscles (Fig. 1C).

Hand contact with the external stable object increased postural stability and gave rise to prominent body sway. It is likely that hand contact with the external object elicits a reorganization of the posture control system and changes the relative contribution of different sources of information to the control of the postural reference. This could explain why the direction of the postural sway was dependent on the feet position relative to the support. Nevertheless, this result points out that the absence of marked postural reactions on the support of $R = 30$ cm was not due to specific properties of that support (large mobility in the ankle joint, relatively small horizontal support displacements, etc.), but due to the postural instability.

Another interesting result of the study consisted of peculiarities of postural reactions to neck muscle vibration. Shin muscles participate directly in balancing on the movable support while neck muscles stabilize only the head position. On the rigid floor, neck muscle vibration did not differ much from vibration of the shin muscles; the main difference was the opposite direction of the body sway (Fig. 3). However, on the movable support postural responses to neck muscle vibration were larger in magnitude than those to Achilles tendon vibration and included the quick initial response.

It has been suggested that the processing of neck and vestibular afferentation interact strongly (Lund, 1980; Lund & Broberg, 1983; Smetanin *et al*., 1993). Owing to the mobility in the neck, the interpretation of vestibular signals should take into account the head orientation relative to the trunk in order to control human posture. It is known that the direction of body sway in response to neck muscle vibration as well as to labyrinth stimulation depends on the head orientation relative to the trunk (Popov *et al*., 1986; Smetanin *et al*., 1993; Hlavacka *et al*., 1995). These facts are understandable if one takes into account the common processing of vestibular and neck proprioception inputs in the system of spatial orientation. This could explain the peculiarities of postural responses to neck muscle vibration on the rigid floor in labyrinthine-defective patients (Popov *et al*., 1996; Lekhel *et al*., 1997).

In order to explain why the intensity of the vestibulomotor reaction depends on postural stability in the frontal plane, Day *et al*. (1997) suggested that vestibular influences on leg muscles were determined by the necessity of involvement of the vestibular system for body position maintenance. Neck vibration may be expected to induce maximum equilibrium disturbances in the least stable posture as in these conditions the vestibular system plays a particularly important part in equilibrium maintenance. According to this assumption, one can probably explain the quick initial body sway on the movable support in response to the transient change in the cervical signal (Fig. 3).

As a general conclusion, we have observed different responses to the same sensory input, depending on the support properties. Support instability strikingly diminished the effect of Achilles tendon vibration. On the other hand the prominent effect of neck muscle vibration might reflect the common processing of vestibular and neck proprioception inputs. The human central nervous system is not just a set of reflexes and is organized according to the meaningful context of multisensory information. These findings are important for understanding the organizational principles which characterize the state of the system of equilibrium maintenance and the use of proprioceptive information.

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## Abbreviations

CG, centre of gravity; EMG, electromyography

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