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Stance- and locomotion-dependent processing of vibration-induced proprioceptive inflow from multiple muscles in humans

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ABSTRACT

We performed a whole-body mapping study of the effect of unilateral muscle vibration, eliciting spindle Ia firing, on the control of standing and walking in humans. During quiet stance, vibration applied to various muscles of the trunk-neck system and of the lower limb elicited a significant tilt in whole body postural orientation. The direction of vibration-induced postural tilt was consistent with a response compensatory for the illusory lengthening of the stimulated muscles. During walking, trunk-neck muscle vibration induced ample deviations of the locomotor trajectory toward the side opposite to the stimulation site. In contrast, no significant modifications of the locomotor trajectory could be detected when vibrating various muscles of the lower as well as upper limb. The absence of correlation between the effects of muscle vibration during walking and standing dismisses the possibility that vibration-induced postural changes can account for the observed deviations of the locomotor trajectory during walking. We conclude that the dissimilar effects of trunk-neck and lower limb muscle vibration during walking and standing reflect a general sensory-motor plan, whereby muscle Ia input is processed according to both the performed task and the body segment from which the sensory inflow arises.

INTRODUCTION

Sensory information conveyed along afferent fibers from muscle proprioceptors plays an important role in the control of posture and gait in humans (Pearson 2004; Schieppati and Nardone 1999). A number of studies have demonstrated that tendon vibration, which almost selectively activates muscle spindle primary endings and elicits a discharge in the fast-conducting large-diameter group Ia afferent fibers (Roll et al. 1989a), can induce oriented postural imbalance (Eklund 1969; Kavounoudias et al. 1999; Lund 1980; Roll et al. 1989b) as well as direction-specific gait deviations (Bove et al. 2001; Bove et al. 2002; Courtine et al. 2003; Courtine et al. 2001; Ivanenko et al. 2000a; 2000b; Verschueren et al. 2002; 2003).

Nevertheless, the extent to which proprioceptive information originating from trunk-neck compared to lower body muscles influences the performance of standing and walking motor activities remains unclear. For example, whereas neck (Courtine et al. 2003) and trunk vibration (Schmid et al. 2005) induce noticeable motor effects during standing and walking, vibration applied to muscles about the ankle elicits large body tilts in standing position but has no or weak effects during gait (Courtine et al. 2001; Ivanenko et
al. 2000a; Verschueren et al. 2002). Processing of sensory inputs originating from lower limb muscles is known to be altered, presumably gated by presynaptic inhibition, when engaging the neuromotor circuits for stepping (Stein and Capaday 1988). Such functional adaptation may explain why the reduction of vibration-induced effects during walking is restricted to lower limb muscles compared to trunk-neck muscles (Courtine et al. 2001; Ivanenko et al. 2000a; Verschueren et al. 2002).

Nevertheless, no study performed a systematic whole body mapping investigation of muscle vibration effects during posture and gait, and no attempts were made to contrast vibration-induced alteration of posture with changes in gait control in the same subjects with the same vibrator location. Considerable differences between subjects in the extent of vibration-induced motor responses have repeatedly been documented (Courtine et al. 2003; Gurfinkel et al. 1998; Ivanenko et al. 2000b) and the direction of vibration-induced motor responses can differ substantially with relatively small displacements of vibrator location (Roll and Gilhodes 1995). Therefore, the smaller efficacy of vibration-induced effects during walking compared to standing for stimulations applied to lower limb muscles but not trunk-neck muscles cannot be generalized on the basis on the available data.

In the current study, we applied unilateral vibration to various aspects of the body muscular chain during quiet stance and overground walking in the same subjects with unchanged vibrator location in both tasks. Our aim was to contrast the effects on posture and on gait induced by a continuous discharge of the spindle group Ia input from lower limb muscles compared to trunk-neck muscles.

METHODS

Participants

Eight healthy subjects (six males and two females, 26 to 58 years old) participated in the present experiment after giving written consent in accordance with the Declaration of Helsinki.

Walking task

From an erect body position with standardized foot position (footprints sketched on the floor), subjects were asked to walk eyes closed in the straight-ahead direction. They performed the task with their own sport shoes. Subjects started the walking task with the left foot according to a verbal signal provided by the investigator, and stopped when so
told, after approximately 8 meters walk. Instructions was given not to oppose any vibration-induced effect during walking (Courtine et al. 2003). Then, subjects opened their eyes and returned to the starting position with the eyes open through a freely chosen trajectory and timing.

They first performed 5 trials under no-vibration condition before any vibration was applied. After completion of the no-vibration condition, participants performed the same locomotor task but a vibratory stimulation was applied to various aspects of the body. Vibration (80 Hz) was triggered at the onset of the second left heel strike by means of a foot switch located under the left heel. A total of 16 vibration conditions were tested, corresponding to the 16 different vibrator positions. The exact positioning of the vibrator for each condition is reported in Fig. 1. The different vibrator positions were randomly dispersed across subjects and sessions. The participants performed 6 trials for each vibration condition. Vibration was not turned on during one of these trials (selected randomly) in order to prevent subjects from anticipating vibration effects and to check that no post-effects of vibration affected locomotion. These trials were also used to ensure that walking with the vibrator attached to the body did not interfere with the production of walking. The absence of significant differences between the control condition and these trials (see Results) confirmed that subjects did not alter their walking trajectory when walking with the vibrator. An interval of 30 s to 1 min separated each trial within a given condition, and there was a rest period of 5 to 10 min between the different conditions. The subjects performed the entire experimental protocol on two different days. Each session lasted approximately 2 to 3 hours.

**Postural task**

After completion of the walking trials under a given condition, the postural effects of vibration were tested on a force platform with unchanged vibrator positioning. The subjects, without vision, were asked to stand for a period of 120 s while the displacement of their center of foot pressure (CFP) was recorded by means of a dynamometric platform (Advanced Mechanical Technologies Inc., Watertown, MA, USA, model SGA6). For each experimental condition, the trial comprised a period of 60 s without vibration immediately followed by a period of 60 s during which continuous vibration was delivered. Therefore a condition without vibration but with the vibrator attached to the subject always preceded a given vibration condition. For each vibration condition, the mean CFP position measured during the no vibration condition was used as a reference to monitor changes in CFP position when the vibrator was turned on. This procedure was repeated for each condition
in order to avoid variability in the mean CFP position under no vibration condition, i.e. to ensure unchanged reference to compare the different vibration conditions.

**Vibration**

The cylinder axis of the vibrator was normal to the presumed direction of muscle fibers. The vibrator was tightly fixed to the muscle by a large elastic band that caused no discomfort to the subjects. The vibrator, of 100 g weight, was custom-made and consisted of a DC motor with an eccentric on the shaft embedded in a plastic tube 3 cm in diameter and 7 cm long, the motor having a servo-control to keep constant the velocity of its shaft. The vibration frequency was 80 Hz. The amplitude of the effective displacement of the vibrator applied to the muscle was about 0.8 mm, as measured by an accelerometer mounted on the vibrator on the direction of its action on the muscle (Schmid et al. 2005).

**Data acquisition and analysis**

*Walking.* For all walking conditions, we analyzed the displacements of the head over a distance of 6 meters by means of the 3D-video ELITE system (eight TV cameras, 100 Hz, BTS, Italy). Subjects wore a light head-frame equipped with four reflective markers (8 mm diameter). Markers were positioned on the vertex, between the eyebrows on the midline, and along the tragus to tragus direction on each side of the body. Only the motion of the marker positioned on the vertex \((x_V, y_V, z_V)\) was analyzed, as previously described (Courtine et al. 2003). The other markers were used to verify the processing of the kinematic data. Briefly, the gait cycle was defined by means of the vertical head movement. Length, duration and speed of each gait cycle were computed. The angle of the instantaneous velocity vector of the vertex marker \((\dot{x}_V, \dot{y}_V, \dot{z}_V)\) with respect to the straight line (x axis) in the horizontal plane defined heading of the body \((\Phi_B)\) at each point of the trajectory:

\[
\Phi_B = \tan^{-1}\left(\frac{\dot{z}_V}{\dot{x}_V}\right)
\]

The orientation of the locomotor trajectory was computed for each gait cycle recorded as the difference in the heading value between the beginning and the end of the cycle period (Courtine et al. 2003). The change in walking direction was defined positive for a right turn, i.e. the direction of vibration-induced deviations.

*Standing.* For all the standing experimental conditions, we measured the mean anterior-posterior and lateral positions of the CFP over a 60-s period of quiet stance under...
continuous vibration, and computed these values with respect to the mean CFP position over the immediately preceding 60-s period without vibration. This procedure ensured that motion of the CFP was defined in the same reference system for all the subjects and conditions.

**Statistical analysis**

For each subject and condition we calculated the mean value of the measured variables. For the postural task these values were submitted to an analysis of variance for repeated measures (within-subject ANOVA) to evaluate significant differences between conditions. Post-hoc differences were assessed by means of the Newman-Keuls test. For the walking tasks, Levene’s test did not confirm the homogeneity of the variance for the deviations of the walking path across vibration spots. Therefore, non-parametric tests were used. The main effect of the vibration was assessed by means of Friedman’s ANOVA for multiple paired samples. Wilcoxon’s test for paired samples was used to evaluate differences between control and each vibration condition. Average values and their standard error (SE) over all trials for all subjects and measured variables were also computed.

**RESULTS**

**Subjects produced straight walking trajectories under no-vibration or vibration applied to upper limb muscles**

Fig. 2A shows average (± SD) locomotor trajectories from a typical subject under the different experimental conditions. The mean values (all subjects, n = 8) of the change in walking direction during the third cycle after walking onset are reported in Fig. 3A. Without muscle vibration, blindfolded subjects showed minor deviations from the requested straight line (Fig. 2A) as revealed by the near-zero values of the change in walking direction per cycle (0.06 ± 0.07 deg) (Fig. 3A). Likewise, when vibration was not delivered during the vibration blocks (in the control trials randomly inserted within the vibration blocks, see Methods), subjects showed no significant veering (ANOVA, main vibration effect, F_{16, 112} = 14, p > 0.3) compared to the no-vibration condition; mean average was 0.66 ± 0.07 deg, all inserted control trials collapsed (not shown). Vibration applied to the left deltoid muscle did not significantly alter (Wilcoxon’s test, Z = 1.2, p > 0.2) the
orientation of the walking path compared to the no-vibration condition (Fig. 2A, upper left, cyan, and Fig. 3A).

**Vibration applied to trunk-neck muscles elicited side-specific gait deviation**

When vibration was applied either to trunk (Th, Lu, AB) or neck muscles (S, SCM, T) (see Fig. 1), a systematic and reproducible locomotor deviation toward the side opposite to the stimulation site - rightward deviation for vibration applied to the left side - was observed for all subjects (Fig. 2A and Fig. 3A; Friedman’s ANOVA, main vibration effect, Chi$^2$ ANOVA (df = 16) = 68.9, p < 0.0001; Wilcoxon’s test, Z > 2.38, p < 0.02 for all no-vibration vs. trunk-neck vibration assessments). Subjects started deviating from the straight ahead direction during the first cycle after the onset of vibration (indicated by circles in Fig. 2A), but vibration effects became marked only during the subsequent cycles. The different conditions of trunk and neck muscle vibration generally induced locomotor deviations that did not differ in amplitude; only vibration applied to the SCM muscle produced significantly larger walking deviations compared to the other trunk or neck vibration sites (Wilcoxon’s test, Z > 1.96, p < 0.05 for all post hoc comparisons between SCM and other trunk-neck vibration conditions, Fig. 3A).

**Vibration applied to lower limb muscles had no or weak effects on gait trajectory**

Contrary to upper body vibration, stimulation applied to lower limb muscles did not induce consistent alterations to the locomotor trajectory (Fig. 2B). Accordingly, none of the statistical comparisons between the no-vibration condition and vibration conditions yielded significant differences (all Wilcoxon’s tests between control and lower limb muscle vibration conditions, Z < 1.4, p > 0.15; Fig. 3A). Only vibration applied to the left BF muscle elicited obvious deviations toward the right side in three out of the eight subjects. Group-averaged values, however, did not reach statistical significance (Wilcoxon’s test, Z = 0.84, p > 0.4). Nevertheless, Levene’s test applied to lower limb muscle conditions did not confirm the homogeneity of the variance (F$^{7, 56}$ = 3.1, p < 0.01), indicating that variability of the gait trajectory significantly increased under lower limb muscle vibration conditions (see Fig. 2B).

**Vibration applied during quiet stance elicited oriented shifts in postural reference**

Fig. 2C and D show the mean position of the CFP during continuous vibration of trunk-neck muscles and lower limb muscles, respectively, for the same subject as in Fig. 2A and
B. With the exception of the deltoid muscle, vibration of all trunk-neck and lower limb muscle groups gave rise to significant (within-subject ANOVA, main effect, $F = 5.25, df = 15, p < 0.0001$) medio-lateral (Newman-Keuls post-hoc comparisons between control and vibration conditions, $p < 0.05$ for S, SCM, T, Lu, TI, TE, AI, AE, Sol muscles) and/or antero-posterior (Newman-Keuls post-hoc comparisons between control and vibration conditions, $p < 0.05$ for S, Th, Lu, AB, GL, RF, BF, TA, Sol muscles) displacements of the CFP compared to the no-vibration condition (Fig. 3B). Neck or trunk muscle vibration resulted in body tilt oriented in the contralateral direction with respect to the vibrated muscle side (Fig. 2C and Fig. 3B top). For example, the shift in mean CFP position was oriented forward and slightly rightward when vibrating the left splenius muscle. Likewise, vibration of the internal and external aspects of the left thigh elicited prominent medio-lateral whole body tilt toward the left and right sides of the body, respectively (Fig. 2D and Fig. 3B). On the contrary, vibration applied at the ankle level (TA, Sol, AI, AE) induced postural responses oriented ipsilaterally with respect to the vibrated muscle (Fig. 2D and Fig. 3B). Finally, vibration of BF, RF, and GL muscles all resulted in forward-oriented body tilts (Fig. 2D and Fig. 3B).

**Relationship between postural responses to muscle vibration during stance and trajectory deviations during walking**

Fig. 4 shows the correlation between the mean amplitude of the change in walking direction and the mean medio-lateral CFP shift during stance with trunk-neck and lower limb vibrations, all subjects averaged. A significant ($R^2 = 0.6; p < 0.001$) relationship was found between the amplitude of postural responses in the medio-lateral direction during quiet stance and the deviations of the locomotor trajectory during walking when vibrating trunk-neck muscles. In contrast, lower limb muscle vibrations could evoke ample medio-lateral responses during stance, as shown for one subject in Fig. 2D, but no deviation during walking. There were no significant relationships between the CFP shift and the orientation of the walking trajectory for the lower limb vibration conditions in any of the tested subjects. On the other hand, vibration of some trunk-neck muscles elicited no significant medio-lateral responses during quiet stance, although it induced ample locomotor deviations during walking, as was the case for the abdominal muscle (Fig. 4).
**DISCUSSION**

The current study represents the first whole-body mapping investigation of muscle vibration effects during posture and gait in the same subjects with unchanged stimulator location between standing and walking tasks. Unilateral vibration of all trunk-neck and lower limb muscle groups elicited a tilt in body orientation during quiet stance. However, only stimulation applied to trunk-neck muscles significantly altered body steering during walking. This study adds to the notion that proprioceptive information is processed not only according to the performed task but also to the muscle from which the message originates.

*Alteration to postural body scheme likely accounts for the effects of muscle vibration during quiet stance*

The vibration-induced postural effects reported in the present study (Fig. 3B) are in agreement with previously published observations showing that vibration elicits tilts in body orientation coherent with a reaction from the nervous system compensating for the illusory lengthening of the stimulated muscle groups (Eklund 1972; Kavounoudias et al. 1999; Lund 1980). Here, we document such postural effects for a variety of vibration locations including muscle groups that had not been studied so far, i.e. abdominal, trunk, and thigh abductor/adductor muscles. It is worth stressing that, for all stimulated muscles, the effects of vibration were not local, i.e. restricted to responses at the stimulated joint, but instead involved global reactions that changed whole body orientation relative to gravity, as originally demonstrated (Eklund 1972). Vibration-induced deformation of the internal representation of the body scheme is usually put forward to interpret such postural modifications. We report that vibration of virtually all body muscles gives rise to significant changes in standing posture. We thus confirm that the proprioceptive messages originating from the uninterrupted muscular chain that extends from the eyes to the feet jointly contribute to elaborate a body postural scheme that is used to regulate balance in humans (Kavounoudias et al. 1999; Massion 1992; Roll et al. 1989b).

Kavounoudias et al. (1999) originally pointed out that the direction of the sway elicited during quiet stance on leg and neck muscle vibration is opposite – compare for example the effects of the vibration of the ventral and dorsal parts of the trunk (Th vs AB) and legs (TA vs Sol) (Fig. 3B). We extend this observation to all trunk-neck vs. lower limb muscles with the exception of the lateral aspect of the thigh (TI and TE). Differences in the direction of the elicited postural responses may reflect the physiological relevance of such changes...
in body orientation for preserving balance, given the different action of leg muscles on the foot and thigh muscles on the pelvis.

**There are striking differences between the effects of vibration of trunk-neck and limb muscles**

Motor effects to vibration-induced muscle-spindle input were different during walking compared to stance. Stimulation of trunk-neck muscles elicited consistent deviation of the locomotor trajectory in all subjects to the side opposite to the vibration site (Fig. 2A and 3A). On the contrary, no significant modifications of the locomotor trajectory were detected when vibrating the lower limb (Fig. 2B and 3A) or upper limb muscles such as the deltoid (Fig. 2A and 3A) or triceps brachii as in Bove et al. (2002). Nevertheless, significant increase in the variability of the locomotor trajectory revealed that the vibratory stimulation did alter, although non-specifically, the normal production of the stepping pattern. For example, vibration applied to the biceps femoris muscle perturbed locomotion, inducing modest deviation of the locomotor trajectory in 3 out of 8 subjects, in keeping with previous studies reporting alteration of joint trajectories during treadmill walking under continuous vibration of the biceps femoris muscle (Ivanenko et al. 2000a; Verschueren et al. 2002). Therefore, the present results provide evidence that, contrary to trunk-neck muscles (Bove et al. 2002; Bove et al. 2001; Courtine et al. 2001; Ivanenko et al. 2000a; 2000b; Schmid et al. 2005; Verschueren et al. 2002), proprioceptive feedback from lower limb muscles, in addition to being reduced during walking (Courtine et al. 2001; Verschueren et al. 2002), has no direct and fast access to the neural centers ultimately responsible for steering. It is worth noting that prolonged stepping on a rotatory platform induces prominent directional changes in locomotor trajectory during a subsequent overground stepping task (Weber et al. 1998). However, such leg proprioception-mediated podokinetic alteration of steering requires a long-lasting stimulus and rather represents an adaptation phenomenon of a different nature than the present vibration effects.

An additional, non-alternative possibility is that for muscles having a greater degree of tonic postural activity during walking, i.e. trunk or neck, the tonic vibration stimulus could have more meaning to the CNS and accordingly produce larger responses. When the muscles are more phasic, as the leg muscles during walking, the tonic vibration may have little task-dependent meaning (Roll et al. 1989) and therefore be ignored. In turn, this would account for the large effects of lower-limb vibration during standing when the muscle activity is of a largely tonic nature. Ad hoc experiments, by means of a vibration input that matches the tonic and phasic activity (Roll and Gilhodes 1995), could
investigate the possibility that the vibration effect are larger when they match the expected pattern of reafference from each muscle and task.

**Postural effects cannot explain alteration to body steering during walking**

The observed deviations of the locomotor trajectory could result merely from the mechanical consequences of vibration-induced alteration in body postural orientation: a shift in the center of foot pressure, as elicited during quiet stance, would cause lateral imbalance during walking, and thus body veering (Ivanenko et al. 2000a). This hypothesis is weakly plausible, however. In fact, vibration of lower limb muscles such as thigh abductors/adductors or peroneus lateralis/tibialis posterior evoked large medio-lateral shift in body orientation during quiet standing (Fig. 2D and 4), but no significant deviation from the straight-ahead direction during walking (Fig. 2B). Furthermore, vibration applied to trunk-neck muscles during walking provoked deviations that could hardly be predicted from the effects observed during standing (Fig. 4). For example, unilateral vibration of abdominal muscles, which induced a forward shift in postural orientation without significant medio-lateral displacements when delivered during quiet stance (Fig. 2B), provoked sharp, whole body lateral deviation during walking (Fig. 2A).

**Task-dependent changes in spinal circuits are unlikely to account for the different effects of vibration during walking and standing**

There are evidences that presynaptic inhibition of Ia-afferent terminals from all lower limb muscles increases when engaging the neuro-motor circuits for stepping (Courtine et al. 2005a; Stein and Capaday 1988). Stepping-associated depression in spinal reflex circuits’ excitability might account for the reduced effects of lower limb muscle vibration during walking. Nevertheless, local reflexes appear to play a modest or negligible role in the genesis of vibration-induced effects during standing and walking (Andersson and Magnusson 2002; Eklund 1972; Roll and Roll 1988). Firstly, lower limb muscle-spindle input conveyed along large-diameter Ia fibers has no or weak modulatory effects on the ongoing EMG activity of the homonymous muscle during walking (Courtine et al. 2001; Grey et al. 2001; Mazzaro et al. 2005a; Verschueren et al. 2003). Secondly, vibration elicits instead global changes involving the whole body during standing (Eklund 1972) and walking (Ivanenko et al. 2000a; 2000b). Consequently, decreased gain in spinal reflex circuits during walking is unlikely to be the main explanation for the negligible effects of vibration of lower limb muscles during walking compared to standing. On the other hand, the excitability of the soleus monosynaptic reflex can be profoundly depressed also during
quiet stance without preventing vibration from eliciting clear-cut effects on body posture (Bove et al. 2003; Bove et al. 2006).

**Task-dependent influences of the Ia input likely account for the different effects of muscle vibration during walking**

The muscle groups contrasted in the present study ensure similar function during standing, i.e., preserve body orientation with respect to gravity, whereas their function differs drastically during walking. Lower limb muscles develop the forces necessary to propel the body forward and control limb endpoint trajectory during swing whereas trunk-neck muscles mainly contribute to preserve body orientation. Consequently, the proprioceptive information originating from trunk-neck and lower limb muscles may also ensure different functions during walking compared to standing. For instance, trunk muscles become active at the time of contralateral heel strike during walking, when the activity of leg extensor muscles diminishes rapidly and flexor muscles are not yet turned on (Courtine et al. 2005b). Activation of trunk muscles at heel strike determines the extent of the subsequent trunk rotation, which influences the future direction of the locomotor trajectory (Courtine and Schieppati 2003). Indeed, lower back extensor muscles’ activity and associated patterns of trunk movements are altered gradually when steering curves of increasing tightness (Courtine et al. 2005b). The information arising from trunk muscles may therefore provide the locomotor system with critical cues for steering the walking body in space (Fig. 3A).

The brain interprets vibration-induced muscle-spindle input as the muscle being longer (Albert et al. 2006). In the case of neck muscle vibration, this illusory relationship between the cephalic segment and the trunk likely induces a mismatch between the expected orientation of the body parts and the monitored direction of gravity (Karnath et al. 2004). The importance of the head reference frame in the construction of internal representations for maintenance of body segment orientation during walking (Courtine and Schieppati 2003; Courtine and Pozzo 2004) would account for the potent motor corrections resulting from neck muscle vibration (Fig. 3A).

Vibration applied to lower limb muscles also provokes misperception of foot location with respect to the body during walking (Ivanenko et al. 2000a). Indeed, such deformation of the body scheme induces shifts in postural orientation during standing (Fig. 3B). Therefore, the question arises as to why vibration applied to lower limb muscles has no or weak effects during walking. Likely, locomotion performed on a flat and solid surface, without demands that require alteration of lower limb trajectory, rely on automatic generation of the motor pattern for walking (Van de Crommert et al. 1998). Accordingly,
continuous vibration-induced Ia input from a given muscle might have weak effects on the
spinal circuits that produce the stepping activity, which receive dynamic information from a
variety of sensory receptors during walking. Furthermore, leg muscle proprioceptive
information conveyed along group-II fibers appears to be more relevant to the control of
human walking than group-Ia originating input (Grey et al. 2001; Schieppati and Nardone
1999; Mazzaro et al. 2005b).

We therefore hypothesize that the absence of motor effects when vibrating lower limb
muscles during walking reflects either or both limited connections between Ia input and
the centers controlling the production of curved walking and task-dependent influences of
proprioceptive information on motor control. Task-dependent integration of sensory
information has been documented repeatedly. For example, the magnitude of locomotor
deviations elicited by lateral neck muscle vibration (Courtine et al. 2003) or vestibular
stimulation (Brandt et al. 1999) dramatically decreases during running compared to
walking.

In conclusion, the present findings emphasize that Ia muscle input is processed
according to both the performed task and the body segment from which the sensory inflow
arises. The importance of trunk-neck proprioceptive information in the control of walking
must be taken into account for the interpretation of posture and movement problems
(Adkin et al. 2005) and for rehabilitation of patients suffering from balance disorders during
locomotion (de Seze et al. 2001).

REFERENCES

Adkin AL, Bloem BR, and Allum JH. Trunk sway measurements during stance and
Albert F, Bergenheim M, Ribot-Ciscar E, and Roll JP. The Ia afferent feedback of a
given movement evokes the illusion of the same movement when returned to the
Andersson G and Magnusson M. Neck vibration causes short-latency
electromyographic activation of lower leg muscles in postural reactions of the standing
Bove M, Courtine G, and Schieppati M. Neck muscle vibration and spatial orientation
Bove M, Diverio M, Pozzo T, and Schieppati M. Neck muscle vibration disrupts


FIGURE LEGENDS

**Figure 1:** Position of the vibratory stimulator for each experimental condition. The stimulator was located on the left side of the upper body or on the left lower limb. The abbreviations used for each condition are indicated.

**Figure 2:** Effect of muscle vibration on locomotor trajectory and postural orientation for a typical subject. Average locomotor trajectories (mean path ± SD) during walking under no vibration condition, and while muscle vibration was delivered to trunk-neck muscles (A) or lower limb muscles (B). Trajectories were obtained from all the trials (n=5 per condition) performed under each experimental condition. The reference point (0, 0) corresponds to the starting spot. The circles indicate the onset of the vibratory stimulation for each condition. (C) Mean medio-lateral and antero-posterior position of the CFP during continuous vibration of trunk-neck muscles and (D) lower limb muscles. All the values are normalized to the mean CFP position measured over a period of 60s without vibration which immediately preceded the onset of the vibratory stimulation.

**Figure 3:** Average values of locomotor deviations during walking and changes in mean CFP position during stance under trunk-neck and lower limb muscle vibration. (A) Mean values (+SE) of the change in walking direction (deg) during the third gait cycle after walking onset, i.e. the second gait cycle after the onset of vibration. *, significant differences between no-vibration and vibration conditions; #, significant differences between SCM vibration and all the other vibration conditions. (B) Mean (± SE) medio-lateral and antero-posterior position of the CFP during stance under continuous vibration of trunk-neck and lower limb muscles.

**Figure 4:** Correlation between postural responses during stance and locomotor deviations during walking. The mean values (all subjects, n = 8) of the average change in walking direction reported in Fig. 3A are plotted versus the mean values of the medio-lateral displacement of the CFP during quite stance, for both trunk-neck and lower limb vibrations. Linear regression analyses were performed independently for trunk-neck and lower limb vibrations. R² values are reported close to the corresponding best fitting lines.
<table>
<thead>
<tr>
<th>Muscle</th>
<th>Abbreviation</th>
<th>Vibrator location</th>
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<tbody>
<tr>
<td><strong>Upper body</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deltoid</td>
<td>D</td>
<td>On the muscle belly</td>
</tr>
<tr>
<td>Splenius</td>
<td>S</td>
<td>2 cm lateral to C3-C4</td>
</tr>
<tr>
<td>Sternocleidomastoidus</td>
<td>SCM</td>
<td>4 cm below the mastoid bone</td>
</tr>
<tr>
<td>Trapezius</td>
<td>T</td>
<td>~ 10 lateral to the acromion</td>
</tr>
<tr>
<td>Trunk thoracic</td>
<td>Th</td>
<td>3 cm lateral to T3-T4</td>
</tr>
<tr>
<td>Trunk lumbar</td>
<td>Lu</td>
<td>3 cm lateral to L3</td>
</tr>
<tr>
<td>Abdominal</td>
<td>AB</td>
<td>3 cm lateral to the ombilic</td>
</tr>
<tr>
<td><strong>Lower limb</strong></td>
<td></td>
<td></td>
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<tr>
<td>Gluteus</td>
<td>GL</td>
<td></td>
</tr>
<tr>
<td>Rectus Femorisis</td>
<td>RF</td>
<td>On the muscle belly</td>
</tr>
<tr>
<td>Biceps Femorisis</td>
<td>BF</td>
<td></td>
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<tr>
<td>Thigh internal</td>
<td>TI</td>
<td></td>
</tr>
<tr>
<td>Thigh external</td>
<td>TE</td>
<td></td>
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<tr>
<td>Tibialis Anterior</td>
<td>TA</td>
<td></td>
</tr>
<tr>
<td>Soleus</td>
<td>Sol</td>
<td>On the Achille's tendon</td>
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<tr>
<td>Ankle internal</td>
<td>AI</td>
<td>On the tibialis posterior</td>
</tr>
<tr>
<td>Ankle external</td>
<td>AE</td>
<td>On the peroneus lateralis</td>
</tr>
</tbody>
</table>

Figure 1
Figure 3
Figure 4

Medio-lateral CFP displacements (cm) vs. Amplitude of change in walking direction (deg)

- Upper body: Deltoid (D), Splenius (S), SCM, Trapezius (T), Trunk Th (Th), Trunk Lu (Lu), Abdominal (AB), Gluteus (GL), Biceps F (BF), Thigh Int (TI), Thigh Ext (TE), Tibialis (TA), Soleus (Sol), Ankle Int (AI), Ankle Ext (AE)
- Lower limb: Rectus F (RF), R2=0.60, R2=0.04

Figure 4