CAN PREPARED ANTICIPATORY POSTURAL ADJUSTMENTS BE UPDATED BY PROPRIOCEPTION?

**H. RUGET,[a] J. BLOUIN,[a] N. TEASDALE[b]
AND L. MOUCHNINO[a]***

[a]*Laboratoire Neurobiologie de la Cognition, Aix-Marseille Université, CNRS, Université de Provence, UMR 6155 case C, 3 place Victor Hugo, F-13331 Marseille cedex 3, France*

[b]*Groupe de Recherche en Analyse du Mouvement et Ergonomie, Université Laval, Faculté de Médecine, Division de Kinésiologie, PEPS, Québec, G1K 7P4 Québec, Canada*

Abstract—Stepping over an obstacle is preceded by a center of pressure (CoP) shift, termed anticipatory postural adjustments (APAs). It provides an acceleration of the center of mass forward and laterally prior to step initiation. The APAs are characterized in the lateral direction by a force exerted by the moving leg onto the ground, followed by an unloading of the stepping leg and completed by an adjustment corresponding to a slow CoP shift toward the supporting foot. While the importance of sensory information in the setting of the APAs is undisputed, it is currently unknown whether sensory information can also be used online to modify the feedforward command of the APAs. The purpose of this study was to investigate how the CNS modulates the APAs when a modification of proprioceptive information (Ia) occurs before or during the initiation of the stepping movement. We used the vibration of ankle muscles acting in the lateral direction to induce modification of the afferent inflow.

Subjects learned to step over an obstacle, eyes closed, in synchrony to a tone signal. When vibration was applied during the initiation of the APAs, no change in the early APAs was observed except in the case of a cutaneous stimulation (low frequency vibration); it is thus possible that the CNS relies less on proprioceptive information during this early phase. Only the final adjustment of the CoP seems to take into account the biased proprioceptive information. When vibration was applied well before the APAs onset, a postural reaction toward the side of the vibration was produced. When subjects voluntarily initiated a step after the postural reaction, the thrust amplitude was set according to the direction of the postural reaction. This suggests that the planned motor command of the APAs can be updated online before they are triggered. © 2008 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: postural control, vibration evoked-signal, somatosensory afferents, stepping over an obstacle.

*Corresponding author. Tel: +33-0-4-88-57-68-14; fax: +33-0-4-88-57-68-72.
E-mail address: laurence.mouchnino@univmed.fr (L. Mouchnino).

The production of voluntary movements is generally accompanied by postural adjustments. In several cases, muscles responsible for these postural adjustments are activated before those acting as prime movers. For instance, step initiation is preceded by the coactivation of tibialis anterior (TA) and medial gastrocnemius muscles of the stepping leg. These activations generate sideward and backward displacements of the center of pressure (CoP), which in turn accelerates the center of mass (CoM) toward the supporting leg and forward (Robert et al., 2004). These postural adjustments are essential because they allow the unloading of the stepping leg and so create the necessary condition for progression (Brénière and Do, 1991). Starting before the step (but continuing during the movement), they are referred to as anticipatory postural adjustments (APAs) (Kaminski and Simpkins, 2001; Malouin and Richards, 2000; Massion, 1992; Timmann and Horak, 2001). Intracerebral recordings in the cat and lesion studies in humans have shown that the coordination between the APAs and the focal leg movement are organized at a supraspinal level and involve the pontomedullary reticular formation, the supplementary motor area and the basal ganglia (Massion et al., 1999; Viallet et al., 1992; Gantchev et al., 1996; Schepens and Drew, 2004). The APAs could be progressively assembled and stored in advance of movement and triggered by corticospinal excitations. MacKinnon et al. (2007) have shown that magnitude and duration of the APAs increased as a startle-like acoustic stimulus (which causes an early release of the planned movement) timing approach the "go" signal for step initiation. The scaling of the APAs before their dispatch to the periphery depends on the ability to use sensory information from various sources (vestibular, cutaneous, visual, proprioceptive) (Mille et al., 1998; Timmann and Horak, 1998). Studying step initiation in response to a backward surface translation (which moved the subjects' CoM forward off their base of support), Timmann and Horak (2001) found that sensory information was integrated rapidly to adjust the APAs. Indeed, the authors showed that although the stepping response had short reaction times (~200 ms), the APAs were well adapted to changes in body state introduced prior to movement onset. They suggested that proprioceptive inputs arising from such postural reactions in addition to activation of mechanoreceptors from the sole of the foot and also vestibular signals, could contribute to the re-setting of the planned motor command. These studies also suggest the APAs could be modulated by somatosensory information originating from the body movement. However, the movement was imposed before the APAs had been initiated. While the importance

of sensory information in the setting of the APAs is undisputed, it is currently unknown whether sensory information can also be used online to modify the feed-forward command of the APAs.

The possibility of controlling the APAs during their execution has been investigated by Bent et al. (2002). The authors stimulated the vestibular apparatus of individuals for 7.5 s (using the galvanic vestibular stimulation (GVS) technique) starting 1.5 s before they started to walk straight-ahead with eyes closed. Despite GVS evoking a slight body tilt toward the anode side, the APAs (i.e. the lateral forces produced to unload the stepping leg) were unaffected by the change in the vestibular afferents. The effect of GVS was only identified at the start of the second step. This led to the suggestion that vestibular information has little influence on both the setting and the online control of the APAs, and that it only becomes relevant during the more dynamic control of the stepping task. In this experiment, we used muscular vibration techniques to investigate whether leg muscle proprioception is processed by the CNS to then control the APAs online, that is once they are initiated. The fact that proprioception-based movement corrections can have short latencies (<100 ms, i.e. shorter than for initiating movement through proprioceptive cues, Gomi et al., 2002; Ito et al., 2005) allows for such a possibility. If proprioceptive signals are used in the online control of the APAs, then erroneous vibration-induced detection of the current body state should be reflected in the APAs.

EXPERIMENTAL PROCEDURES

Subjects stood barefoot on a force platform. In the main experimental condition, they were asked to make a complete step over an obstacle (height: 23 cm×width: 45 cm×depth: 12 cm) with the right leg and to stop just beyond it. In order to generate the vibration at specific times with respect to APAs onset, subjects were asked to synchronize their step initiation with the fifth 1-s-interspaced tone produced by a computer (Fig. 1A). A few practice trials were required for the subject to comply with this requirement. The subjects' eyes were open, looking at the obstacle and then closed at the first tone. Eccentrically loaded motors inserted in plastic cylinders provided the vibration stimuli. The vibrators were securely fixed with an elastic belt, one vibrator on each leg, just above the external malleolus on the fibularis longus muscle and above the medial malleolus on the tibialis posterior muscle. With such arrangement, the vibrations acted on both the right-side of one leg and left-side of the other leg (Fig. 1B). The vibrators were activated simultaneously, and the stimulation consisted of small amplitude vibrations (1.2 mm) of high (80 Hz) or low (40 Hz) frequencies. High frequency vibrations (80 Hz) applied to muscle tendons produce micro stretches of the muscle spindles which are interpreted by the CNS as resulting from a muscular stretch (Roll and Vedel, 1982; Roll et al., 1989; Gurfinkel et al., 1996). In free standing subjects, the vibration of hip abductor muscles acting in the frontal plane evokes spatially oriented postural responses (PR) with a latency of ~650 ms (Popov et al., 1999) which is aimed at correcting for perceived changes with respect to the vertical posture. The 40 Hz vibration frequency (hereinafter called Mecha Vib condition) favors activation of cutaneous afferents, essentially the Meissner corpuscles (Mountcastle, 1984). In the low frequency range (20–40 Hz), tactile stimulation of the sole of the foot gives rise to more powerful postural effects than those elicited by proprioceptive stimulation; conversely, this tendency is
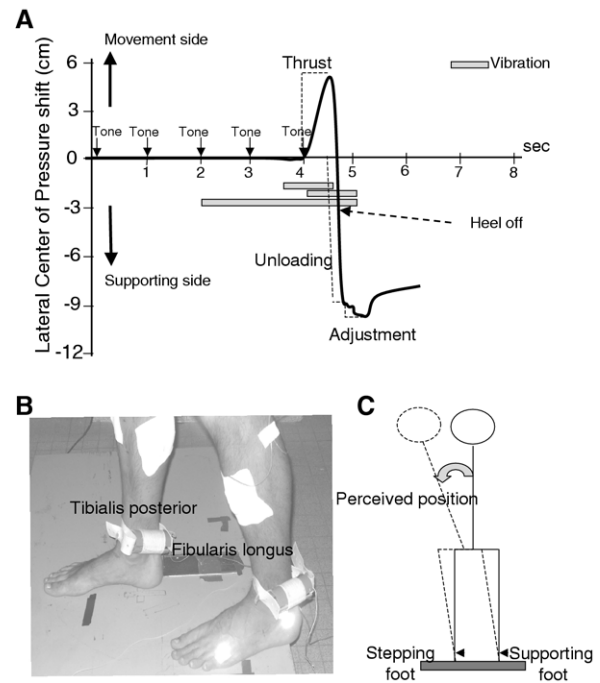
Fig. 1. (A) CoP lateral displacement during step avoidance task. After an initial displacement toward the stepping side (Thrust), the CoP moved toward the supporting side (Unloading and Adjustment). The dotted lines represent the onset and offset of each phases. The "heel off" indicates the onset of the stepping movement. Time 0 corresponds to the start of the data recordings, the vibration had been applied at different times during the preparation and APAs initiation. (B) Example of vibrators placement. (C) Illustration of the effect of the sensory message induced by vibration when the vibrators are placed as shown in B.

reversed with stimulation at higher frequencies. As the 40 Hz vibration would allow effects of the mechanoreceptive afferents to be separated from effects of proprioceptive signals (80 Hz), any confounding effect of mechanical cues with proprioceptive inputs are a priori excluded.

Seven subjects aged 24–29 years (mean age 25 years) without any known neurological and motor disorders, participated in the experiment. None of the participants was familiar with the purpose of the experiment. They all gave their informed written consent prior to undertaking the experiment, which was approved by the Ile de France ethic committee.

The experimental sessions consisted of 70 trials and started after verifying that the vibration induced lateral body tilt when the subjects stood still with the eyes closed. Subjects stepped over the obstacle in four conditions which were presented in a pseudo-randomized manner (no more than three trials of the same condition were presented consecutively). In 30% of these trials, no vibration was delivered (No Vib). In the remaining 70% of the trials, a 1 s-vibration was applied at low or high frequencies 400 ms before the fifth beep (i.e. on average −488 ms±150 before the APAs onset defined by the onset of the lateral force: Vib before) or at high frequency when the lateral force exceeded 2 N (on average +61 ms±128 after the APAs onset: Vib during).

The 80 Hz vibrations that occurred before the APAs onset were deliberately not early enough to evoke a PR. Here, the vibrations were used to induce afferent proprioceptive inflow analogous to the pattern resulting from body tilt in the opposite side to the vibrated muscles. This information, which arises from the Ia afferent inputs, could be seen as being conflicting with the forth-

coming CoM shift as it provided reversed direction information (i.e. virtual body displacement toward the stepping leg) with respect to the actual concomitant CoM shift (i.e. body displacement toward the supporting leg, Fig. 1C). We hypothesized that if the APAs are subjected to online control during their execution, they would be modified in order to increase the lateral body shift toward the supporting side.

Data collection and analysis

Ground reaction forces were recorded at 500 Hz with an AMTI (BTS Bioengineering, Milano, Italy) force platform to compute the CoP displacement. The movement of the stepping leg was recorded by fixing a semi-spherical reflexive marker on the malleolus lateralis and tracking its position with an automatic optoelectronic system (E.L.I.T.E. system®, Ferrigno and Pedotti, 1985) at a frequency of 100 Hz. Three-dimensional reconstruction of the marker kinematic was performed through off-line data processing techniques.

Bipolar surface electromyogram (EMG) signals were recorded on the TA and on gastrocnemius medialis (GM) of the stepping leg. These muscles are responsible for the lateral shift of the CoP during gait initiation (Robert et al., 2004). EMG signals were pre-amplified at the skin site and sampled at 500 Hz (band-pass filtered 20–250 Hz). To determine the baseline EMG activity level, we computed, for each trial, the mean rectified activity recorded in a 500 ms time window during quiet standing (Staude et al., 2001). The onset of the burst activity was defined as the time at which the EMG activity exceeded the mean baseline activity by two standard deviations. The offset of the bursts was defined as the time at which the rectified EMG dropped below two standard deviations following the onset. Due to some burst profile inconsistencies the onsets and offsets of the EMG activity were subsequently visually inspected and manually corrected when necessary. To quantify the EMG bursts of TA and GM muscles, the area associated with the burst of EMG activity was determined for each muscle by computing the integral over the entire burst duration of each trial. The base-line activity was then subtracted to the areas computed over the 500 ms that preceded the onset of the EMG burst of each trial.

All signals were recorded during 8 s from the first tone.

All dependent variables (which are detailed below) were submitted to one-way analyses of variance (ANOVAs) with repeated measures (No vib, Vib before, Vib during and Mecha Vib). Significant effects were further analyzed using Newman-Keuls post hoc tests. The level of significance was set at 5%.

RESULTS 1

The obstacle clearance typified in this experiment can be clearly divided into three phases according to the profile of the CoP displacement in the medio-lateral (M/L) direction (Fig. 1A). Firstly, the CoP shifts toward the movement side. This CoP shift corresponds to a vigorous lateral pressure onto the ground ("thrust") exerted mainly by the forthcoming moving leg while still on the ground. Then, the CoP moves toward the supporting side in order to unload the leg to be moved. During the "unloading," the leg movement (heel-off) is initiated. This unloading is completed by an "adjustment" corresponding to a slow CoP shift onto the supporting foot.

The APAs onset (i.e. thrust) occurred, on average, 10 ms (±83) after the 5th tone signal in the no vibration condition. The ANOVA showed a condition effect [$F_{(2,12)}=8.83$, $P=0.004$] on the latency between the tone signal and the thrust onset; in Vib before the thrust onset
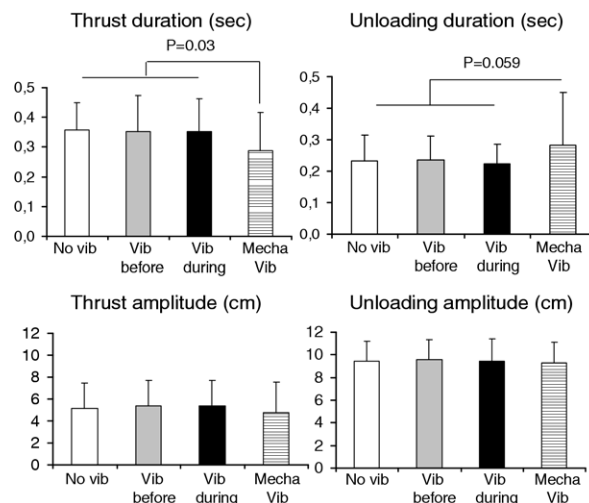

Fig. 2. Mean maximum M/L displacement of the CoP toward the stepping (thrust) and the supporting (unloading) sides (defined as the difference between the neutral position and the maximum displacement in each direction) and duration of the separate phases. The error bars indicate the standard deviations of the means.

preceded by -63 ms (±58) the tone signal and in Mecha Vib, the thrust onset followed the tone by $+90$ ms (±85). Overall, the subjects succeeded in synchronizing their step initiation with the tone signal, if not ($+200$ ms) the trials were discarded from the analyses (less than 3% of the trials).

The ANOVA showed a significant effect of condition on the thrust duration [$F_{(3,18)}=4.36$, $P=0.017$]. Post hoc analyses showed that, the thrust duration was significantly shorter in Mecha Vib (285 ms±76) than in the "No Vib" (357 ms±92), "Vib Before" (345 ms±119) and "Vib During" (364 ms±112) conditions (Fig. 2). On the other hand, this duration did not vary significantly among the 80 Hz vibration conditions (Vib before and Vib during). The peak amplitude of the thrust was not affected by the different vibration conditions [global mean=5.27 cm±2.32; $F_{(3,18)}=1.66$, $P=0.21$].

The sideward acceleration of the body from the initial quiet standing position was produced by the thrust, which was associated with the activation of both GM and TA muscles. Fig. 3 shows that GM activation was smaller in Mecha Vib than in all other conditions. This was confirmed by a significant effect of condition on the iEMG [$F_{(3,12)}=3.26$, $P=0.05$] but not on the EMG burst duration [mean duration 213 ms±70, $F_{(3,12)}=0.55$, $P=0.65$]. As expected a less vigorous thrust onto the ground is associated with a weak GM muscle activation in Mecha Vib condition which decreases the body acceleration toward the supporting leg. Neither the iEMG ($F_{(3,15)}=2.70$, $P=0.08$) nor the duration (641 ms±157; $F_{(3,15)}=2.15$, $P=0.13$) of the TA muscle activation varied significantly across conditions.

In addition, the unloading phase (Fig. 2) tended to be longer in Mecha Vib (282 ms±168) compared with both 80 Hz vibration conditions (global mean 230 ms±40). However, the difference did not reach significant level
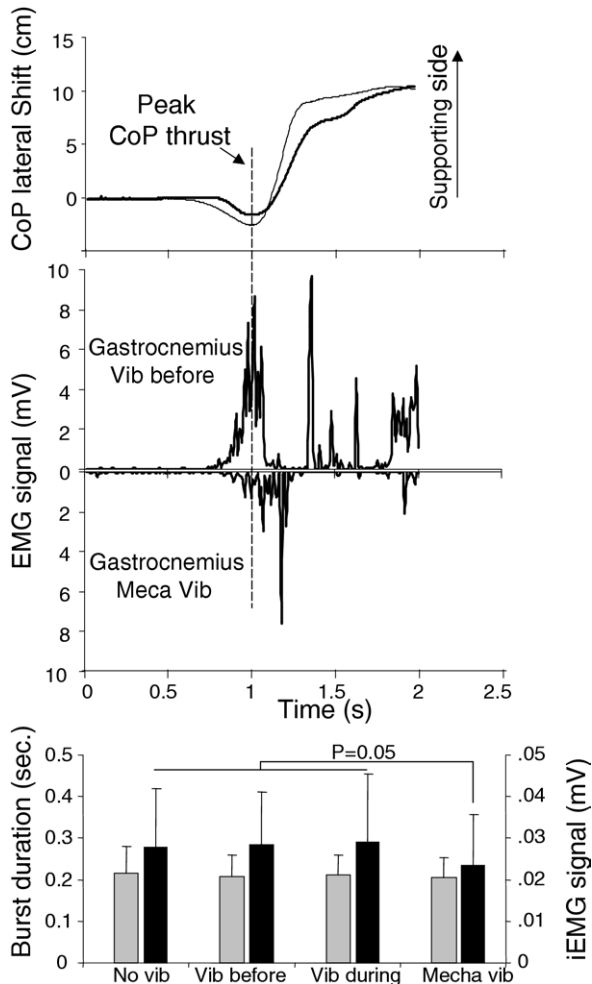
Fig. 3. Top and middle mean CoP shift and mean iEMG trace for one subject in two experimental conditions. The thin CoP line represents the No Vib condition and the thick line shows the Mecha Vib condition. The mean iEMG trace for the Mecha Vib condition is inverted for clarity. The time of maximal thrust is shown by the vertical dashed line. Bottom: Mean integral (in black) and duration (in gray) of the gastrocnemius burst in all conditions. The P value revealed a condition-effect on iEMG, even though the duration remained constant across conditions.

[$F(3,18)=2.96$, $P=0.059$]. Similarly to the thrust, the unloading amplitude did not vary significantly across conditions (global mean=9.47 cm±1.84; $F(3,18)=0.59$, $P=0.62$). The duration and the amplitude of the adjustment phase of the unloading (measured between the end of the rapid component of the unloading and the subsequent maximal lateral displacement of the CoP) did not vary significantly between the conditions (respective global means of 421 ms±243 and 1.61 cm±1.14).

The final position reached by the malleolus of the stepping foot was analyzed relative to its starting position in the M/L direction. On average, at the end of the step, the foot was slightly deviated from its initial position by 0.7 cm (±1.1) outward. However, this final foot position did not vary significantly across conditions [$F(3,15)=1.03$ $P=0.40$].

DISCUSSION 1

The only change observed in the APAs during vibratory stimulation occurred in the 40 Hz condition. The vibration may have elicited unexpected (by the subject) cutaneous information on the ankle area which may have been interpreted by the CNS as a potential hazard for the tissues of the ankle joint or as balance perturbation. The decreased integrated EMG and thrust duration observed in this condition could therefore represent a protective strategy as it decreased the CoM acceleration toward the supporting leg.

Contrary to our predictions, the change in afferent signals induced by the 80 Hz vibration did not modify the APAs. In the present experiment, the vibrators were configured in order to elicit afferent information related to body tilt toward the stepping leg. All other somatosensory (i.e. cutaneous of the plantar sole) and vestibular information provided a massive flow of information related to body tilt toward the supporting leg during the CoM shift. This could have somewhat cancelled the illusory effect of the vibration. In experiment 2, we tested the contribution of the afferent information in the control of the APAs when the vibration-induced afferent signals were in the same direction than the actual body tilt toward the supporting side. Vibration evoking movement perception in the same direction than the actual movement is known to greatly enhance the intensity of the illusion (Cordo et al., 2005).

Experiment 2

A separate group of nine subjects participated to this second experiment (aged 20–39 years, mean 24 years). The experimental procedures were identical to those used in experiment 1 with the only exception that the vibrator configuration elicited afferent information relating to body tilt toward the supporting leg (by changing the position of the vibrators). Three conditions were tested: No vib, Vib before (80 Hz, on average −380 ms±200 before the APAs onset) and Vib during (80 Hz, on average +154 ms±110 after the APAs onset).

RESULTS 2

There was no significant change in any of the CoP (amplitude and duration) and EMG activity (area and duration) parameters for the thrust and the unloading components. A summary of the statistical analyses across the dependent variables is shown in Table 1. However, the ANOVAs and the post hoc test showed that the adjustment phase was significantly smaller [$F(2,16)=8.84$, $P=0.002$] in both conditions with vibration (Vib Before: 1.48 cm±1.22 and Vib During: 1.67 cm±1.15) than in "No Vib" condition (2.13 cm±1.15) (Fig. 4). The vibratory stimuli had no significant effect on the duration of the adjustment phase [global mean=487 ms±257 ms, $F(2,16)=0.76$, $P=0.48$].

Compared with the "no Vib condition," the final position reached by the malleolus of the stepping foot exhibited a larger eccentric position of 12 cm in both vibration conditions [$F(2,10)=4.99$, $P<0.05$]. Increasing the support surface at the end of the movement could be a response to

Table 1. Summary of the statistical analyses of the dependent variables

Variables	Repeated measures ANOVA	Mean value
Thrust amplitude	$F(2,16)=0.043$, $P=0.95$ NS	4.33 cm$\pm$1.5
Thrust duration	$F(2,16)=0.098$, $P=0.99$ NS	0.367 s$\pm$0.10
GMmov duration	$F(2,14)=0.543$, $P=0.59$ NS	0.254 s$\pm$0.098
GMmov iEMG	$F(2,14)=1.14$, $P=0.34$ NS	0.067 V$\pm$0.059
Unloading amplitude	$F(2,16)=0.198$, $P=0.82$ NS	7.9 cm$\pm$1.3
Unloading duration	$F(2,16)=1.40$, $P=0.27$ NS	0.266 s$\pm$0.09
Adjustment amplitude	$F(2,16)=8.84$, $P<0.05$**	No vib: 2.13 cm$\pm$1.15 Vib Before: 1.48 cm$\pm$1.22 Vib During: 1.67 cm$\pm$1.15
Adjustment duration	$F(2,16)=0.76$, $P=0.48$ NS	0.487 s$\pm$0.257

The significant result (**) is observed for the adjustment amplitude which decreases in both vibration conditions as compared to no vibration. All other dependent variables remained constant.

the less eccentric CoP position reached at the end of the unloading that could threaten body equilibrium.
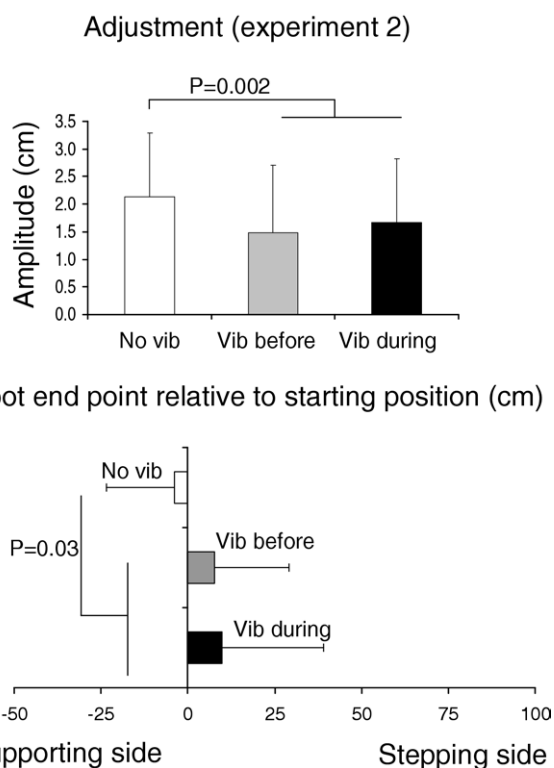
DISCUSSION 2

Results of experiment 2 showed significant modifications in the late phase of the APAs (adjustment) during the vibrations which evoked here proprioceptive-afferent inflow relating to body tilt toward the supporting leg. The lateral displacement of the CoP toward the supporting side

Fig. 4. Top: Mean maximum M/L displacement of the CoP during the adjustment toward the supporting side (defined as the difference between the end of the fast unloading and the maximum displacement in the supporting direction). Bottom: Mean stepping foot endpoint at heel strike relative to the foot initial position. A positive value means an increase of the supporting area as compared with the initial position. The error bars indicate the standard deviations of the means.

was indeed smaller with the vibration. The congruence between afferents from vibrated muscle and afferents signaling the actual body movement (e.g. vestibular) may have led to an exaggerated sense of movement toward the supporting side prompting the CNS to decrease the CoP excursion. However, the change in the APAs was only observed in the adjustment phase (on average 633 ms after the APAs onset), that is after the initial rapid shift of the CoP toward the supporting leg.

Overall, the results from the first and second experiments suggest that the early APAs can be controlled online when a mechanical stimulus was applied but not in the case of a proprioceptive stimulus. This suggests that step initiation is unaffected by proprioceptive afferents in the early stage of the APAs (thrust) but is controlled at a latter stage (adjustment) through these signals. A recent study by Voss et al. (2006) showed that movement preparation induces a corticofugal gating of somatosensory inflow. This gating mechanism could explain the lack of effect of the vibration in the early phase of the APAs. To test whether the preparation of stepping movements modulates the transmission of proprioceptive signals, we compared in a third experiment the PR evoked by the vibration in conditions with or without stepping movement. In the latter case, the vibration occurred 2 s before the cue that indicated subjects to initiate their gate. This timing was chosen because the latency of vibration-induced PR in free standing subject is shorter than 2 s and because the setting of the APAs is known to be progressively stored 1–2 s before step initiation (MacKinnon et al., 2007).

Experiment 3

Twelve subjects aged 20–28 years (mean age 22 years) without any known neurological or motor disorders, participated in this experiment. All participants gave written consent according to Laval University ethic committee. Two tasks were performed in this experiment and the trials sequence of the complete experimental session is presented in Table 2. Subjects were instructed to step over an obstacle (height: 23 cm$\times$width: 45 cm$\times$depth: 12 cm) and to stop just behind it (stepping task). They had to initiate the crossing over at a tone signal. In two conditions, 3-s vibrations were applied 2 s before the tone. In these con-

Table 2. Trial organization used in the experiment 3

Trials	Type of trials
1–5	Stepping task: no vibration
6–10	Static task: "stepping" side vibration
11–15	Static task: "supporting" side vibration
16–25	Stepping task: stepping side vibration
26–35	Stepping task: supporting side vibration
36–40	Static task: "stepping" side vibration
41–45	Static task: "supporting" side vibration
46–50	Stepping task: no vibration

For the static task, the use of the terms "stepping" or "supporting" vibration was meaningless but used for the comparison with the conditions of the stepping task. Since no statistical differences were found between the four sequences of the static task, we then pooled together all the trials and considered as static condition.

ditions, the vibrators were positioned in order to elicit PR either toward the supporting or the stepping leg. No vibratory stimulus was provided in the third condition. In order to determine whether a gating occurs during the preparation of stepping movements, a baseline reference for the vibration-induced postural effect was obtained by applying the vibrations in an additional session where no step movement was required (static task, Fig. 5). All dependent variables were submitted to an ANOVA with repeated measures with two levels: the sessions (stepping task vs. static task) and the side (supporting vs. stepping sides).

RESULTS 3

In all static and stepping tasks, the vibration induced a PR which consisted of a shift of the CoP toward the vibrator side. Off-line analyses showed that, on average, the vibration-induced CoP shifts (PR) toward the supporting or the stepping legs occurred 1.47 s (± 0.08) before the onset of the APAs (Fig. 5), that is during the preparation phase of the APAs. ANOVA revealed a significant main effect of the task (static vs. stepping) on the latency of the PR relative to the vibration onset [$F(1,11)=8.52$, $P=0.013$]. The shortest latencies of the PR were observed in the stepping (709 ms± 207) as compared with the static (760 ms± 220) tasks. No significant interaction between side (stepping and supporting) and task (static and stepping) factors was found.

The amplitude of the PR during static task (measured as the maximal CoP shift between PR onset and the tone (Fig. 5)) was significantly different from the value 0 in both vibration side (supporting: -0.74 cm± 0.26, $P<0.001$ and stepping: $+0.71$ cm± 0.23, $P<0.001$).

Contrary to the results predicted from somatosensory gating mechanisms during step preparation (i.e. smaller PR in stepping- than in static-tasks) the amplitude of the PR was significantly greater in the stepping task when PR was directed toward the supporting side than for all other conditions (Fig. 5). This was shown by the significant interaction between task and side [$F(1,11)=0.29$, $P=0.0008$].

We also examined the possibility of modifying the APAs according to current postural reaction evoked by

vibration. Fig. 6 shows that the thrust was smaller (7.03 cm± 1.85) when the vibration induced a PR toward the supporting leg than in the no vibration condition (7.49 cm± 2.54) and greater (8.29 cm± 1.66) when the vibration evoked a PR toward the stepping leg. This was confirmed by the main effect of the vibratory conditions [$F(2,22)=16.56$, $P<0.001$] and post hoc analyses. No significant differences were observed in the thrust duration (mean duration: 273 ms± 46, $F(2,22)=2.18$, $P=0.13$).

On the other hand, the amplitude and duration of the unloading did not show significant differences between conditions (global mean amplitude: 9.38 cm± 1.59, $F(2,22)=1.51$, $P=0.24$ and global mean duration: 183 ms± 41, $F(2,22)=2.69$, $P=0.09$). However, amplitude and duration of the adjustments varied significantly across conditions (respectively $F(2,22)=19.28$, $P<0.001$ and
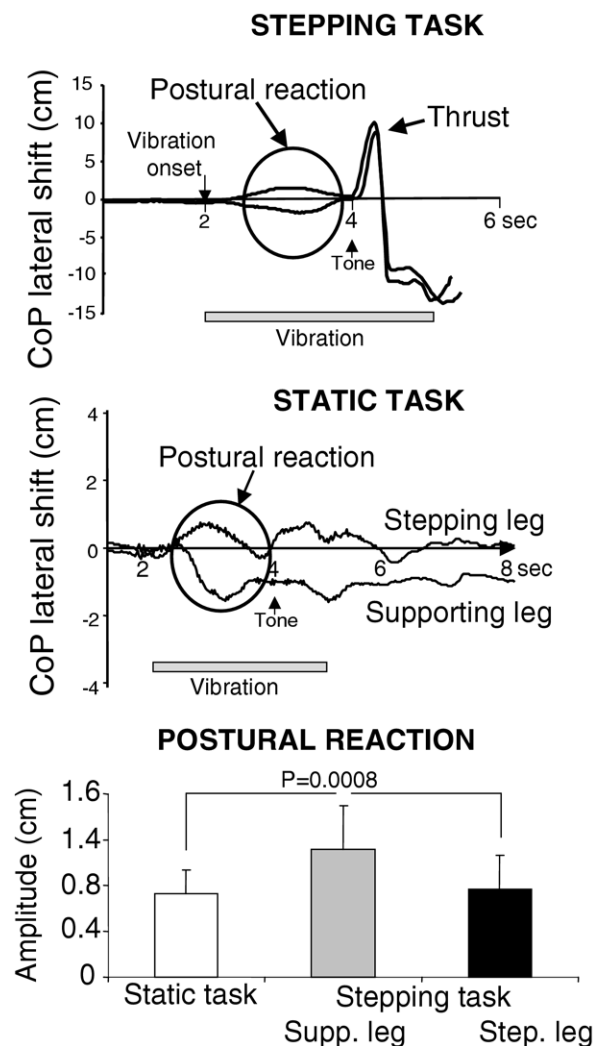
Fig. 5. Postural reactions oriented toward the vibration side during the stepping (top) and static (middle) tasks for experiment 3. Bottom: Mean maximum M/L displacement of the CoP during the PR (defined as the difference between the neutral initial position and the maximum displacement in each direction) in static task (white) and in stepping task (PR oriented toward the supporting leg in gray and PR oriented toward the stepping leg in black).

Thrust (experiment 3)

Adjustment (experiment 3)
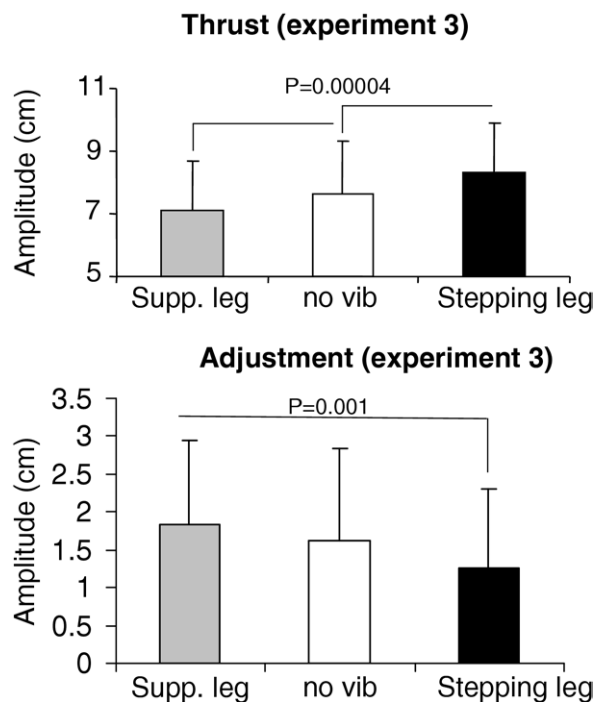
Fig. 6. Mean thrust and adjustment amplitudes of CoP in stepping task for all conditions. The error bars indicate the standard deviations of the means.

$F(2,22)=12.39$, $P<0.001$). The adjustment was greater (1.84 cm$\pm$1.11) and longer (344 ms$\pm$146) when the vibration induced a PR toward the supporting leg than in the no vibration conditions (1.63 cm$\pm$1.21 and 284 ms$\pm$154) and smaller (1.26 cm$\pm$1.05) and shorter (241 ms$\pm$173) when the vibration evoked a PR toward the stepping leg (Fig. 6).

In both vibration-side conditions the foot reached a more eccentric position (PR toward the supporting side: 1.99 cm$\pm$7.40 and PR toward the stepping side: 1.97 cm$\pm$5.97) relative to "No Vibration" (-1.15 cm$\pm$8.25 toward the stepping side), thus increasing the support surface at the end of the focal movement i.e. "safety attitude."

DISCUSSION 3

The absence of the expected decreased amplitude of the PR when comparing stepping to static tasks indicates that sensory attenuation did not occur during the preparation of the APAs. Such attenuation has been reported during the planning phase (i.e. -400 ms) of wrist movements in primates (Seki et al., 2003) as well as in humans (Collins et al., 1998) and -100 ms before an index movement in humans (Voss et al., 2006). In contrast we found a facilitation of the lateral PR (i.e. shorter latencies and greater magnitude of the PR in stepping as compared with static tasks). It is suggested that this facilitation of the postural reaction could be due to a general increase of the activation level of the sensory motor system during the planning phase of the stepping movement. This facilitation is in accordance with the 60 ms shortening of the reaction time

observed for movement that are prepared in advance. Carlsen et al. (2004) have shown when comparing simple (prepared movement) and choice (not prepared movement) reaction time movements that a startle acts as an early trigger for subcortically stored prepared movement and not for the others.

GENERAL DISCUSSION

The experiments presented here tested the hypothesis that the APAs observed in the frontal plane when producing a step are under proprioception-based online control. This was done by evaluating the effect of vibration applied on the tibialis posterior and fibularis longus at various times with respect to the onset of the APAs. This method and results allow us to expand the current knowledge on the APAs by showing that the APAs in the frontal plane can be modified online, during their execution. These results complement those which demonstrate the importance of the sensory-detected initial standing condition on the APA setting (Mille and Mouchnino, 1998; Timmann and Horak, 1998) and those showing that this setting is progressively stored prior to the APAs execution (MacKinnon et al., 2007). Below, we discuss the different features of these online APAs modifications and what can be inferred for their control during step initiation.

Online control of the early component (thrust) of the APAs

Online modification of the initial component of the APAs was observed during the 40 Hz vibration frequency and not during the 80 Hz vibration. This change was typified by a decrease in EMG area and shorter duration of the CoP shift toward the stepping leg (i.e. thrust phase) which initiates the CoM acceleration toward the supporting side. This early component of the APAs corresponds to a phase where forces are exerted onto the ground without any lateral body movement (Mouchnino et al., 1992). The latencies between the tone signal and the APAs onset were similar in all four conditions. Thus, the decrease of the thrust duration cannot be accounted for by an early release of the planned APAs (not completely stored) due to a startle stimulus as reported by MacKinnon et al. (2007). Hence, the reduced thrust phase observed in our study must come from online modification of the APAs, responding to cutaneous information. These results highlight a multisensory control which includes signal not directly devoted to stance and postural control. The low vibration frequency corresponds to the peak sensitivity of the cutaneous Meissner corpuscle receptors stimulated around the ankle joint and not those originating from the sole of the foot. Indeed the absence of any 80 Hz vibration effect may suggest that proprioception is not used by the CNS to exert a fine control over that early motionless phase. The thrust component of the APAs was not shortened in this phase by vibration of the primary endings of the leg muscles. This may suggest that the planning and the online control of this motionless phase of the APAs are not primarily based on proprioception.

Scaling of the APAs according to a previous postural reaction

Results of experiment 3 indicated that when the body moves just before the setting of the APAs, the thrust is scaled according to the direction of the postural reaction and therefore to the associated afferent inflow related to whole body movement. For instance, when the vibration led to a PR oriented toward the supporting leg there was a smaller lateral CoP displacement which decreases the CoM acceleration toward the supporting side. Inversely, when the vibration induced a PR oriented toward the stepping leg, a larger lateral CoP displacement was observed. Hence, the actual postural reaction can interfere with the programmed motor command of the APAs. These results indicate that afferent inputs, signaling the actual standing position, are monitored and appropriately processed by the CNS independently from the vibration-evoked Ia afferences still stimulated during the PR up until the initiation of the APAs. This suggestion is in line with the results of Burleigh et al. (1994) and Timmann and Horak (1998) in step initiation in response to an antero-posterior surface translation. However, our results may appear in opposition to those of Bent et al. (2002) who have shown that subjects submitted to GVS stepping to a lateral shift of the CoP position, did not exhibit modification of the initial phase of the APAs. These authors concluded that step initiation may be unaffected by vestibular influences and suggested that APAs may be programmed as a feedforward, ballistic phase. The lateral postural reaction induced by GVS (i.e. a 1.7 mm shift of the CoP) was, however, four times smaller than that induced by muscle vibrations in the present study. This postural reaction may be too small to elicit any change in the APAs.

Proprioceptive-based control of the final adjustment

Because the vibration lasted 3 s in experiment 3, the leg muscles were still being vibrated following the APAs onset (i.e. the thrust). Whereas this early phase was scaled with respect to the side of the vibration-evoked PR, the subsequent adjustment phase was modulated according to the vibration-induced afferent signals. As in experiment 2, the lateral displacement of the CoP toward the supporting leg was smaller when the vibration elicited afferent information related to body tilt toward the supporting leg. However, contrary to experiment 1, the CoP displacement increased when the vibrated muscles provided information related to a body displacement toward the stepping leg. The effect of the vibration is known to increase with the duration of the vibration (Capicikova et al., 2006). It is therefore likely that the 1-s stimulations in experiment 1 were not sufficiently long to elicit a change in the APAs when the information provided by the vibration and the information produced by the actual body movements were in conflict. This is in line with recent findings obtained by Ivanenko et al. (2000) and Cordo et al. (2005) who showed that when movement and vibration evoked-signal are of opposite direction, the kinesthetic illusion diminishes or even stops.

In light of the present experiments a proprioceptive-based control of the APAs is shown to be phase-dependent. The Ia afferents would be considered as being non-relevant in the early phase of the APAs where no lateral body movement was observed to the benefit of cutaneous inputs that can modify this early APA. During the latter and more dynamic phase of the APAs, the weight of proprioceptive afferents could increase in order to modify the final adjustment accordingly.

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