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Several studies have shown that the transmission of afferent inputs from the periphery to the somatosensory cortex is attenuated during the preparation of voluntary movements. In the present study, we tested whether sensory attenuation is also observed during the preparation of a voluntary step. It would appear dysfunctional to suppress somatosensory information, which is considered to be of the utmost importance for gait preparation. In this context, we predict that the somatosensory information is facilitated during gait preparation. To test this prediction, we recorded cortical somatosensory potentials (SEPs) evoked by bilateral lower limb vibration (i.e., proprioceptive inputs) during the preparation phase of a voluntary right-foot stepping movement (i.e., stepping condition). The subjects were also asked to remain still during and after the vibration as a control condition (i.e., static condition). The amplitude and timing of the early arrival of afferent inflow to the somatosensory cortices (i.e., P1-N1) were not significantly different between the static and stepping conditions. However, a large sustained negativity (i.e., late SEP) developed after the P1-N1 component, which was larger when subjects were preparing a step compared with standing. To determine whether this facilitation of proprioceptive inputs was related to gravitational equilibrium constraints, we performed the same experiment in microgravity. In the absence of equilibrium constraints, both the P1-N1 and late SEPs did not significantly differ between the static and stepping conditions. These observations provide neurophysiological evidence that the brain exerts a dynamic control over the transmission of the afferent signal according to their current relevance during movement preparation.

sensory facilitation; proprioception; EEG; anticipatory postural adjustments; microgravity

IN HUMANS, it has been shown that afferent information transmission is attenuated when executing a voluntary movement (Chapman 1994; Williams and Chapman 2000). This afferent "gating" can also be observed during the preparation of voluntary movements (Collins et al. 1998; Morita et al. 1998; Seki et al. 2003; Voss et al. 2006). For instance, the sensitivity to somatosensory inputs decreases ~100 ms before the onset of finger movements (Voss et al. 2006) and 60 ms before the onset of ankle joint movement (Morita et al. 1998). This sensory attenuation appears to be independent of the activity of the primary motor cortex, because it is also present when the motor command is delayed by transcranial magnetic stimulation (TMS). On the basis of these results, Voss et al. (2006)

suggested that the sensory suppression emerges upstream of M1, from premotor areas.

Although the somatosensory attenuation precedes the onset of motor activity, the fact remains that the characteristics of the forthcoming movement have a strong effect on the amplitude of the attenuation. Indeed, Collins et al. (1998) identified a speed-dependent attenuation of proprioceptive afferents that occurs before single flexion-extension wrist movement performed at different speeds. Specifically, the sensory gating was stronger when the speed of the movement was larger. This phenomenon is observed before the movement (Collins et al. 1998). However, the speed of the movement has no effect on the magnitude of the sensory attenuation when the limb is displaced passively. This centrally driven attenuation of afferent signals could be due to increased neuromuscular spindle discharge associated with the preparation of the fusimotor system prior to a forthcoming fast movements. Furthermore, the mere expectation to receive a sensory signal to move body segments suffices to evoke sensory suppression (Shimazu et al. 1999) even if the movements are not subsequently executed (Voss et al. 2008).

Whereas the afferent attenuation phenomenon has been extensively studied, surprisingly, the possibility to either alleviate this suppression or even facilitate the sensory inputs before or during motor actions is rarely considered. Nevertheless, there is growing evidence that in some contexts, motor tasks can unfold without triggering somatosensory gating. For instance, McIlroy et al. (2003) showed that the sensory suppression in the primary sensory cortex was alleviated prior to randomly occurring perturbations of a pendulum that had to be actively stabilized by the subject's feet. Likewise, the sensory attenuation was minimal or absent prior to foot contact during a locomotion task in human (Altenmüller et al. 1995; Duysens et al. 1995) as well in rats just before the forepaw touched the ground (Chapin and Woodward 1982). Furthermore, tactile gating is also absent when the speed of finger movement is below 200 mm/s, that is, when the speed favors tactile exploration and perception (Cybulska-Klosowicz et al. 2011). Sensory attenuation during volitional actions thus appears to be mediated by task requirements.

There is also some evidence of sensory facilitation during movement preparation. For example, Ruget et al. (2008) found behavioral evidence for sensory facilitation in a study employing a gait initiation task. In their study, the postural reaction evoked by musculotendinous vibration of the ankle joints was more pronounced when the vibration occurred just prior to stepping forward than when the subjects stood still. Given that muscular proprioception provides crucial information about body segment configuration and that stepping may threaten

equilibrium if not appropriately planned, the increased postural response (i.e., center of pressure displacement) to the vibration may have reflected a functional greater sensitivity of the sensory cortex to afferent inputs. Note that such facilitation of sensory information use during a movement has also been observed in fast visually guided upper limb movements (Tremblay and Nguyen 2010) and thus may not be limited to movement preparation. However, these studies only provided behavioral evidence for sensory facilitation.

On the basis of putative functions of the somatosensory information in setting the balance constraints prior to step movement execution (Timmann and Horak 2001), we hypothesized that in tasks requiring a high "proprioceptive vigilance," facilitation of somatosensory inputs should be observed at a cortical level. Furthermore, when reducing the balance requirements of the stepping task by removing the gravitational forces, we should on the other hand observe the well-known movement-induced gating of the transmission of the somatosensory inputs (Seki et al. 2003; Voss et al. 2006; Williams and Chapman 2000) prior to step movement execution. To test these hypotheses, we recorded cortical somatosensory evoked potentials (SEPs) of individuals in response to proprioceptive stimulation (by means of muscle tendon vibration) during the preparation phase of a stepping movement in two environments: normogravity (*experiment 1*) and microgravity (*experiment 2*). We reasoned that a forthcoming step should enhance the vibration-related SEPs relative to a quiet standing position when the presence of gravity is likely to threaten equilibrium (*experiment 1*) and that the SEPs should remain unaffected or decreased during the microgravity phase of parabolic flights (*experiment 2*), that is, in the absence of gravitational equilibrium constraints.

MATERIALS AND METHODS

Experiment 1

Experimental procedures. Eight subjects without any known neurological and motor disorders participated in the first experiment (mean age 36 ± 7 yr). All participants gave their written informed consent to take part in this study, which conforms with the standards set in the Declaration of Helsinki. The local Ethics Committee (Sud Méditerranée 1, ID RCB: 2010-A00074-35) specifically approved this study. Subjects stood barefoot on a 60×120-cm force platform leveled with the ground floor. Their posture was erect, symmetric, and stable. At the start of the trials, the subjects looked at a fixed target in front of them, at eye level. They were asked to close the eyes at a signal indicating either to stand still (hereafter referred to as the static condition) or to make a complete step forward with the right leg (hereafter referred to as the stepping condition). Each subject performed 60 trials that were equally and randomly distributed between the static and stepping conditions. In all trials, bilateral leg vibration was applied for 1 s. Specifically, tendons of the peroneus longus (stepping leg) and tibialis posterior (supporting leg) muscles (Fig. 1A) were vibrated simultaneously. These muscles are responsible for moving the ankle joints laterally and primarily sense leftward lateral body tilts. The vibratory stimulus consisted of small-amplitude vibrations (1.2 mm) of high frequencies (80 Hz), which are known to produce microstretches of muscle spindles and are interpreted by the central nervous system (CNS) as resulting from muscular stretching (Eklund and Hagbarth 1966; Gurfinkel et al. 1996; Roll and Vedel 1982). We used such bilateral tendon vibration to induce afferent volleys mimicking the pattern arising from leftward lateral body tilt (i.e., opposite side to the vibrated muscles: see Fig. 1B). When applied on standing individuals, such vibratory stimulation evokes spatially oriented postural responses toward the stepping (i.e., right) leg with a latency of ~700 ms (Ruget et al. 2008).

The vibration started ~1 s after the verbal cue for remaining either static or for producing a step (Fig. 1C). In the latter condition, the subject had to synchronize step onset with the offset of the 1-s vibration. Note that subjects succeeded in doing so because the onset of the center of pressure displacement, which is responsible for the body shift toward the supporting leg, occurred on average 23 ± 154 ms after the vibration offset (Fig. 1C). This allowed identification of a preparation phase (i.e., between vibration onset and vibration offset), before any motor execution.

Behavioral recordings and analyses. The ground reaction forces and moments were recorded with an AMTI force platform (Advanced Mechanical Technology) at a sampling rate of 500 Hz. From these

Fig. 1. Experimental set up. *A*: vibrator positioning on the ankle joints. *B*: illustration of the effect of the sensory message induced by vibration when the vibrators are placed as shown in *A*. *C*: condition procedures (static and stepping) performed in both normogravity (nG) and microgravity (μG). Schematic represents the center of pressure (CoP) lateral displacement, which indicates the onset of the anticipatory postural adjustments for the stepping condition (in nG). The "foot off" indicates the onset of the stepping movement on the foot vertical velocity.
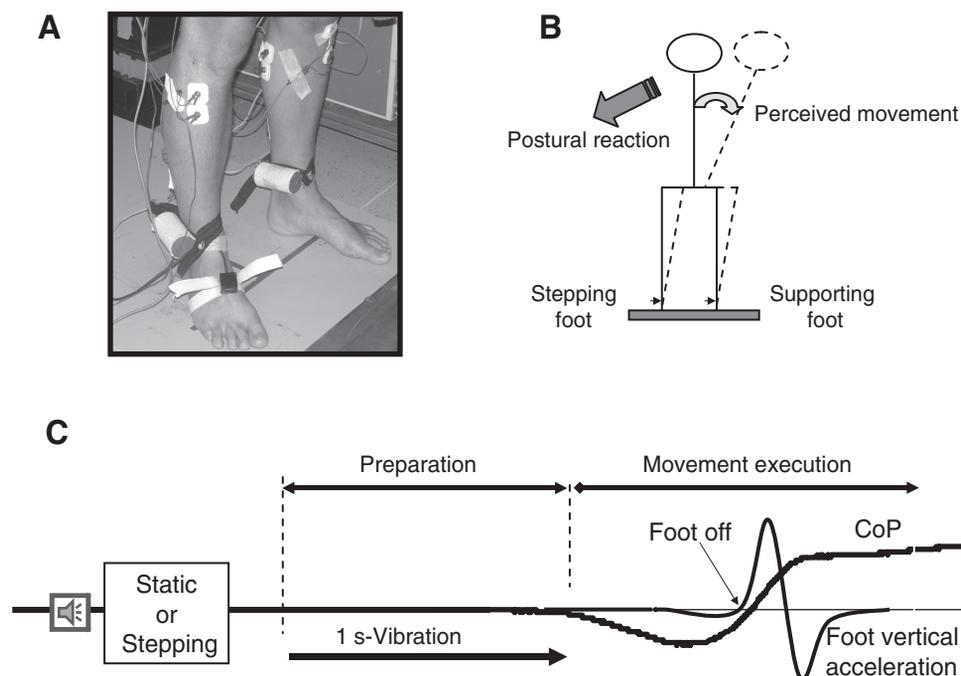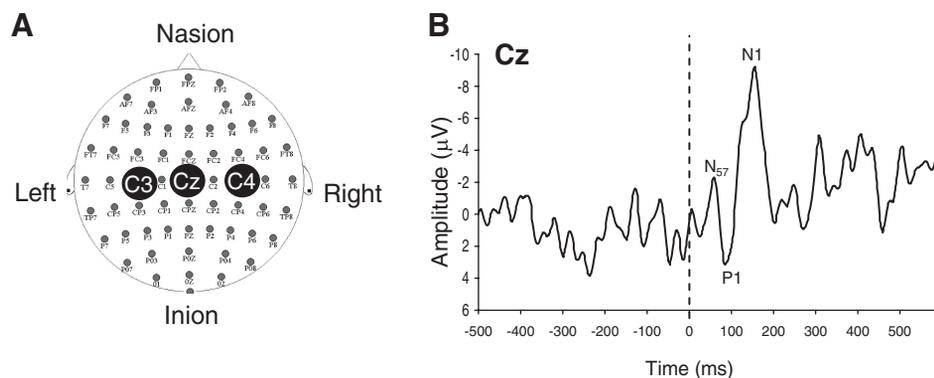
Fig. 2. *A*: image displaying the position of the electrodes of interest (i.e., C3, Cz, and C4). *B*: grand-average evoked potentials for 1 subject recorded over Cz electrode during quiet standing (static condition), which exhibits a first peak negativity (N57), and following the P1-N1 somatosensory evoked potential (SEP) component.

kinetics data, the position of the center of pressure (CoP) was calculated along the mediolateral axis. The primary change of the CoP position was directed toward the stepping leg. The onset of CoP shift was considered as the onset of the motor execution (i.e., forces exerted onto the ground). After reaching a peak toward the stepping side, the CoP moved toward the supporting leg until a stable position was reached, allowing the stepping leg to be unloaded.

The kinematics of the stepping movement were recorded using a triaxial accelerometer (model 4630; Measurement Specialties) placed on the top of the right foot (Fig. 1*A*). Foot kinematics along the forward direction and the vertical acceleration (foot-off, Fig. 1*C*) of the foot movement were analyzed to determine the onset of the step, which occurred 388 ± 100 ms after the vibration offset.

Bipolar surface electromyography (EMG; Bortec AMT-8 system; Bortec Biomedical, Calgary, AB, Canada) was used to record the activity of the tibialis anterior (TA) and the gastrocnemius medialis (GM) muscles of both legs. Activation of the TA and GM muscles of the stepping leg are responsible for the rightward and backward shift of the CoP during gait initiation (Brunt et al. 1991; Mouchnino et al. 1996, Robert et al. 2004). EMG signals were preamplified at the skin site ($\times 1,000$), sampled at 1,000 Hz, bandpass filtered 20 to 250 Hz, and rectified. To quantify the muscle activity, we computed the integral of the EMG activity (iEMG) for each muscle during two time windows identified from electroencephalographic measures, as described below.

Electroencephalography recordings and analyses. Electroencephalographic (EEG) activity was recorded continuously from 64 Ag-AgCl surface electrodes embedded on an elastic cap (BioSemi Active-Two system; BioSemi, Amsterdam, The Netherlands). Specific to the BioSemi system, "ground" electrodes were replaced by "common mode sense" active and "driven right leg" passive electrodes. The signals were preamplified at the electrode sites and postamplified with DC amplifiers, filtered online with a 0.16-Hz high-pass filter (Actiview acquisition program), and digitized at a sampling rate of 1,024 Hz. The signals were further filtered offline with 50-Hz notch filters (digital filters, 24 dB/octave), 40-Hz (high cutoff) and 0.1-Hz (low cutoff) filters (digital filters, 48 dB/octave; BrainVision Analyzer 2; Brain Products, Gilching, Germany). Impedance was kept below 20 kΩ. Vertical electro-oculograms were recorded bipolarly with electrodes placed above and below the left eye; horizontal electro-oculograms were recorded bipolarly with electrodes positioned near the outer canthus of each eye. EEG signals were corrected for eye blinks according to the statistical method of Gratton et al. (1983), as implemented in BrainVision Analyzer 2 software.

SEPs were obtained by averaging, for each subject and each condition, all synchronized epochs relative to the vibration onset. The average amplitude of the 50-ms prestimulus epoch served as baseline. The SEPs were maximal over C3, Cz, and C4 electrodes, which overlay the sensorimotor cortices (Fig. 2). The activity recorded at these electrodes was therefore used to assess the vibration-evoked proprioceptive cortical potentials. The earliest discernible positive peak over the precentral region in most of the EEG recordings could

be distinguished 100 ms after the vibration onset. However, an earlier negative peak evoked by vibration was observed for some subjects and occurred at a mean latency of 57 ms. Such negative peak latency is comparable to latencies (i.e., 45–55 ms) evoked by the ankle joint movement induced by support surface translation (Dietz et al. 1985a) or by vibration of the arm segment (Münte et al. 1996). We primarily focused on the P1-N1 wave following the vibration. Its amplitude was measured peak to peak (Figs. 2 and 3). Its latency was measured as the time of the first positive or negative peak relative to vibration onset (i.e., synchronized signal). After visual inspection for artifact rejection, 88% of trials were included in the analyses. The EMG analyses were performed during the time window defined from vibration onset to N1 offset (i.e., first opposite deflection after N1), which lasted on average 233 ± 17 ms.

Following the P1-N1 component, a clear negative wave over the somatosensory cortices (i.e., late SEP) was observed in both the stepping and static conditions (Fig. 3). We quantified this late activity by computing the integral of the EEG activity (iEEG) over the interval elapsed between N1 offset (i.e., on average 240 ± 26 ms after
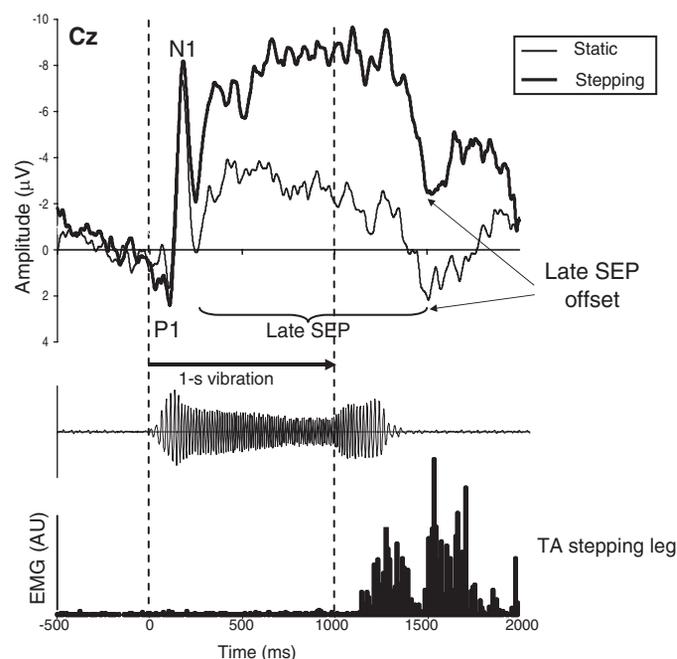

Fig. 3. Electroencephalographic (EEG) and electromyographic (EMG) recordings in nG (*experiment 1*). Grand-average SEPs for 8 subjects were recorded at electrode Cz for the static and stepping conditions. We identified the offset of the late SEP when monotonic trends (strictly increasing) in time series were disrupted. The vertical dotted lines indicate the vibration onset and offset. The vibratory oscillations were recorded by the accelerometer placed on the skin of the foot for 1 subject. Tibialis anterior (TA) muscle activity is shown for a representative trial in the stepping condition.

vibration onset) and 500 ms after vibration onset (i.e., lasting on average 260 ± 26 ms). This time window was also used for iEMG analysis. Because the onset of the TA muscle activity occurred on average $1,039 \pm 113$ ms after the vibration onset, this time window was virtually free of step-related muscular activity.

Statistical analyses. The data related to the EEG signals over the sensorimotor cortices were submitted to repeated-measures analysis of variances (ANOVAs) combining two conditions (static, stepping) with three electrodes (C3, Cz, and C4). Behavioral data (e.g., muscle activity) were submitted to repeated-measures ANOVAs combining two conditions (static, stepping) with two sides (left, right) and two muscles (TA, GM). Significant effects were further analyzed using Newman-Keuls post hoc tests. The level of significance was set at 5%. All significant effects and interactions are reported.

Experiment 2

This experiment was approved by the flight-testing center. All participants gave their written informed consent to take part in this study, which conforms with the standards set in the Declaration of Helsinki. The local Ethics Committee (Sud Méditerranée 1, ID RCB: 2010-A00074-35) specifically approved this study. The experiment was conducted in the A-300 Zero-G aircraft chartered by the French Centre National d'Etudes Spatiales (CNES) for parabolic flight studies. Six flights over two parabolic flight campaigns (nos. 82 and 88) were necessary to complete the experiment with 6 subjects (mean age 35 ± 7 yr). During the flight, the aircraft alternated rises and descents to carry out parabolic profiles, which were interspersed with flat trajectories. Each parabolic maneuver was composed of three distinct phases: 20 s of hypergravity (1.8 g, pull-up phase), followed by 22 s of microgravity (0 g, or μG), before a second period of 20 s of hypergravity (1.8 g, pull-out phase). The aircraft ran a sequence of 30 parabolas per flight separated by 2- to 8-min periods of level flight. The μG phase provided enough time to perform two experimental trials per parabola and thus 60 trials for each subject. The procedure was identical to that in *experiment 1* with one exception that pertained to preventing the subjects from floating away in the experimental bay. To this end, subjects wore shoes with adapted metal soles and stood on a platform comprising four electromagnets (i.e., 2 under each foot). Each set of electromagnets could be activated independently allowing the release of the right foot 200 ms before the vibration offset. After visual inspection of the EEG signals for artifact rejection, 84% of the trials were included in the analyses. The electrode C4 turned out to be defective for one subject due to a wiring fault and the data have been discarded from the analyses for this subject.

RESULTS

Experiment 1

Electrophysiological results. The ANOVA on P1 latency did not show significant effects of condition ($F_{1,7} = 2.03$; $P = 0.19$) or electrode ($F_{2,14} = 0.45$; $P = 0.64$). On average, P1 peaked 100 ± 8 ms after vibration onset. Its amplitude was not significantly affected by the experimental conditions ($F_{1,7} = 0.51$; $P = 0.49$) but was significantly greater at Cz (2.49 ± 1.27 μV) than at C3 and C4 electrodes (overall mean 1.14 ± 0.8 μV) ($F_{2,14} = 6.24$; $P = 0.01$). This positive waveform was followed by a large negativity (i.e., N1, Fig. 3). The ANOVA showed that neither the amplitude ($F_{1,7} = 4.26$; $P = 0.07$) nor the latency ($F_{1,7} = 1.96$; $P = 0.20$) of N1 significantly differed between the static and stepping conditions (Table 1). However, the amplitude of N1 was significantly greater at Cz than at C3 and C4 electrodes (Fig. 4A; $F_{2,14} = 31.54$; $P < 0.001$), and the latency of N1 was shorter at both Cz and C3 electrodes than at C4 (Table 1; $F_{2,14} = 5.05$; $P = 0.02$).

Table 1. *Mean latencies, amplitudes, and iEEG of the SEP components for C3, Cz, and C4 eletrodes in normogravity (experiment 1)*

| Task Condition | Cortical Site | P1-N1 | | Late SEP |
		Average peak latency, ms	Average peak amplitude, μV	iEEG
Static	C3	169 ± 11.7	-3.92 ± 0.71	-0.006 ± 0.28
	Cz	165 ± 14.8	-10.05 ± 2.8	-0.68 ± 0.60
	C4	177 ± 10.4	-4.70 ± 1.92	-0.03 ± 0.29
Stepping	C3	160 ± 12.3	-3.62 ± 1.20	-0.38 ± 0.35
	Cz	161 ± 13.6	-11.81 ± 4.11	-1.65 ± 1.96
	C4	172 ± 13.8	-5.34 ± 1.77	-0.65 ± 0.73

Values are means $\pm$ SD for mean latency, amplitude, and integral of electroencephalographic activity (iEEG) of the somatosensory cortices (P1-N1) and late somatosensory evoked potential (late SEP) components in normogravity (*experiment 1*).

A second negative waveform developed over the somatosensory cortices shortly after the P1-N1 component (Fig. 3). The amplitude of this late and sustained SEP (i.e., iEEG) was markedly of greater amplitude in the stepping than in the static condition (Fig. 4B) as confirmed by the ANOVA, which revealed a significant effect for condition ($F_{1,7} = 56.76$; $P < 0.001$). As for the previous SEP (i.e., P1-N1), the late SEP was greater over the Cz electrode than over the C3 and C4 electrodes (main effect for electrode: $F_{2,14} = 8.22$; $P = 0.004$). In addition, the post hoc comparisons did not yield any differences between C3 and C4 electrodes ($P = 0.57$) in both the static and stepping conditions. The offset of the late SEP was identified at the end of the large deflection strictly increasing (i.e., toward a positivity) in the time series after vibration offset (Fig. 3). The late SEP offset did not differ between static and stepping conditions ($t_7 = 0.36$; $P = 0.97$). It occurred on average 234 ms after the vibration offset command, which was overestimated when considering the inertia of the cylinder (i.e., delay between vibration offset command and actual vibration offset).

One additional analysis confirmed that the late SEP was related to the evoking stimulus and not to the step initiation onset. Two groups of participants (4 in each group) were categorized (hereafter referred to as high-responsive and low-responsive participants) with regards to the different time intervals between the evoking stimulus and the step initiation onset. The high-responsive group triggered anticipatory postural adjustment (APAs) 884 ± 32 ms after the vibration onset, and the low-responsive group, $1,163 \pm 50$ ms after. The latencies between the two groups were significantly different ($t_6 = -9.28$; $P < 0.05$, about 280 ms) because there was a marked effect of the categorization (included as a factor in the ANOVA) of the participants (Fig. 5A). The amplitude of the late and sustained SEP (i.e., iEEG) was greater for the high-responsive participants (in static as well as in stepping conditions) than for the low-responsive participants as confirmed by the ANOVA ($F_{1,6} = 7.51$; $P < 0.033$).

The more striking result was that the amplitude of the late SEP was markedly of greater amplitude in the stepping than in the static condition (condition main effect: $F_{1,6} = 18.9$; $P = 0.04$) regardless of the participants' responsiveness because no interaction between conditions and participants' responsiveness was observed ($F_{1,6} = 2.06$; $P = 0.20$). These results
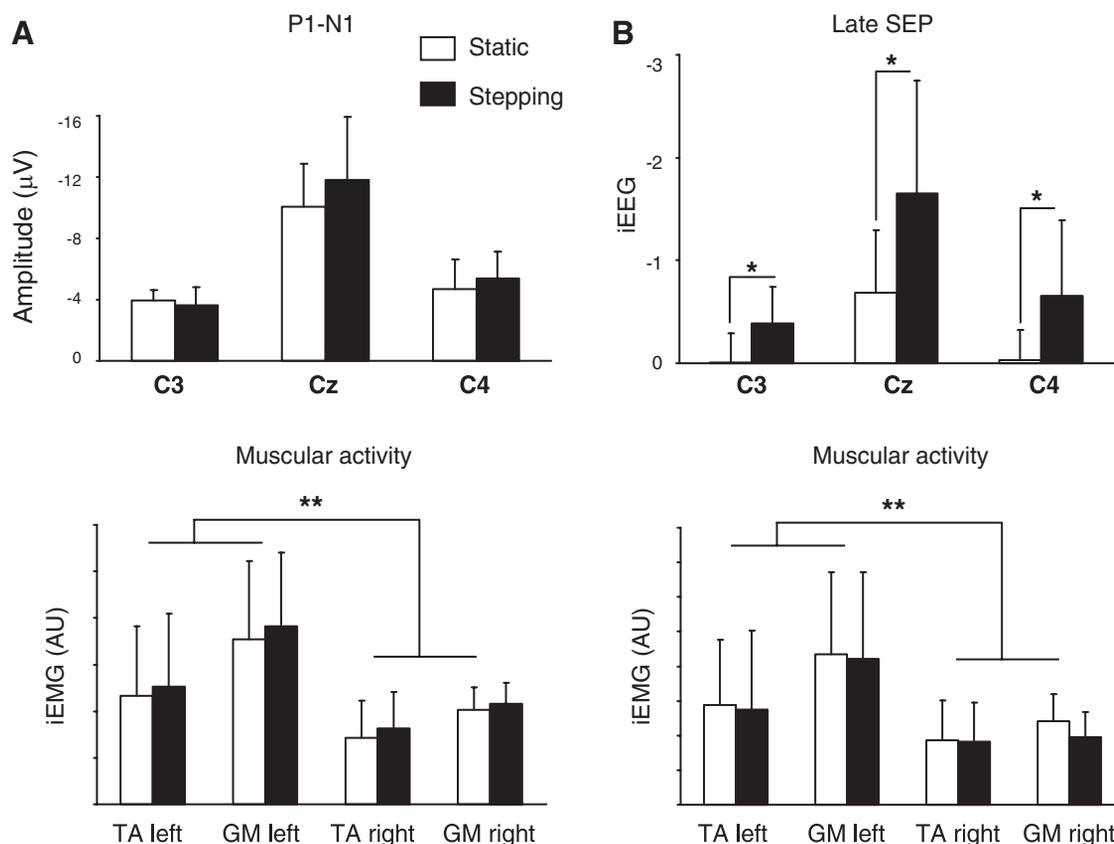
Fig. 4. SEPs and EMG activity in nG (*experiment 1*). *A, top*: mean amplitude of the P1-N1 component for C3, C4, and Cz electrodes in 8 subjects. *Bottom*, integral of the EMG activity (iEMG) of TA and gastrocnemius medialis (GM) muscles of both sides computed in a time window defined from vibration onset to P1-N1 offset. *B*: mean iEEG (late SEP; *top*) and iEMG (*bottom*) computed in a time window defined from the P1-N1 offset to 500 ms following the vibration onset. *$P < 0.05$; **$P < 0.01$.

suggested that the facilitation was preserved in the stepping condition within each group of participants (Fig. 5*B*).

Behavioral results. None of the behavioral data recorded during the preparation phase differed significantly between the stepping and static conditions. The ANOVA did not show a significant effect of condition on iEMG during the P1-N1 or during the late SEPs ($F_{1,7} = 1.82$; $P = 0.21$ and $F_{1,7} = 0.93$; $P = 0.36$, respectively). It is noticeable that a significant effect for side (left, right) was observed on iEMG during both the

P1-N1 ($F_{1,7} = 24.73$; $P = 0.002$) and the late SEP ($F_{1,7} = 17.67$; $P = 0.004$) (Fig. 4). This effect resulted from a slight asymmetric weight bearing toward the supporting side in both the static and stepping conditions. The randomized presentation of the static and stepping trials could explain why subjects also adopted an asymmetric position in the static condition. Overall, similarities of the iEMG variables between the stepping and static conditions suggest that the late and large frontocentral negativity (i.e., Cz, C3, C4) observed in the
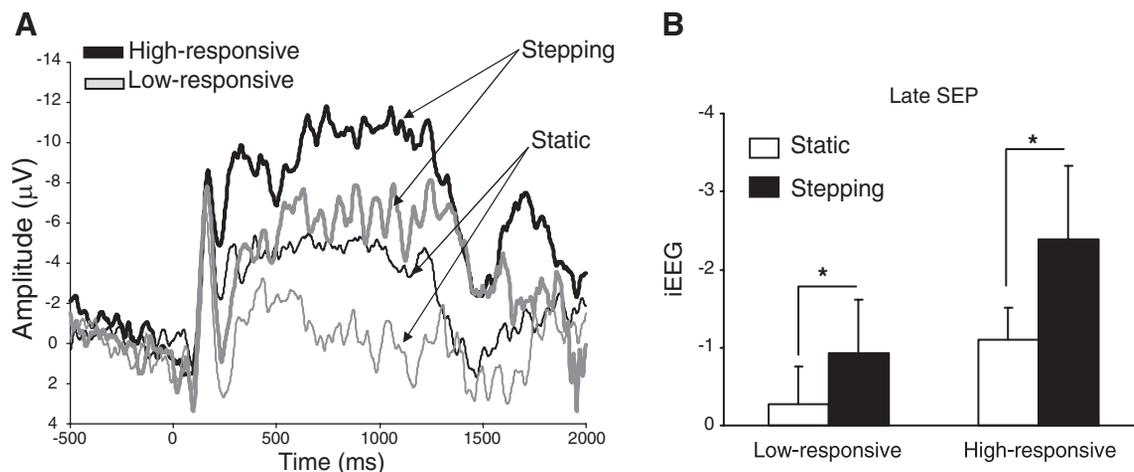

Fig. 5. SEPs in high- and low-responsive participants. *A*: grand-average SEPs for 4 high-responsive (black traces) and 4 low-responsive participants (gray traces) recorded at electrode Cz for the static (thin traces) and stepping conditions (thick traces). *B*: mean iEEG (late SEP). *$P < 0.05$.

stepping condition resulted from somatosensory processes rather than from changes in motor activity.

Conclusion. Results of *experiment 1* revealed a marked increased of negativity (i.e., late SEP) when subjects prepared to produce a step compared with when they stood still. The APA stepping sequence is known to be progressively assembled and stored up to 1.5 s before step initiation (MacKinnon et al. 2007). The scaling of these APAs relies on the ability to use sensory information to determine the body configuration relative to the ground prior to step execution (Timmann and Horak 2001). Although gait is normally initiated with ease and fluency in healthy individuals, this process most likely requires accuracy given the motion of the body's center of mass and the unipodal weight bearing during gait. The large negativity observed at electrodes overlaying the somatosensory cortices during step preparation may thus reflect a sensory facilitation or "proprioceptive vigilance" linked to the balance constraints of the task.

Alternatively, this additional increased negativity could be linked to general preparatory processes analogous to movement-related contingent negative variation (CNV) as identified by Walter et al. (1964). The CNV corresponds to the slow increase negativity that predominantly develops at the vertex after subjects receive a warning stimulus and before they receive an imperative stimulus to initiate their voluntary movements (Yazawa et al. 1997). The CNV has also been evidenced prior to postural reactions (Jacobs et al. 2008; Slobounov et al. 2000, 2005). In the present study, the onset and the offset of the vibration, which were constantly spaced by 1 s, could well be interpreted by the subject as the warning and imperative signals, respectively.

To determine whether the increased negativity that we observed in *experiment 1* reflected either sensory processing mechanisms related to balance control (*hypothesis 1*) or rather movement-related arousal mechanisms (*hypothesis 2*), *experiment 1* was replicated in a μG environment. Indeed, microgravity suppresses gravitational equilibrium constraints and the anticipatory postural adjustments that are normally associated with leg movements (Mouchnino et al. 1996) while maintaining movement kinematics (Papaxanthis et al. 2005). Thus *experiment 2* involved subjects performing the same stepping task as in *experiment 1*, but this time during the μG of parabolic flights.

Experiment 2

Electrophysiological results. As in *experiment 1*, the waveform observed in μG was composed of a P1-N1 and late components (Fig. 6). Similarly to *experiment 1*, the amplitude of P1-N1 was greater over the Cz than over C3 and C4 electrodes (Fig. 7A; $F_{2,8} = 10.36$; $P = 0.006$) and the latency of N1 was not significantly different between the three electrodes ($F_{2,8} = 0.40$; $P = 0.67$). Also as in *experiment 1*, neither the amplitude nor the latency of the P1-N1 significantly differed between the static and stepping conditions ($F_{1,4} < 0.01$; $P = 0.97$ and $F_{1,4} = 0.28$; $P = 0.62$ for amplitude and latency, respectively) (Table 2). However, both the P1-N1 and late components drastically differed from those revealed in normogravity (cf. Figs. 3 and 6).

On one hand, the amplitude of P1-N1 was twice as small in μG than in normogravity (nG; *experiment 1*). On the other hand, but also in sharp contrast with *experiment 1*, no large
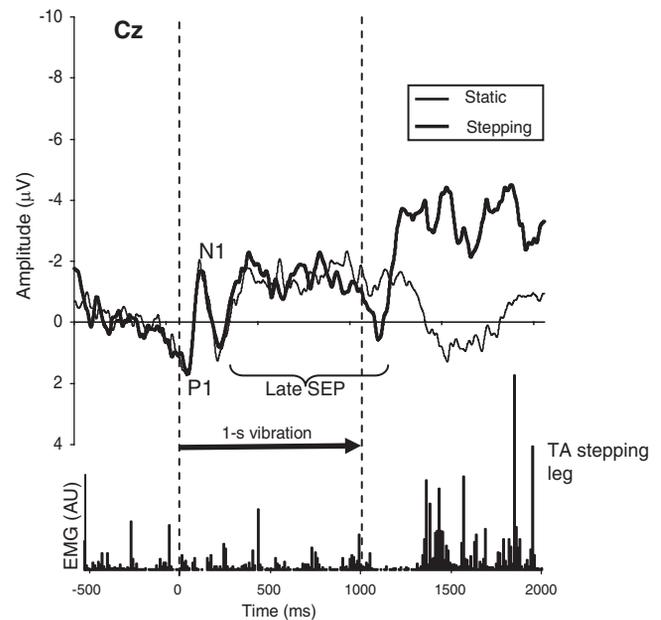

Fig. 6. EEG and EMG recordings in μG (*experiment 2*). Grand-average SEPs were recorded at electrode Cz for the static and stepping conditions for 6 participants during parabolic flight of the Airbus A300 Zero-G. TA muscle activity is shown for a representative trial in the stepping condition. The vertical dotted lines indicate the vibration onset and offset.

negativity was observed after the P1-N1 component in the absence of gravitational constraints. As a result, no significant effects of condition ($F_{1,4} = 0.24$; $P = 0.64$) or electrode ($F_{1,4} = 1.48$; $P = 0.28$) were found on iEEG during the late SEP (Fig. 7B).

Behavioral results. None of the measured behavioral variables significantly differed between the static and stepping conditions. This was confirmed by the ANOVA, which did not reveal significant effects of condition on the iEMG during the P1-N1 (Fig. 7A; $F_{1,5} = 2.36$; $P = 0.18$) or the late SEP (Fig. 7B; $F_{1,5} = 1.77$; $P = 0.23$). Contrary to *experiment 1*, the absence of gravitational constraints failed to yield significant differences between the muscular activity (i.e., iEMG) of both legs during either the P1-N1 or late SEP ($F_{1,5} = 0.20$; $P = 0.66$ and $F_{1,5} = 0.02$; $P = 0.94$, respectively).

In the μG environment, a well-known change in postural tonic muscle activity was observed (Lestienne and Gurfinkel 1988). In the static condition, the tonic activity of the TA muscles was profoundly enhanced and, inversely, the tonic activity of the GM muscles reached a level near zero. This effect of microgravity on the activity of the antagonistic muscles of the leg was confirmed by the ANOVA on iEMG data, which showed a significant effect for muscle during the P1-N1 (Fig. 7A; $F_{1,5} = 18.82$; $P = 0.0074$) as well as during the late SEP (Fig. 7B; $F_{1,5} = 7.61$; $P = 0.039$). This main effect of muscle was observed in both the static and stepping conditions. A few contrasts with experiment 1. *Experiment 2* yielded some differences from *Experiment 1* that could be explained by either artifacts due to differences in the actual stepping movements and/or differences in EEG measurements made in μG and nG. We thus opted to perform careful comparisons between the experiments while correcting for the unequal number of subjects as well as acknowledging limitations associated with between-subject comparisons. To compare the stepping condition under both μG (*experiment 2*) and nG environments
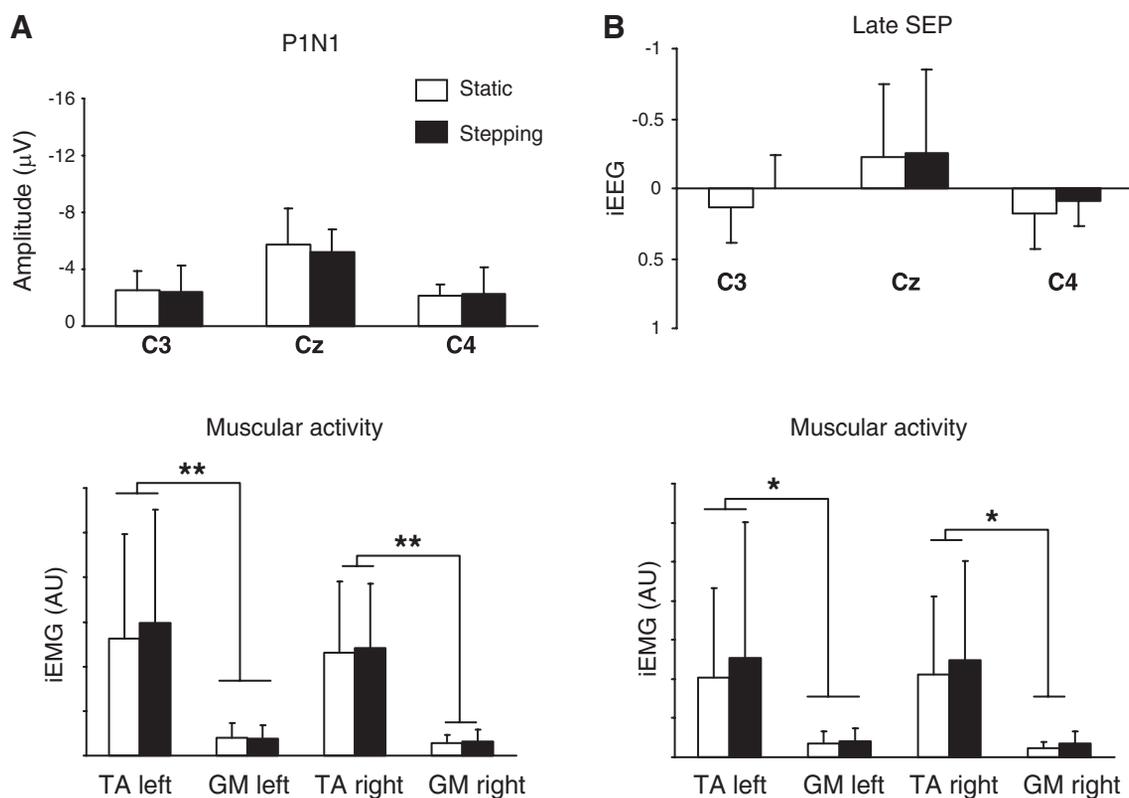
Fig. 7. SEPs and EMG activity in μG (*experiment 2*). *A*, *top*: mean amplitude of the P1-N1 component for C3, C4, and Cz electrodes. *Bottom*, iEMG of TA and GM muscles of both sides computed in a time window defined from vibration onset to P1-N1 offset. *B*: mean iEEG (late SEP; *top*) and iEMG (*bottom*) computed in a time window defined from the P1-N1 offset to 500 ms following the vibration onset. *$P < 0.05$; **$P < 0.01$.

(*experiment 1*), we exceptionally opted to conduct independent *t*-tests to determine if the stepping movement produced in both gravitational environments were significantly different. As in nG, the foot-off occurred after the vibration offset in μG; its onset time was not significantly different in both environments ($t_{12} = -1.22$; $P = 0.24$; 450 ± 80 ms in μG and 388 ± 100 ms in nG). Moreover, the peak acceleration reached by the stepping foot (Fig. 8*A*) did not significantly differ between the μG (1.9 ± 1.2 m/s^2) and nG environments (2.3 ± 0.4 m/s^2) (Fig. 8*B*; $t_{12} = 0.90$; $P = 0.38$). However, the peak deceleration was lower in μG (0.9 ± 0.6 m/s^2) than in nG (2.9 ± 1.2 m/s^2) ($t_{12} = 3.33$; $P = 0.005$), whereas the duration of the step movement was longer in μG than in nG (Fig. 8*C*; $t_{12} = -3.61$; $P = 0.003$). The latter results can be explained by the down-

Table 2. *Mean latencies, amplitudes, and iEEG of the SEP components for C3, Cz, and C4 eletrodes in microgravity (experiment 2)*

Task Condition	Cortical Site	P1-N1		Late SEP
		Average peak latency, ms	Average peak amplitude, μV	iEEG
Static	C3	182 ± 33.9	-2.50 ± 1.37	-0.171 ± 0.27
	Cz	197 ± 32.5	-5.76 ± 2.45	-0.085 ± 0.43
	C4	181 ± 40.3	-2.07 ± 0.83	0.184 ± 0.24
Stepping	C3	181 ± 37.5	-2.39 ± 1.89	-0.050 ± 0.20
	Cz	187 ± 27.7	-5.17 ± 1.65	-1.035 ± 0.31
	C4	190 ± 49.7	-2.31 ± 0.76	-0.094 ± 0.17

Values are means $\pm$ SD for mean latency, amplitude, and iEEG of P1-N1 and late SEP components in microgravity (*experiment 2*).

ward part of the step movement to reach the ground. Indeed, in the nG environment the downward step movement can be passively achieved by the action of gravitational forces on the limb (i.e., without voluntary muscle activity). In contrast, removing gravity requires muscular activation to move the foot toward the ground. Another potential concern was related to the overall levels of evoked potentials in μG, which were markedly lower than in nG. These lower evoked potentials could indeed arise from nonphysiological origins and could stem, for instance, from lesser adherence of the electrodes with the scalp in μG than in nG. To test for potential differences in EEG measures in both environments, we compared iEEG over the same window duration as the ones used to calculate the late SEP but just following vibration offset. We contrasted these iEEG values using a two-environment (μG, nG) $\times$ two-task (stepping, static) ANOVA. As anticipated (Fig. 8*D*), we observed a main effect for task ($F_{1,5} = 9.64$, $P = 0.03$) but not for environment ($F_{1,5} = 1.72$, $P = 0.24$). In addition, we conducted an independent *t*-test on the stepping iEEG data separately, which also failed to exhibit significant differences between μG and nG ($t_{12} = -1.37$, $P = 0.2$). As such, we were confident that the absence of differences in iEEG between stepping and static conditions in μG was not due to methodological limitations of conducting EEG measurements in μG.

DISCUSSION

We used protocols that enabled us to appraise changes in transmission of somatosensory signals during the preparation of a complex motor task, namely, gait initiation. Together, the results of *experiments 1* and *2*, which were respectively carried out in normogravity and microgravity, clearly show that the
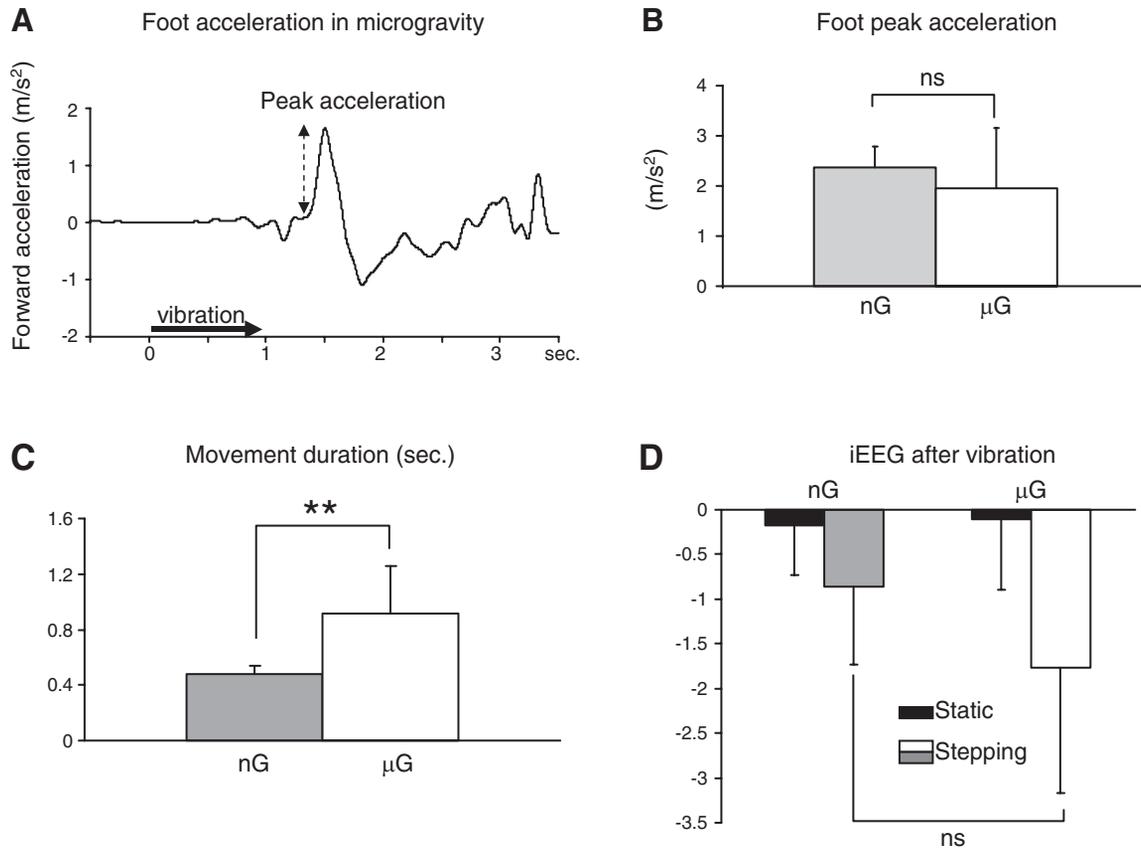
Fig. 8. Kinematics and iEEG during the step movement. *A*: foot vertical acceleration for a representative trial in μG (stepping condition). *B*: mean peak acceleration of the foot in nG and μG. *C*: mean movement duration in nG and μG. *D*: iEEG following the end of the vibratory stimulus in static and stepping conditions (i.e., during movement execution). *$P < 0.05$. ns, No significant difference.

sensitivity of sensorimotor cortices to somatosensory cues increases during the planning phase of a step only when gravitational equilibrium constraints are present.

The first important information revealed by the present study is that the early detectable arrival of somatosensory afferents to S1 (i.e., P1-N1 component), which is known to be greatly reduced during finger and wrist movement planning (Seki et al. 2003; Voss et al. 2006), remains unmodified during step preparation. The lack of effects of motor preparation on the early SEP both in normal gravitational conditions and in microgravity suggests that this component was impervious to the processes engaged during the step motor preparation. This cortical waveform recorded over the sensorimotor region most likely resulted from the proprioceptive afferent volley evoked by the vibration, and not from another sensory system (e.g., cutaneous receptors of the skin under the vibrators). Indeed, SEPs recorded over the same scalp regions as in the present study were reported to be unaffected after ischemic blockade of the foot (Dietz et al. 1985b) or after cutaneous anesthesia (Münte et al. 1996). As such, it is unlikely that the skin afferents contributed significantly to the generation of the SEPs we observed.

The lack of difference in the amplitude of the P1-N1 component between the static and stepping conditions in both environments sharply contrasts with the results reported in previous studies using nonpostural movements (Seki et al. 2003; Shimazu et al. 1999; Voisin et al. 2011; Voss et al. 2006, 2008;). For instance, Seki et al. (2003) found large gating of afferent inflow,

starting some 400 ms before voluntary wrist movements in monkeys, whereas Voss et al. (2006) reported a sensory attenuation occurring ~100 ms before finger movements in humans. It is important to note that the P1-N1 observed here, which peaked some 850 ms before the step initiation, can be considered as occurring during the preparation phase because the motor preparation of a step movement starts as early as 1,400 ms before the beginning of step-related motor activity (see MacKinnon et al. 2007). Therefore, the P1-N1 observed in the present experiments occurred during the preparation phase of the stepping movement, but this motor preparation had no effects on the magnitude of the SEP. The modulation of attenuation appeared specifically related to the postural task, likely improving sensory transmission related to the equilibrium constraints associated with executing a stepping movement. A recent study by Cybulska-Klosowicz et al. (2011) confirmed such a functional role of absence of gating: during tactile exploration, subjects optimized the speed of movement to avoid speed-associated tactile gating. This strategy thus optimized the quality of the tactile feedback.

After the P1-N1 component, the electroencephalograms revealed a clear and sustained negative waveform over the somatosensory cortices. Unlike P1-N1, the late SEP was markedly enhanced when subjects were about to produce a step compared with when they stood still in a normogravity environment (*experiment 1*). As such, this additional increased negativity is analogous to movement-related CNV, which rises in expectation of the imperative stimulus. However, this component shows marked cortical asymmetry that depends on the

responding motor segment side (i.e., greater amplitude over the contralateral hemisphere). The fact that the present EEG recordings arising from bilateral ankle muscle vibration did not show asymmetric activation of the somatosensory cortices (recorded by electrodes C3 and C4) before the right foot movement is not compatible with a putative role of CNV.

In addition, Rohrbaugh et al. (1976) have shown that the readiness potential increased in relation with short reaction time. Thus greater late SEPs in high-responsive participants would suggest some contribution from this readiness potential. However, the increase in high-responsive participants was observed for the stepping as well as the static condition (i.e., when the high-responsive participants stood still). These observations are in conflict with the above interpretation. Still, the most convincing argument against a significant contribution of the CNV in the late SEP increase is probably the fact that the SEP increase was not observed when subjects performed a step in weightlessness. This was true despite the fact that the stepping movements had many features comparable to those produced in normogravity (e.g., similar latency, foot acceleration, and, arguably, iEEG after vibration offset). Rather than being strictly linked to general preparatory processes, the increase of the late SEP observed during step preparation in normogravity may reveal sensorimotor system facilitation associated with equilibrium constraints (i.e., absent in microgravity). Such preparatory sensorimotor facilitation mechanisms could thus be linked to the generation of APAs (i.e., CoP shift before step movement), which are not observed in microgravity (Mouchnino et al. 1996). The sensory facilitation revealed here would be predictive in nature, as opposed to postdictive (see for instance, Voss et al. 2008), because it would be enabled by the preparation of the upcoming APAs, thereby facilitating the role of proprioceptive inputs, a phenomenon that could be termed "task-relevant sensory vigilance." The most convincing argument in favor of a proprioception-based sensory vigilance explanation is probably the fact that the late SEP ended at the offset of the oscillatory stimuli produced by the vibrators in both the static and stepping conditions (see Fig. 3). The importance of muscle spindle inputs for generating the late SEP is also supported by results obtained by Nelson et al. (2000). These authors showed an increase delay of the late SEP evoked by the nerves stimulations at the ankle level when the conduction velocity of the primary afferents endings was slowed down by cooling the lower limb. In the current study, the upregulation of proprioceptive afferents in normogravity contrasts with the absence of "sensory facilitation" in microgravity. This difference could highlight the rapid adaptation of predictive feedforward motor commands in microgravity, where a proprioception-based postural control became pointless. For instance, the position of the center of mass is no more controlled in weightlessness, where the equilibrium is not endangered by the gravitational forces (Casellato et al. 2012; Ruget et al. 2010). Therefore, the irrelevant aspects of the performance (here, equilibrium aspect) would not be taken into account in the movement control as evidenced either in short-term (Casellato et al. 2012; Ruget et al. 2010) or during long-term microgravity (Pedrocchi et al. 2002).

The presence of facilitation of the late SEP, while the early P1-N1 SEP was not modulated, suggests the presence of at least two somatosensory processes: one being linked to the afferent inflow and the second representing a later stage of processing in proprioceptive-motor integration. The early SEP could be related to signal processing and independent of context (i.e., task factors) while the other signals information that is relevant to ongoing behavioral demands (i.e., proprioceptive vigilance). These two processes observed in our study could account from different origins and be consistent with reports of the role of primary (S1) and secondary (S2) somatosensory cortex, respectively (see for review, Romo et al. 2002). For example, Chapman and Meftah (2005) have shown, using single-unit recordings, that neuronal responses from S1 were not changed with directed attention on the textures scanned under the digit of a macaque monkey, whereas a large enhancement was observed in S2. The S2 region, which comprises the parietal ventral area (PV), has strong connections with the posterior parietal and premotor cortex. Indeed, data from monkeys (Disbrow et al. 2003) and humans (Hinkley et al. 2007) demonstrated that PV receives and sends projections to premotor cortex. This pathway is thought to provide the substrate for sensorimotor integration in movements that require constant online feedback.

The increased brain activation in the sensorimotor cortices is consistent with recent findings obtained by Mizelle et al. (2010) using event-related desynchronization (ERD) analyses. These authors showed a large increase of brain activation over the premotor, sensorimotor, and parietal areas with increased spatial demand when sitting subjects prepared a knee extension movement to a small target compared with a knee extension free of spatial constraints. This is also in line with the study of Quant et al. (2004), which reported a facilitation of the late SEP at the electrode overlying the vertex (Cz) in sitting subjects who had to stabilize an inverted pendulum with their feet. One likely structure responsible for setting the "sensory vigilance" is the prefrontal cortex. This region is known to project toward the sensorimotor cortex (Christensen et al. 2007; Jones 1986) and to regulate the transmission of sensory inputs to primary sensory areas according to their task relevance (Knight et al. 1999; Staines et al. 2002; Yamaguchi and Knight 1990). This function of the frontal lobe is also supported by the fact that patients with damage to the prefrontal cortex fail to distinguish between relevant and irrelevant sensory information (Knight et al. 1999).

Another salient feature of the EEG recordings made in microgravity (*experiment 2*) was the large decrease of the cortical response to the vibratory stimulation compared with normogravity. To our knowledge, this finding provides the first electrophysiological basis for the decreased sensitivity to proprioceptive inputs, which has been alluded to in several behavioral studies conducted in microgravity. For instance, Roll et al. (1998) have reported decreased postural responses and kinesthetic illusions in microgravity in response to vibrations, suggesting decreased proprioceptive transmission. Experiments in microgravity, including limb matching tasks under muscle vibration (Lackner and DiZio 1992) and perceptual estimates of limb position (Bringoux et al. 2012; Young et al. 1993), have also suggested that the use of proprioception is not as effective in microgravity as in normogravity. Illusory motion induced by muscle vibration also diminished in microgravity relative to that in normal gravity (Lackner and DiZio 1992). A suggestion was made that it could result from the absence of gravity-based vestibular inputs, which would lead to a decreased vestibulospinal influence on muscle spindle

sensitivity (Lackner and DiZio 1992). This hypothesis is supported by the observation made by Popov et al. (1999): a balanced bilateral vibration of the hip abductors, which is inappropriate for eliciting a postural response, does evoke a body sway when it is combined with a near-threshold galvanic vestibular stimulation, which is too weak to elicit a postural response on its own. Another explanation for the decreased SEP in microgravity could be related to the absence of gravity-induced joint torques. Indeed, restoring gravity-like torque during movements with a pair of elastics that were attached to each side of the right arm's gutter at the elbow level allowed subjects to perceive their limb position in microgravity with similar levels of accuracy compared with normogravity (Bringoux et al. 2012). Whereas this result provides compelling evidence for the importance of joint torque, it also suggests that the hypergravity phase that occurs at the beginning of the parabolas has no effect on the processing of somatosensory information during the forthcoming weightless phases.

Altogether, the present study shows that somatosensory inputs are not suppressed, but rather facilitated during the preparation of a step movement only when the gravitational circumstances offer postural stability constraints. These results indicate that humans can not only inhibit but also facilitate sensory signal processing based on the relevance of the specific sensory signals for the task they are about to perform.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.H.S. and L.M. conception and design of research; A.H.S., L.T., J.P., J.B., and L.M. performed experiments; A.H.S., L.T., J.P., and L.M. analyzed data; A.H.S., L.T., J.B., and L.M. interpreted results of experiments; A.H.S. and L.M. prepared figures; A.H.S., J.B., and L.M. drafted manuscript; A.H.S., L.T., J.B., and L.M. edited and revised manuscript; A.H.S., L.T., J.P., and L.M. approved final version of manuscript.

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