

Modulation of proprioceptive inflow when initiating a step influences postural adjustments

Hélène Ruget · Jean Blouin · Thelma Coyle ·
Laurence Mouchnino

Received: 15 April 2009 / Accepted: 25 September 2009 / Published online: 16 October 2009
© Springer-Verlag 2009

Abstract A synergistic inclination of the whole body towards the supporting leg is required when producing a stepping movement. It serves to shift the centre of mass towards the stance foot. While the importance of sensory information in the setting of this postural adjustment is undisputed, it is currently unknown the extent to which proprioceptive afferences (Ia) give rise to postural regulation during stepping movement when the availability of other sensory information relying on static linear acceleration (gravity) is no longer sensed in microgravity. We tested this possibility asking subjects to step forward with their eyes closed in normo- and microgravity environments. At the onset of the stepping movement, we vibrated the ankle muscles acting in the lateral direction to induce modification of the afferent inflow (Ia fibres). Vibration-evoked movement (perceived movement) was in the same direction as the forthcoming body shift towards the supporting side (current movement). A control condition was performed without vibration. In both environments, when vibration was applied, the hip shift towards the supporting side decreased. These postural modifications occurred, however, earlier in normogravity before initiating the stepping movement than in microgravity (i.e. during the completion of the stepping movement). Our results suggest that proprioceptive information induced by vibration and afferent inflow related to body movement exaggerated sense of movement.

This biased perception led to the postural adjustment decrease. We propose that in both environments, proprioceptive inflow enables the subject to scale the postural adjustments, provided that body motion-induced afferences are present to activate this postural control.

Keywords Anticipatory postural adjustments · Gait · Tendon vibration · Microgravity

Introduction

The execution of voluntary movements by standing subjects is generally accompanied by postural adjustments. In most cases, the muscles responsible for these postural adjustments are activated before those acting as prime movers. For instance, electromyographic activity of the leg muscles usually precedes that of the upper limb's muscles when an individual rapidly raises the arm while standing (Aruin and Latash 1995). The activity of antigravity muscles minimizes the postural perturbations that are likely to occur during movement execution by stabilizing the body's centre of mass (CoM) (Massion 1984; Bouisset and Zattara 1987). Tightly linked to the magnitude and direction of the forthcoming focal movement, these postural adjustments are known as anticipatory postural adjustments (APAs).

The stabilization of the CoM is not always required during movements. Indeed, the normal execution of several motor actions relies rather on the displacement of the CoM. This is the case for instance when reaching for an object located beyond arm's length (Pozzo et al. 2002; Berret et al. 2009), initiating gait or raising a leg (Brénière and Do 1991; Malouin and Richards 2000; Mouchnino et al. 1992; Robert et al. 2004; Rogers and Pai 1990, 1995; Timmann and Horak 2001). These movements are indeed preceded by

H. Ruget · J. Blouin · L. Mouchnino (✉)
Laboratoire Neurobiologie de la Cognition,
CNRS and Aix-Marseille Université, 3 place Victor Hugo,
13331 Marseille cedex 3, France
e-mail: laurence.mouchnino@univmed.fr

T. Coyle
Laboratoire Mouvement et Perception,
CNRS and Aix-Marseille Université, Marseille, France

initial postural adjustments whose goal is to set up the condition required for the execution of the focal leg movement. Starting before the step, these initial postural adjustments (which also unfold during the stepping movement) are also considered as APAs (Kaminski and Simpkins 2001; Malouin and Richards 2000; Massion 1992; Timmann and Horak 2001). For instance, step initiation is preceded by a shift of the CoM both laterally towards the supporting side to unload the stepping leg and forward to create the condition for progression (Brénière and Do 1991). More specifically, when producing a step with the right leg, the leftward displacement of the CoM is produced by an initial rightward shift of the centre of pressure (CoP) whereas the forward displacement of the CoP is produced by an initial posterior shift in the CoP. These early shifts of the CoP form the “thrust” component of the APAs and precede the earliest motion of any body segments which are usually observed at the trunk level (Brénière and Do 1991; Mouchnino et al. 1992). Indeed, the earliest body displacement occurs only after the CoP had reached its maximal amplitude and is starting its displacement toward the supporting side. Starting before the focal step movement, these late APAs correspond to the unloading of the stepping leg.

The setting of the postural adjustments that anticipate and accompany leg movements are largely based on sensory information processing (e.g. vestibular, cutaneous, visual, proprioceptive). However, the way this information is integrated varies during the execution of the movement and depends on the overall sensory context. For instance, recent studies have shown that the early APAs (that is the thrust) of a forward stepping movement are robust to vestibular (i.e. galvanic stimulation, Bent et al. 2002) or proprioceptive (i.e. muscle vibration, Ruget et al. 2008) stimulations. One interpretation for the lack of effect of the muscle vibration and vestibular galvanic stimulation in the early postural adjustments is that the body motion information evoked by these techniques was superimposed and presumably masked by the massive sensory inputs (from all other sensors) that informed about body stability. In this context, we hypothesized that the contribution of leg muscle proprioception should be greater when the availability of other sensory information relying on static linear acceleration (gravity) is no longer sensed in microgravity.

For instance, the microgravity takes away gravity and consequently the reaction force normally used to resist the acting force of gravity no longer exists. Therefore, under microgravity, Golgi organs and mechanoreceptors from the plantar sole cannot provide relevant information on body position prior stepping movement as their activation depends on contact forces opposing gravity (Lackner and Dizio 1996), also evidenced by immersion (Dietz and Colombo 1996). Nevertheless, muscular proprioceptive inputs are known to remain functional in microgravity during quiet standing (Roll et al. 1993, 1998). In addition, the

otolith organs no longer provide information on the linear gravitational acceleration and the static otolith-spinal and otolith-oculomotor influences that depend on head orientation relative to gravity are absent (Watt et al. 1986). The high frequency otolith and semicircular canals input are, however, preserved (Moore et al. 2003). In microgravity, the vestibular system no longer provides information about the vertical orientation of the body although the lack of vestibularly detected linear acceleration in such environment is indicative of a stationary posture.

Since it also prevents detection of the vertical standing position through load (Golgi and plantar) receptors, microgravity environment, therefore, provides a unique opportunity to investigate the extent to which proprioceptive information contributes to postural control. Despite that the equilibrium is not challenged in microgravity, APAs are still observed in microgravity. For instance, the trunk inclination in the opposite direction to the leg movement is preserved in microgravity during leg raising (Mouchnino et al. 1996; Gueguen et al. 2004). These simultaneous and opposite movements of the leg and trunk account for the CoM stabilization and serve to ease the leg movement. Other evidences of preserved APAs in microgravity were also reported by Vernazza-Martin et al. (2000) in subjects moving the whole body and by Bouisset and Zattara (1987) and Clément et al. (1984) during arm raising. The goal of these APAs is to stabilize the CoM position. However, in normogravity, the execution of several motor activities relies rather on the displacement of the CoM. For instance, step initiation is preceded by a shift of the CoM both laterally towards the supporting side to unload the stepping leg and forward to create the condition for progression (Brénière and Do 1991). The goal of these APAs is to set up the condition required for the execution of the focal movement. These APAs are either reduced or abolished in microgravity (Mouchnino et al. 1996).

Here, we asked subjects to step forward with their eyes closed during the microgravity phases of parabolic flights. Vibratory stimulus was delivered to the leg muscles and was synchronized with the stepping movement initiation. The vibrations evoked proprioceptive-afferent inflow related to body tilt towards the supporting leg. If proprioceptive signals are used to control the APAs, then erroneous vibration-induced detection of the current body state should be reflected in the forthcoming body shift. More specifically, the body shift towards the supporting side should be decreased during the vibration, due to an exaggerated sense of movement towards the supporting side.

Materials and methods

Six subjects participated in the experiment (mean age 34 ± 8 years). They gave their informed consent to take

part in this study which is in conform to the standard set by the Declaration of Helsinki and the protocol was approved by the local Ethics Committee.

The experiment was performed in an A 300 Airbus especially adapted for parabolic flights. Trials were performed during the microgravity phases of the parabolic flight and also under normogravity environment when the aircraft was on the ground. During the flight, 30 parabolas were carried out, each providing ~ 20 s of microgravity, allowing two trials per parabola.

Subjects wore shoes with adapted metal soles and stood with their hands behind their backs on a platform comprising of four electromagnets (two under each foot). Their posture was erect, symmetrical and stable. They were asked to perform with their eyes closed a normal step forward with the right leading leg. Each set of two electromagnets could be activated independently allowing the release of the right foot, while holding the left supporting foot to the deck of the aircraft during microgravity. A second electromagnetic platform was placed 50 cm in front of them. The trials were validated when the heel of the right foot successfully reached the electromagnet (i.e. a circle with a diameter of 6 cm) located in the second platform (about 2–3 trials per subject and condition did not meet this criterion).

Subjects performed the task under two conditions in both microgravity (μG) and normogravity (nG) environments: Vibration “on” and Vibration “off” conditions. Eccentrically loaded motors inserted in plastic cylinders provided the vibration stimuli. The vibrators were securely fixed with an elastic belt, one on each leg, just above the right external malleolus on the fibularis longus muscle and above the left medial malleolus on the tibialis posterior muscle (Fig. 1a).

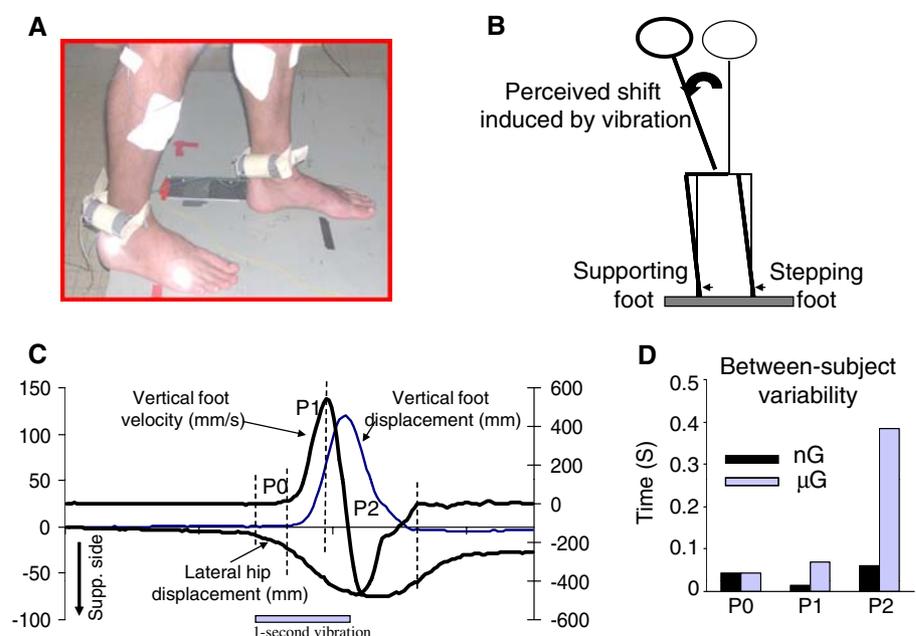
The vibrators were activated simultaneously, and the stimulation consisted of 1 s small amplitude vibration (1.2 mm) of high (80 Hz) frequencies. Such vibration applied to muscle produces microstretches of the muscle spindles which are interpreted by the CNS as resulting from a muscular stretch (McCloskey 1973; Roll and Vedel 1982; Roll et al. 1989a, b) analogous to the pattern resulting from a real body tilt in the opposite side to the vibrated muscles. The vibration of muscles acting in the frontal plane evokes spatially oriented postural responses with a latency of ~ 650 ms (Popov et al. 1999) which is aimed at correcting for perceived changes with respect to the vertical posture.

Subjects were asked to synchronize their step with the third of three 1-s interspaced tone produced by the computer. At the third tone, the vibration was activated and the electromagnets of the right foot deactivated. With the selected spatial configuration of the vibrators, the vibrations induced afferent proprioceptive inflow (conveyed by Ia afferent inputs) analogous to the pattern resulting from lateral body tilt to the opposite side of the vibrated muscles. Therefore, the direction of the perceived body motion elicited by the vibration (i.e. towards the left supporting leg) was similar to the direction of the current concomitant body shift toward the supporting leg (Fig. 1b).

Under each gravitational environment, subjects performed 30 trials, i.e. 15 trials per vibration condition which were presented in a randomized order. No practice trials were performed by the subjects in μG and nG environments.

Kinematic data were recorded at 100 Hz using an automatic opto-electronic system with passive markers (ELITE system, Ferrigno and Pedotti 1985). Markers (15 mm in

Fig. 1 **a** Position of vibrators on the subject's ankles. **b** Schematic representation of actual and vibration-evoked whole body movements towards the supporting side. **c** Mean foot vertical velocity, and lateral hip and vertical foot displacements during the step from a representative subject in normogravity. **d** Mean between-subject variability for each phase (P0, P1, P2)



diameter) were placed on the right side of the body (leg movement side) on the anterosuperior iliac spine (trunk) and infraorbital margin (head) (to provide information on body displacement), lateral malleolus and big toe (to provide information on the focal foot movement). The kinematic data were filtered with a seventh-order Butterworth filter (10 Hz low-pass cut-off frequency).

The APAs were investigated analysing the postural adjustments and EMG recordings. Postural adjustments were analysed in the medio-lateral (M/L) direction as because the APAs during stepping movement essentially occur in this direction and changes evoked by the vibratory stimuli were also expected to occur in this direction. The amplitude of the M/L displacements of the head and hip was computed from the starting (neutral) position to their maximal displacements towards the supporting side (left side). The data were normalized. This normalization was performed, for each subject, with respect to the duration of each phase (in percentage) with respect to the leg movement duration.

EMG activity of both tibialis anterior (TA, ankle flexor and dorsiflexor) and both gastrocnemius medialis (GM, ankle extensor and plantarflexor) muscles was recorded by means of bipolar preamplified surface electrodes spaced 2 cm apart. We focused the analyses on these muscles as they are responsible for the early postural adjustments which accelerate the whole body towards the supporting side during stepping movements (Robert et al. 2004). The EMG signals were amplified ($\times 1,000$), band-pass filtered (20 to 250 Hz), digitized at 1,000 Hz and rectified. To analyse EMG activity, we first computed, for each trial, the mean activity recorded in a 500 ms time window during quiet standing to determine the baseline EMG activity level (Staude et al. 2001). Then, the muscular activity onset was identified at the instant that the activity level 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. These automatically determined onsets and offsets were afterwards visually inspected and manually corrected when necessary. The baseline activity was subtracted from the burst EMG activity. Burst durations and EMG integrals (iEMG) were evaluated for each subject.

Also, from the vertical velocity curve of the malleolus marker, two phases of the focal movement were identified and analysed (Fig. 1c): phase 1 (P1, stepping initiation phase) defined as the time elapsed from the onset of the malleolus movement to its peak vertical velocity. In normogravity, this phase corresponds to the time during which the subjects unload the stepping leg in order to produce the step (Rugot et al. 2008). Phase 2 (P2) corresponded to the completion of the stepping movement and was measured from the time-to-peak velocity to stepping movement

offset; defined as the time at which the foot's velocity returned to zero after peak velocity. An additional phase (P0), which represents the subjects' error in synchronizing their stepping movement with the last tone, is defined as the elapsed time between the last tone and the stepping movement onset.

Finally, the landing position of the stepping foot relative to its initial starting position was also analysed in the lateral direction (negative values representing leftward position with respect to the initial foot position).

In the text, mean values (\pm standard deviations) computed for the different dependent variables are presented. Dependent measures were analysed using 2 Environments (nG/ μ G) \times 2 Vibration conditions (on/off) repeated measures analysis of variance (ANOVA). The Newman–Keuls post hoc test was used to determine the locus of the differences. Significant threshold was set at $p < 0.05$. We also used when specified the t test and the comparison of a mean to a standard value test.

Results

Foot movement characteristics

Overall, the subjects succeeded in producing the required stepping movement in both gravitational environments. Since the postural adjustments associated with stepping are dependent upon the foot movement characteristics, peak vertical velocity reached by the foot, final landing position and phases' duration were analysed.

The vertical peak velocity reached by the foot did not show differences between vibration conditions, no Environments \times Vibration interaction was found, $F_{(1,5)} = 0.20$; $p = 0.66$. However, the peak velocity was significantly lower in μ G (overall mean: 0.6 ± 0.2 m/s) than in nG (overall mean: 0.87 ± 0.18 m/s), $F_{(1,5)} = 6.79$; $p < 0.5$. The foot landing position did not significantly differ between Vibration conditions, no Environments \times Vibration interaction was found, $F_{(1,5)} = 0.45$; $p = 0.53$. However, the mean landing position was more leftward (i.e. towards the supporting side) relative to its initial position in μ G (overall mean: -4.8 ± 3.7 cm) than in nG (overall mean: -2.6 ± 2.6 cm), $F_{(1,5)} = 8.87$; $p < 0.5$.

Finally, a 3 Phases (P0, P1 and P2) \times 2 Environments (nG/ μ G) \times 2 Vibration (on/off) repeated measures analysis of variance was used to analyse the durations. The duration of the phases did not show differences between Vibration conditions, $F_{(1,5)} = 3.74$; $p = 0.11$, no Phases \times Environments \times Vibration interaction was found, $F_{(2,10)} = 0.14$; $p = 0.86$. Since the between-subject variability did not exceed 50 ms for P0 and 70 ms for P1 in μ G, the absence of differences in these phases duration cannot

account for a high variance between different subjects. However, P2 duration was significantly longer in μG ($1,335 \pm 374$ ms) than in nG (577 ± 58 ms) as shown by the Phases \times Environments interaction, $F_{(2,10)} = 23.26$; $p < 0.05$. On the contrary, the Environments did not significantly affect either the initiation of the stepping movement (P1: 228 ± 62 ms) or the latency to initiate the stepping movement relative to the tone signal (P0: 235 ± 51 ms).

Taken together, the results, therefore, indicate that the movement performance was not affected by the Vibration conditions, thus any postural adjustments modifications could be attributed to the vibration.

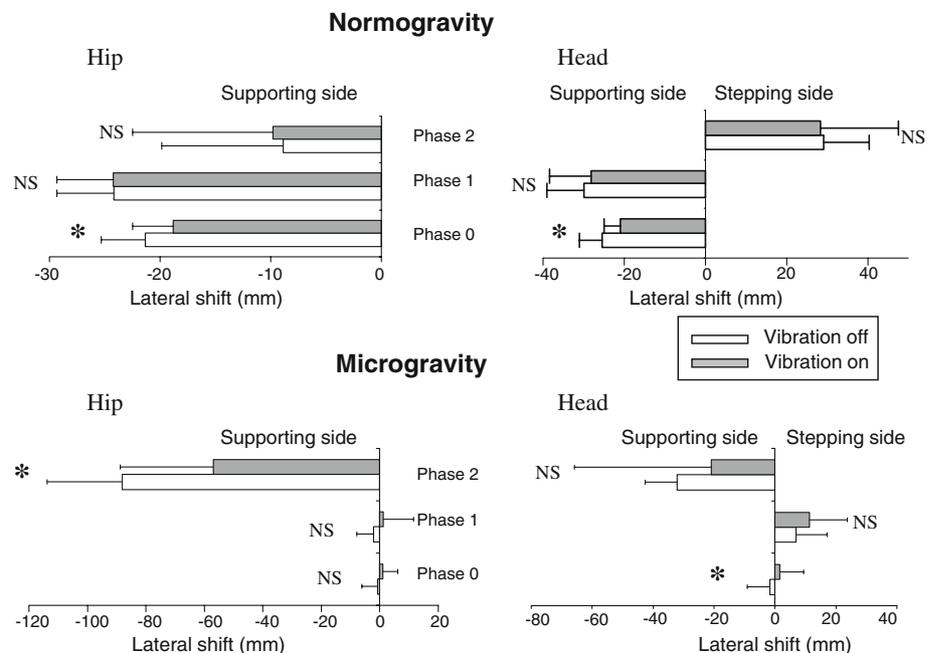
Postural segments kinematics

Vibration of the right side of the body should evoke afferences signalling a body shift towards the left side (i.e. towards the supporting side). If this information is used to control the APAs, it should lead to a decrease of the current body inclination over the supporting side which in turn would require a redistribution of the activity of the leg muscles. To determine if such postural adjustments were observable in the present experiment, we computed the head and trunk lateral displacements for the three phases of the stepping movement. The ANOVA did not show significant effects of Environment ($F_{(1,5)} = 0.02$; $p = 0.89$) or Vibration ($F_{(1,5)} = 1.55$; $p = 0.26$) on the total displacement of the head (i.e. P0 + P1 + P2). Similarly, neither the Environment ($F_{(1,5)} = 0.17$; $p = 0.17$) nor the Vibration ($F_{(1,5)} = 6.3$; $p < 0.053$) had a significant effect of the total displacement of the hip.

During P0, however, the ANOVA revealed a significant Environment \times Vibration interaction, $F_{(1,5)} = 62.06$; $p < 0.05$, on the amplitude of the hip displacement. The decomposition of the interaction showed that the vibration had a significant effect on the hip shift only in nG where the hip displacement was found to be smaller in Vibration “on” (18.8 ± 3.6 mm) than in Vibration “off” (24.3 ± 3.9 mm) (Fig. 2). On the other hand, in μG , the comparison test to a standard revealed that the hip displacement in both Vibration “on” ($p = 0.63$) and Vibration “off” ($p = 0.76$) did not differ significantly from 0. The hip remained in its initial position during P0; this is likely due to the absence of body weight transfer before leg stepping initiation which became useless in microgravity. In both gravitational environments, the head shift towards the supporting side was smaller in Vibration “on” than in Vibration “off” as revealed by the significant main effect of Vibration, $F_{(1,5)} = 19.2$; $p < 0.05$ (Fig. 2). In nG, the head shift towards the supporting side was smaller in Vibration “on” (-20.9 ± 4 mm) than in Vibration “off” (-25.4 ± 5.6 mm). In μG , despite the difference between Vibration “off” (-1.6 ± 7.4 mm) and “on” (1.6 ± 7.7 mm), the head remained in its initial position in both Vibration conditions ($p = 0.64$). The differences in head behaviour relative to gravity were confirmed by the significant main effect of the Environment, $F_{(1,5)} = 168.8$; $p < 0.05$.

During the initiation of the stepping movement (P1), the vibration had no significant effect on the hip behaviour, $F_{(1,5)} = 1.68$; $p = 0.25$. The hip continued to move towards the supporting side in nG (on average -24.2 ± 4.8 mm) and remained in its initial position in μG (on average

Fig. 2 Mean lateral shift of the hip and head during each of the three defined phases in Vibration “on” and “off” conditions in both normo- and microgravity. The error bars indicate the standard deviations of the means



0.14 ± 7.7 mm). This was confirmed by the significant Environment main effect ($F_{(1,5)} = 40.12$; $p < 0.05$) and by the comparison of the mean hip displacement measured in μ G with the reference value 0 in both the Vibration “on” ($p = 0.78$) and “off” ($p = 0.41$) conditions. As for the hip, the head continued to move towards the supporting side in nG (on average -29 ± 9.3 mm) whereas, in μ G, the head slightly shifted towards the stepping side (average 7.4 ± 7.9 mm) as revealed by the significant main Environment effect, $F_{(1,5)} = 39.12$; $p < 0.05$ (Fig. 2).

During the longest phase of the stepping movement (P2), the ANOVA revealed a significant Environment \times Vibration interaction, $F_{(1,5)} = 8.11$; $p < 0.05$, on the amplitude of the hip displacement. The decomposition of the interaction showed that the vibration had a significant effect on the hip shift only in μ G where the hip displacement was smaller in the Vibration “on” (-57 ± 32 mm) than in “off” (-88 ± 25.6 mm). In nG, the hip continued slightly to move towards the supporting side (-9.3 ± 11.3 mm). The head exhibited two different gravity-dependent behaviours as revealed by a significant Environment effect, $F_{(1,5)} = 16.61$; $p < 0.05$. In nG, the head reversed its displacement towards the stepping side by 28.7 mm (± 15) whereas in μ G the head was shifted by -28.2 mm (± 32) towards the supporting side. In neither Environments was the head shift significantly affected by the Vibration, $F_{(1,5)} = 0.39$; $p = 0.55$.

EMG activity

The hip movement towards the supporting side is usually initiated by the activation of both TA and GM muscles (i.e. some 450 ms before heel off, Robert et al. 2007). These activations shift the whole body towards the supporting leg and

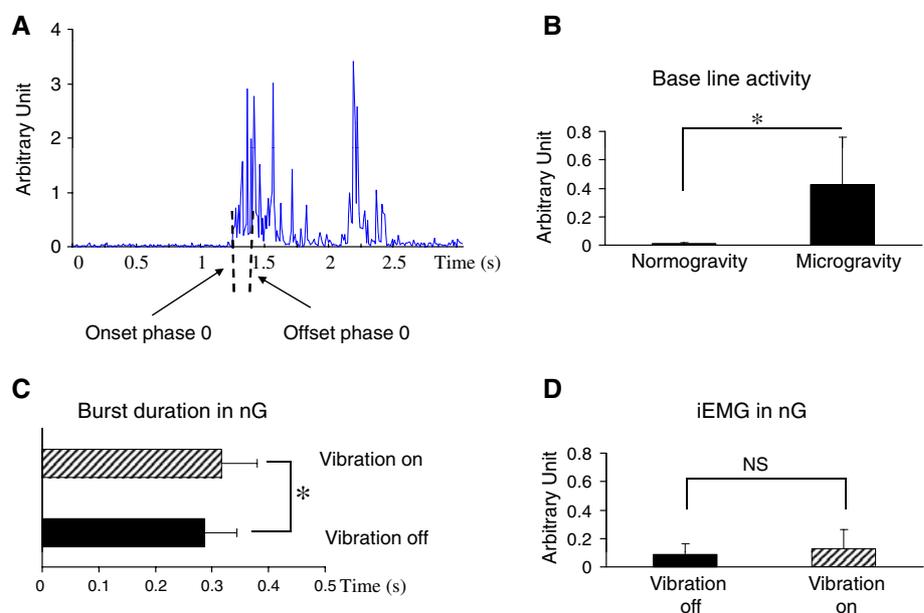
unload the leg to be moved prior to step initiation. In nG, we found that for four subjects, this unloading was essentially performed activating the TA of the supporting leg in order to pull the body towards the supporting side. The remaining two subjects showed predominant activation of the GM muscle in the moving leg (Fig. 3a) that pushed the body towards the supporting side. In μ G, the EMG activity analyses did not reveal clear EMG bursts. However, the baseline activity of the TA muscles in μ G was significantly greater in μ G than in nG, $F_{(1,4)} = 8.01$; $p < 0.05$ (Fig. 3b).

In nG, the decrease hip shift amplitude observed in P0 during Vibration “on” presumably resulted from a change in the activity of the TA and GM muscles. To determine if these changes occurred, we analysed the duration and integral of the EMG activity of the most active muscles from the beginning of P0. The results showed that the EMG activities were significantly longer in Vibration “on” (316 ± 123 ms) than “off” (282 ± 112 ms) (Student’s paired t test: $p = 0.03$) (Fig. 3c). No difference between Vibration conditions on the iEMG of these muscles ($p = 0.18$) was observed (Fig. 3d). Thus, the combined effects of a similar level of activation (i.e. iEMG) associated with longer burst duration lead to exert weaker force during P0. This reduced muscle activation was very likely the origin of the decrease in the hip shift amplitude that was found in Vibration “on”.

Discussion

In a previous study, we found that altering leg muscle proprioception using the vibratory technique had no effect on the early component of the APAs (i.e. the thrust) which is

Fig. 3 **a** Gastrocnemius muscle activity on the stepping leg for a representative trial. **b** Mean iEMG of the baseline activity for TA muscle of the supporting side recorded during quiet standing position well before vibration was applied. **c** Mean duration of the TAsup ($n = 4$) and GMmov ($n = 2$) bursts in nG. The asterisk indicates the conditions for which the t -tests revealed significant differences. **d** Mean iEMG during P0 in nG



responsible for unloading the leading foot during step initiation (Ruget et al. 2008). During this phase, forces are exerted on the ground while the body remains motionless. Here, we tested the hypothesis that the negligible contribution of leg muscle proprioception could be due to conflicting afferent inflow introduced by the vibration. Indeed, vestibular and somatosensory afferents provided a massive flow of information relative to a stationary body that could have likely cancelled out the effect of the vibration. We exploited the fact that, in microgravity, the vertical quiet standing position cannot be detected by vestibular and load receptors (Golgi and plantar), to determine if the importance of proprioception for controlling the APAs increases when the conflict between afferent signals is reduced.

The results showed that in both μ G and nG, changing proprioceptive inflow through leg muscle vibration had a significant impact on the postural adjustments. The vibration, which evoked proprioceptive-afferent inflow related to body tilt towards the supporting leg, decreased the current lateral body displacement towards the supporting side. In nG, these modifications were associated with a smaller activation of the ankle muscles which are responsible for tilting the body towards the supporting leg. In μ G, the analyses of EMG activity did not show bursts in the activity of distal muscles. The increased activation of TA muscles that we observed in microgravity and which is frequently reported in weightlessness experiments during quiet standing (e.g. Lestienne and Gurfinkel 1988) may have masked additional muscular activation. The absence of bursts may also suggest a proximal control of the hip and trunk movements in μ G. Such proximal strategy for moving the leg in μ G has already been reported in lateral leg raising tasks (Mouchnino et al. 1996). For instance under μ G, the tensor fasciae latae (hip flexor and leg abductor) and gluteus medius (hip extensor and leg abductor) muscle activations have been shown to precede leg movement initiation by about 90 ms (Mouchnino et al. 1996). The coactivation of these muscles likely serves to tilt the trunk laterally towards the supporting side and to stabilize the hip in the antero-posterior direction. As it conveys information about body position and movement, it is reasonable to assume that afferent inflow from ankle muscles would still be processed in a proximal strategy leading to a significant effect of vibration.

The hip shift towards the supporting side could be interpreted as a way to ease the initiation of the stepping movement. For instance, it could be used to exert a torque in order to free the stepping leg and facilitate the leg stepping movement. However, this mechanical interpretation is not supported by the present results because the amplitude of the hip shift was adjusted according to the proprioceptive sensory information (vibration-evoked) whereas the spatio-temporal characteristics of the focal foot movement did not depend on the vibration conditions. The decrease of the hip

shift following leg muscle vibration cannot be accounted by such biomechanical factors. Our results rather suggest a central control which adjusts the configuration of body segments during the APAs according to the current proprioceptive-afferent inflow.

The decrease in body excursion observed in both nG and μ G suggests the use of a common reference system for the interpretation of proprioceptive vibration-induced afferents even in the absence of vision and gravitational force as in μ G. This reference system would be based on an internal representation of the body that would take into account the geometry of the body and its dynamics. It would be issued from a proprioceptive chain formed by the Ia afferents (Roll et al. 1989a, b) and from sensing the gravitational forces acting on the body. Once this internal representation formed, it would show resistance to the changes encountered during short and long periods of microgravity (i.e. parabolic and orbital flights, respectively), i.e. in conditions where vestibular gravitational sensors and the proprioceptive input no longer convey information related to the gravity forces (Clément et al. 1984; Lestienne and Gurfinkel 1988; Vernazza-Martin et al. 2000). A good illustration for the use of a stable reference frame to control movement was provided by McIntyre et al. (2001). These authors have shown that when catching a ball projected downwards, astronauts initiate their catching movements earlier (relative to the impact with ball) in 0 g than in 1 g. The results support the view that the brain gives credence to an internal model of the physical world in which a downward moving object should accelerate.

The effects of the muscle vibration on the lateral trunk movement observed in both μ G and nG most certainly arose from an overestimated vibration-induced sense of movement towards the supporting leg prompting the CNS to decrease body excursion. Consistent with this finding, several lines of evidence suggest that a facilitation mechanism occurs when vibration-evoked afferences and those provoked by the movement itself are congruent. For instance, Cordo et al. (2005) have shown, by applying vibration to the triceps brachii tendon (which activates Ia fibres), that a passive movement of the elbow (which activates skin and group II muscle spindle afferents) in the same direction of the vibration illusion (i.e. an elbow flexion) enhances the amplitude and the velocity of the perceived arm movement.

On the other hand, the greater effect of the muscle vibration in μ G than in nG may have resulted from a facilitation of the sensory (Ia) input in μ G, i.e. in the context of impoverished sensory stimulation. This is supported by the studies showing increased sensitivity of a given sensory input in the absence of other sensory modalities (e.g. Blouin et al. 1995, 2007; Horak and Hlavacka 2001; Day and Cole 2002). For instance, Horak and Hlavacka (2001) showed an

increase in the sensitivity of the postural control system to vestibular stimulation when somatosensory information from the surface is disrupted either by peripheral neuropathy or by standing on a compliant foam surface. Finally, the fact that the motor commands largely decrease in μG (because movements are not performed against gravity) may have also resulted in an increase sensitivity to afferent signals. This alternate but not exclusive hypothesis is in line with studies that give importance to centrally motor commands to the sense of position (e.g. Ansems et al. 2006; Smith et al. 2009; Walsh et al. 2006, 2009). For instance, in a forearm position matching task in the vertical plane, Walsh et al. (2006) have reported a more erratic matching performance when removing sensation of effort (i.e. decreased motor commands) from holding the arm against gravity with a counterweight.

Another salient result of the present experiment is that the effect of the muscle vibration was observed only during the dynamic phase of the stepping movement, i.e. when the whole body was moving towards the supporting side. This appeared later in μG (i.e. during P2) than in nG (i.e. during P0). The fact that body motion information was necessary for the vibratory stimuli to have an impact may suggest that the transmission of proprioceptive (Ia) and other afferents consequent to the movement was enhanced by a sensori-sensory facilitation. For instance, the vestibular stimulation elicited by the trunk motion during the dynamic phase (i.e. P2) may have facilitated proprioceptive transmission in microgravity. Sensori-sensory facilitations have previously been reported during quiet standing by Popov et al. (1999). These authors have shown that descending volleys generated by near threshold galvanic stimulation of the vestibular system give rise to a postural response when superimposed on peripheral tonic activity generated by muscle vibration. In another elegant neuroimaging study, Indovina et al. (2005) have shown activation of a vestibular cortical network when the acceleration of a visual target was coherent with natural gravity. By contrast, when visual information on the target acceleration was not coherent with natural gravity, the vestibular network was less activated.

The hypothesis of sensori-sensory facilitation may appear as being not supported by the results obtained by Staines et al. (2001). These authors have reported that vibration of the knee extensors leads to a gating of vestibular information in securely seated subjects submitted to a backward translation. The discrepancies between Staines et al.'s (2001) and our results could stem from the fact that, contrary to the present study, the task used by their study did not challenge subjects' equilibrium. In this light, while we do not have explanation for the sensory gating observed by Staines et al. (2001), it would appear counter intuitive and non-functional to suppress sensory inputs conveying information about body motion in a task

likely to threaten equilibrium such as producing a step. In the present study, any body motion could endanger balance or leg movement performance. Grounds for such a hypothesis come from findings obtained by McIlroy et al. (2003) providing evidence of sensory inputs facilitation in threatened balance tasks that increase the demand for proprioceptive cues.

Acknowledgments The authors wish to thank the Centre National d'Etudes Spatiales (CNES) and the Délégation Générale de l'Armement (DGA) for their financial support and Franck Buloup for technical assistance.

References

- Ansems GE, Allen TJ, Proske U (2006) Position sense at the human forearm in the horizontal plane during loading and vibration of elbow muscles. *J Physiol* 576:445–455
- Aruin AS, Latash ML (1995) The role of motor action in anticipatory postural adjustments studied with self-induced and externally triggered perturbations. *Exp Brain Res* 106:291–300
- Bent LR, Inglis JT, McFadyen BJ (2002) Vestibular contributions across the execution of a voluntary forward step. *Exp Brain Res* 143:100–105
- Berret B, Bonnetblanc F, Papaxhantis C, Pozzo T (2009) Modular control of pointing beyond arm's length. *J Neurosci* 29:191–205
- Blouin J, Vercher J-L, Gauthier GM, Paillard J, Bard C, Lamarre Y (1995) Perception of passive whole-body rotation in the absence of neck and body proprioception. *J Neurophysiol* 74:2216–2219
- Blouin J, Teasdale N, Mouchnino L (2007) Vestibular signal processing in a subject with somatosensory deafferentation: the case of sitting posture. *BMC Neurology* 7:1–8
- Bouisset S, Zattara M (1987) Biomechanical study of the programming of anticipatory postural adjustments associated with voluntary movement. *J Biomech* 20:735–742
- Brénière Y, Do MC (1991) Control of gait initiation. *J Mot Behav* 23:235–240
- Clément G, Gurfinkel VS, Lestienne F, Lipshits MI, Popov KE (1984) Adaptation of postural control to weightlessness. *Exp Brain Res* 57:61–72
- Cordo PJ, Gurfinkel VS, Brumagne S, Flores-Vieira C (2005) Effect of slow, small movement on the vibration-evoked kinesthetic illusion. *Exp Brain Res* 167:324–334
- Day BL, Cole J (2002) Vestibular-evoked postural responses in the absence of somatosensory information. *Brain* 125:2081–2088
- Dietz V, Colombo G (1996) Effects of body immersion on postural adjustments to voluntary arm movements in humans: role of load receptor input. *J Physiol* 497:849–856
- Ferrigno G, Pedotti A (1985) ELITE: a digital dedicated hardware system for movement analysis via real-time TV signal processing. *IEEE Trans Biomed Eng* 32:943–950
- Gueguen N, Coyle T, Craig C, Bootsma R, Mouchnino L (2004) Is perception of upper body orientation based on the inertia tensor? Normogravity versus microgravity conditions. *Exp Brain Res* 156:471–477
- Horak FB, Hlavacka F (2001) Somatosensory loss increases vestibulo-spinal sensitivity. *J Neurophysiol* 86:575–585
- Indovina I, Maffei V, Bosco G, Zago M, Macaluso E, Lacquaniti F (2005) Representation of visual gravitational motion in the human vestibular cortex. *Science* 308:416–419
- Kaminski TR, Simpkins S (2001) The effects of stance configuration and target distance on reaching. *Exp Brain Res* 136:439–446

- Lackner JR, DiZio P (1996) Motor function in microgravity: movement in weightlessness. *Curr Opin Neurobiol* 6:744–750
- Lestienne G, Gurfinkel V (1988) Postural control in weightlessness: a dual process underlying adaptation to an unusual environment. *Trends Neurosci* 11:359–363
- Malouin F, Richards CL (2000) Preparatory adjustments during gait initiation in 4–6-year-old children. *Gait Posture* 11:239–253
- Massion J (1984) Postural changes accompanying voluntary movements. Normal and pathological aspects. *Hum Neurobiol* 2:261–267
- Massion J (1992) Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol* 38:35–56
- McCloskey DI (1973) Differences between the senses of movement and position shown by the effects of loading and vibration of muscles in man. *Brain Res* 61:119–131
- McIlroy WE, Bishop DC, Staines WR, Nelson AJ, Maki BE, Brooke JD (2003) Modulation of afferent inflow during the control of balancing tasks using the lower limbs. *Brain Res* 961:73–80
- McIntyre J, Zago M, Berthoz A, Lacquaniti F (2001) Does the brain model Newton's laws? *Nat Neurosci* 4:693–694
- Moore ST, Clément G, Dai M, Raphan T, Solomon D, Cohen B (2003) Ocular and perceptual responses to linear acceleration in microgravity: alterations in otolith function on the COSMOS and NeuroLab flights. *J Vestib Res* 13:377–393
- Mouchnino L, Aurenty R, Massion J, Pedotti A (1992) Coordination between equilibrium and head-trunk orientation during leg movement: a new strategy built up by training. *J Neurophysiol* 67:1587–1598
- Mouchnino L, Cincera M, Fabre J-C, Assaiante C, Amblard B, Pedotti A, Massion J (1996) Is the regulation of the center of mass maintained during leg movement under microgravity conditions? *J Neurophysiol* 76:1212–1223
- Popov KE, Kozhina GV, Smetanin BN, Shlikov VY (1999) Postural responses to combined vestibular and hip proprioceptive stimulation in man. *Eur J Neurosci* 11:3307–3311
- Pozzo T, Stapley PJ, Papaxanthis C (2002) Coordination between equilibrium and hand trajectories during whole-body pointing movements. *Exp Brain Res* 144:343–350
- Robert G, Gueguen N, Avogadro P, Mouchnino L (2004) Anticipatory balance control is affected by load less training experiences. *Hum Mov Sci* 23:169–183
- Robert G, Blouin J, Ruget H, Mouchnino L (2007) Coordination between postural and movement controls: effect of changes in body mass distribution on postural and focal component characteristics. *Exp Brain Res* 181:159–171
- Rogers MW, Pai YC (1990) Dynamic transition in stance support accompanying leg flexion movements in man. *Exp Brain Res* 81:398–402
- Rogers MW, Pai YC (1995) Organization of preparatory postural responses for the initiation of lateral body motion during goal directed leg movements. *Neurosci Lett* 187:99–102
- Roll JP, Vedel JP (1982) Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. *Exp Brain Res* 47:177–190
- Roll JP, Vedel JP, Ribot E (1989a) Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. *Exp Brain Res* 76:213–222
- Roll JP, Vedel JP, Roll R (1989b) Eye, head and skeletal muscle spindle feedback in the elaboration of body references. *Prog Brain Res* 80:113–123
- Roll JP, Popov K, Gurfinkel V, Lipshits M, André-Deshays C, Gilhodes JC, Quoniam C (1993) Sensorimotor and perceptual function of muscle proprioception in microgravity. *J Vestib Res* 3:259–273
- Roll R, Gilhodes JC, Roll JP, Popov K, Charade O, Gurfinkel V (1998) Proprioceptive information processing in weightlessness. *Exp Brain Res* 122:393–402
- Ruget H, Blouin J, Teasdale N, Mouchnino L (2008) Can prepared anticipatory postural adjustments be updated by proprioception? *Neuroscience* 155:640–648
- Smith JL, Crawford M, Proske U, Taylor JL, Gandevia SC (2009) Signals of motor command bias joint position sense in the presence of feedback from proprioceptors. *J Appl Physiol* 106:950–958
- Staines WR, McIlroy WE, Brooke JD (2001) Cortical representation of whole-body movement is modulated by proprioceptive discharge in humans. *Exp Brain Res* 138:235–242
- Staude G, Flachenecker C, Daumer M, Wolf W (2001) Onset detection in surface electromyographic signals: a systematic comparison of methods. *J Appl Sign Process* 2:67–81
- Timmann D, Horak FB (2001) Perturbed step initiation in cerebellar subjects: 2. Modification of anticipatory postural adjustments. *Exp Brain Res* 141:110–120
- Vernazza-Martin S, Martin N, Massion J (2000) Kinematic synergy adaptation to microgravity during forward trunk movement. *J Neurophysiol* 83:453–464
- Walsh LD, Allen TJ, Gandevia SC, Proske U (2006) Effect of eccentric exercise on position sense at the human forearm in different postures. *J Appl Physiol* 100:1109–1116
- Walsh LD, Smith JL, Gandevia SC, Taylor JL (2009) The combined effect of muscle contraction history and motor commands on human position sense. *Exp Brain Res* 195:603–610
- Watt DG, Money KE, Tomi LM (1986) M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 3. Effects of prolonged weightlessness on a human otolith-spinal reflex. *Exp Brain Res* 64:308–315