ANCESTRAL PERSISTENCE OF VESTIBULO-SPINAL REFLEXES IN AXIAL MUSCLES IN HUMANS

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ABSTRACT

Accurate control of the trunk is essential for maintaining balance in an upright subject. Most studies addressing vestibulo-spinal reflexes have investigated the role of the lower limbs, while limited attention has been paid to the back muscles. To address this issue, we challenged the persistence of vestibular evoked myogenic potentials (VEMPs) in back muscles in situations in which the leg muscle responses were modulated. Nineteen subjects were submitted to galvanic vestibular stimulations (GVS). Body sway and VEMPs were recorded in the paraspinal and limb muscles. During treadmill locomotion, the VEMPS in the lower limbs were observed only during the stance phase, whereas the axial VEMPs were observed during all phases. In upright standing subjects, slight head contact was sufficient to abolish the VEMPs in the lower limbs, while the VEMPs remained present in the paraspinal muscles. Similarly, during parabolic flight-induced microgravity, the VEMPs in the lower limb muscles were suppressed, while those in the axial muscles persisted despite the absence of gravitational information from the otolithic system. Our results depict a differentiated control mechanism of axial and appendicular muscles when a perturbation is detected by vestibular inputs. The persistent feature of axial myogenic adjustments suggests that a hard-wired reflex is functionally efficient to maintain posture. By contrast, the ankle responses to perturbations occur only when the accompanying sensory feedback is congruent, challenging the balance task and gravity. Overall, this study using GVS in microgravity is the first to present an approach delineating feed-forward vestibular control in the absence of all feedback.

INTRODUCTION

During evolution, locomotion has adapted from propulsion by undulation to quadrupedal and finally bipedal propulsion. Despite its decisive advantages, an erected posture strengthens the difficulty of maintaining balance. This ability to adjust the body orientation, particularly during dynamic tasks, highly relies on the vestibular system. This sensorial input provides adequate information related to head movement and orientation and may evoke responses in limb muscles and postural adjustments (Britton et al., 1993; Fitzpatrick et al., 1994). Despite their high degree of automaticity, vestibulomotor responses are extremely flexible and may vary in a task-dependent manner. Various studies have demonstrated that motor responses in the upper and lower limbs following the vestibular detection of motion directly depend on limb engagement in the current task. For instance, using galvanic vestibular stimulation (GVS, Goldberg et al., 1984; Fitzpatrick and Day 2004), arm motor responses were observed during reaching (Bresciani et al., 2002; Mars et al., 2003; Smith and Reynolds, 2017) or body stabilization when the hand is used to help maintain balance (Britton et al., 1993). This response was absent in the contralateral arm, which was not engaged in the task (Britton et al. 1993). Comparable results have been observed in the lower limb muscles since in seated subjects or subjects standing upright while bearing a support, vestibular evoked responses were no longer present in the leg muscles (Fitzpatrick et al., 1994). A recent study (Forbes et al., 2016) showed that a reverse relationship exists between balancing motor command and associated vestibular sensory feedback in a task conducted in the reverse direction of the vestibular evoked compensatory response. The flexibility of vestibulo-spinal processes has also been documented during walking (Bent et al., 2004; Iles et al., 2007; Forbes et al., 2017; Blouin et al. 2011). Altogether, these findings suggest that new relationships between vestibular signals and consequent motor commands can be established according to the context, even in similar tasks.

However, most studies addressing the control of balance in upright subjects have mainly investigated the role of the lower limbs, while limited attention has been paid to the vestibulo-spinal reflexes that occur in the back muscles. This is surprising because the trunk, which represents more than 60% of the total body mass and is located above the center of gravity, is a potential source of major instability. Because this body part is highly articulated and actuated by many muscles, it should be accurately controlled during displacement. Ali et

al. (2003) recorded functional vestibular evoked responses in the erector spinae muscles in both sitting and upright postures, and any response was detected in the limb muscles in the sitting posture. Interestingly, the subjects' responses in the erector spinae recorded at L3/L4 displayed latencies of 59 ms, while the latencies in the lower limb muscles were much longer (≈85 ms). These results suggest that axial trunk muscles and leg muscles may be controlled by different vestibulo-spinal mechanisms.

Therefore, in this paper, our objective was to challenge the persistence of vestibular evoked responses in the back muscles under conditions in which the lower-body muscle responses are modulated by a task and/or context using GVS. In the first experiment, we compared the GVS phase effect dependency on back muscles and lower limb muscles during walking. In the second experiment, we tested two conditions in which vestibular evoked myogenic potentials (VEMPs) were suppressed in the lower limbs, i.e., in upright subjects bearing a support and upright subjects sustained in a harness. In the third experiment, which represented our "most challenging" condition, we tested the persistence of vestibulo-spinal reflexes in floating subjects in the absence of gravity (during parabolic flight) as no postural adjustments were required. To the best of our knowledge, this study represents the first time GVS responses were studied in microgravity. Altogether, we demonstrate that under all these contextual and/or gravitational conditions, balance and posture were persistently controlled using back muscles whereas the lower limb responses could be flexibly modulated.

MATERIAL AND METHODS

Nineteen adults participated in this study. The subjects provided written informed consent prior to participating in each experiment. The procedures conformed to the Declaration of Helsinki and were approved by the French National Research Ethics Committee (Comité de Protection des Personnes Sud-Ouest et Outre Mer III) under agreement number 2011-A00424-37. In all experiments, we used similar tools and methods, including pulse GVS stimulation, electromyography and 3D kinematics.

Vestibular stimulations

99 Bipolar binaural galvanic electrical stimulations were applied to the mastoid processes.
100 The electrodes were circular with a contact surface of 9 cm^2 (Axelgaard Pals Platinium, Ø32
101 mm). Square pulse stimulations (3.5 mA; 175 ms) were delivered using an isolated constant
102 current stimulator (Digitimer DS-5, CE mark certification for medical devices) with randomized
103 and unpredictable delays (5 s minimum between two stimulations).

104 **Electromyographic recordings and analysis**

105 EMGs were recorded bilaterally on the *medial gastrocnemius*, *anterior tibialis*, and
106 *erector spinae* at the C7, T7 and L4 levels (De Sèze et al., 2008; Cecatto et al., 2009). During
107 walking on a treadmill, we used a wireless EMG system (Kine ehf, Iceland; 1.562 KHz, x10,000
108 amplifier), while all other recordings were performed using an analogical amplifier (TeleEMG,
109 BTS, Milano, Italy; x1000 amplifier) linked to an ITC-18 A/D interface (Heka, Lambrecht,
110 Germany; 2KHz). The same A/D card was used to start the GVS and simultaneously record the
111 EMG signals (except for during the walking experiment).

112 From the EMG signals from the erector spinae, the GVS artifacts (shifts due to voltage)
113 were removed *a posteriori* by digitized data shift compensation. During the walking
114 experiment, the presence of GVS artifacts on the EMG traces (voltage shift) was automatically
115 detected (and then controlled for by subsequent visual inspection) on the left C7 erector
116 spinae signal (the recorded muscle nearest the GVS electrode). During the other experiments,
117 we simultaneously recorded EMG and a copy of the GVS stimulator output to precisely and
118 unambiguously identify the GVS artifacts. For each EMG channel, the drift observed in the 40
119 ms following the GVS onset was modeled by a third order polynomial and removed from the
120 signal. The same method was simultaneously applied to remove the artifact at the end of GVS.
121 Then, the EMGs were numerically high-pass filtered (reverse Butterworth filter at 30 Hz),
122 rectified, and smoothed with a 20 samples moving average.

123 For each stimulation, a 4 s time window was defined on both sides of the GVS onset (2
124 s before and 2 s after). For each subject, the EMGs were subsequently synchronized and
125 averaged for each GVS polarity and condition and normalized by the activity measured before
126 the occurrence of GVS (tonic activity during normal standing = 100%). The detection threshold
127 to identifying VEMPs during the 300 ms following the GVS start was two standard deviations
128 from the baseline. The baseline was defined as the median EMG during the 500 ms that

preceded the GVS start. The medium latency of the VEMPs (ML; Fig. 4; Britton et al., 1993) was visually identified by comparing the EMGs following GVS to those at baseline or comparing the EMGs following GVS to those from opposed polarities if any.

The area of the VEMPs was computed by trapezoidal numerical integration of the rectified EMGs. The portions of EMGs used to compute the areas for each muscle in each subject in each experiment were the portions between the starting and ending time of the identified VEMPs averaged across all subjects. Then, we could compute the EMG areas in portions where VEMPs were expected, even if VEMPs were absent, allowing a between conditions comparison.

Center of pressure

Static balance was assessed in a laboratory using a force plate (AMTI BP600900 with 6 degrees of freedom), and the position of the center of pressure was recorded at a 50 Hz sampling frequency. The data from the force plate were synchronized to the GVS start and averaged by subject, condition and GVS polarity.

Kinematic recordings

We used a 3D-motion analysis system for the body segment analysis (Natural Point, Corvallis, USA). Twelve Optitrack Flex3 (640 × 480 pixels, 100 Hz) cameras were used in the gait experiment, and five Optitrack S250e (832 × 832 pixels, 250 Hz) cameras were used in the parabolic flight experiment. Prior to the data collection, calibration was performed to determine the camera orientation in relation to the working volume and the relative position of each camera to the other camera. Spherical reflecting passive markers (15 mm in diameter) were positioned on the head, trunk and body segments (see below). The data acquisition was performed using custom built software developed in MATLAB R2013a (MathWorks, Natick, MA, USA), enabling the simultaneous collection of synchronized kinematic and EMG data.

Experiment 1: GVS during walking

Eleven subjects participated in the experiment (5 females and 6 males, 29.1 [±7] years old). The subjects walked on a treadmill (Pulsar 4.0, HP-Cosmos, Nußdorf Germany) at 0.75

157 m.s^{-1} with their eyes closed and gaze straight ahead. The subjects performed a 10-minute
158 training before the first GVS stimulation. The subjects were secured by a harness, and the
159 treadmill automatically stopped in case of falls in the harness (which never occurred). Each
160 subject performed 12 trials, and each trial lasted 90 s with 5-minute pauses between each
161 trial. During the experiment, each subject received more than 160 GVS (inter-subject
162 mean=172) with unpredictable delay and pseudo-randomized laterality (anode right or left).

163 We placed three reflective markers on each of the following segments: head, scapular
164 girdle, pelvic girdle, hands, and feet. A real-time kinematic measurement of foot
165 displacements was performed using a custom software developed with MATLAB to determine
166 the phase of the gait cycle during which GVS occurred. Using this setup, we detected heel
167 strikes based on the antero-posterior velocity of each foot. On the treadmill, the foot velocity
168 shifted from positive to negative at the heel strike. GVS could be delivered at this time event
169 with a latency as short as 40 ms (approximately 3% of the gait cycle). For each subject, the
170 average gait cycle duration was determined during a ten-minute training, allowing GVS to be
171 applied during the following four different phases of the cycle: (1) the first double support
172 phase (immediately after the right heel strike); (2) the left swing (15% after the right heel
173 strike); (3) the second double support phase (immediately after the left heel strike); and (4)
174 the right swing (15% after the left heel strike). During the data analysis, each locomotor cycle
175 was identified based on the right heel strike. During the post hoc analysis, we checked that
176 GVS occurred at the proper phase.

177 To compare the effects of GVS during different phases of the gait cycle, we
178 synchronized all kinematic signals to the GVS start, and the data were averaged to obtain one
179 measure per subject, segment, cycle phase and GVS polarity. The anode right vs. left GVS
180 induced medio-lateral deviations in opposite directions with the same delay. We compared
181 the averaged medio-lateral velocities at both polarities to visually identify the latencies of the
182 kinematic deviation. The maximum magnitude of the medio-lateral deviation was measured
183 during the 500 ms following the GVS start.

184 The EMG signals were analyzed by performing a cycle categorization according to the
185 phase of GVS occurrence (right heel strike, left swing, left heel strike, right swing, or no GVS).
186 To analyze the phase effect on the VEMPs, the data were synchronized and averaged to obtain

187 one sample synchronized to the GVS start per subject, muscle, and phase of the cycle. Finally,
188 the EMGs of each muscle from each subject were normalized and expressed as a percent of
189 the median activity during the No-GVS gait cycles. The occurrence and latencies of the VEMPs
190 were visually identified by comparing the EMGs following GVS at opposite polarities.

191 **Experiment 2. GVS during upright standing with or without upper body contact**

192 Nine subjects participated in this experiment (5 females and 4 males, 25.3 [±4] years
193 old). We measured the effects of GVS on upright standing subjects under the following two
194 conditions: (1) "freestanding" in which the subjects had to stay upright with their head turned
195 to the right and their eyes closed and (2) "head contact" in which the subjects remained in the
196 same position but with their head slightly in contact with a wall mounted on wheels allowing
197 for precise proprioceptive feedback regarding body sway but could not be used as a firm
198 support. Each subject was submitted to bipolar GVS with the anodal stimulation randomly set
199 on the left or right mastoid process. Each condition included 20 trials, and each trial included
200 4 GVS with randomized polarity and an unpredictable delay (>5 s). The condition occurrence
201 was randomized throughout the test session. Each subject experienced 160 GVS (2 conditions
202 x 20 trials x 4 stimulations).

203 **Experiment 3. GVS in the postural muscle of free-floating subjects**

204 This experiment occurred in the Zero-G airplane (A300, Novespace, Mérignac, France)
205 chartered by the Centre National d'Etudes Spatiales (CNES, France) during two parabolic flight
206 campaigns (VP-92 and VP-95, 2011-2012; 6 flights in total). During each flight, 30 parabolas
207 were performed, and two subjects were tested (15 parabolas per subject). Each parabola
208 provided a time lapse of 22 s of zero gravity (Fig. 5A), which was preceded and followed by 20
209 s time lapse of increased gravity (1.8 g; Fisk et al. 1993). Due to the influence of scopolamine
210 on motor control (Bestaven et al., 2016), the subjects were not medicated.

211 Twelve subjects were tested in the upright standing position with their heads turned
212 to the right, anode on the posterior mastoid process, and vision occluded by a mask. GVS
213 occurred during normogravity (4 stimulations during each steady flight period between the
214 parabolas), the first hyper-gravity period (n=4), and micro-gravity (n=4), resulting in a total of
215 180 GVS. All GVS were delivered at the same polarity to trigger VEMPs in the gastrocnemius

and back muscles (anode posterior). Because the feet usually leave the floor in micro-gravity, the subjects did not have any contact with their environment and were secured. Three conditions were tested. Under the first condition, designated "Free-floating", a scapular harness on the upper body secured the subjects (n=6) with distended tether (Fig. 5A). This harness did not apply any force on the subject, except for in the case of exceptional excursion (usually prevented by an operator situated in front of the subject during the experiment). The results of the first campaign (i.e., microgravity VEMPs remained present in the trunk only) prompted us to add other conditions to confirm that the observed effects were not due to (1) the presence of the harness on the upper body and/or (2) the lack of feet contact and external support. Thus, during the second campaign (VP95), the subjects (n=6) were tested under a second condition designated "Foot-strapped". The subjects were submitted to different gravity conditions without a harness while being efficiently linked to the floor with their feet strapped to soft pads. The straps and pads we used (Concept X Kitesurf) allowed the ankle to be actuated in all directions with very good proprioceptive feedback. The same stimulation and recording protocols were performed during the first and the second campaign.

The third condition, i.e., “Harness”, was a control condition that was performed at our laboratory to consider the influence of gravitational detection and/or spine loading on the VEMPs of the lower limbs. In this experiment, the subjects were sustained in an upright position in a pelvian harness with their feet 10 cm above the floor. As in microgravity, the subjects stayed upright with an unloaded lower limb, but proprioceptive, visceral and otolithic perception of the gravitational field was present. The subjects also had their heads turned to the right, their vision was occluded, and they received 40 GVS with the anode on the posterior mastoid process and unpredictable delays. The same subjects (n=9) were tested under the standing upright (experiment 2) and Harness conditions.

Kinematics

We placed three reflective markers on each of the following segments: head, scapular girdle, and pelvic girdle. The 3D data were captured by 5 cameras (Optitrack s250e) at 250 Hz. The EMG data were synchronized and averaged to obtain one sample synchronized to the GVS start per subject, segment, Gravity and condition. Based on the averaged data, we manually identified the latencies of the GVS induced deviation based on the antero-posterior

displacement velocity (sagittal plane). We computed the maximal posterior sway during the 1500 ms following the GVS start.

Statistical analysis

For each experiment, a repeated-measures analysis of variance was performed using the MATLAB R2017a "ranova" function, and a post hoc analysis was performed using the comparison test of Scheffé. ANOVAs were computed to analyze the EMG area and latencies and kinematic magnitude and latencies. For each experiment, all conditions were considered within factor with repeated measures, except for the Free-floating vs. Foot-strapped conditions, which were considered between-factor because not all subjects participated in both campaigns (one condition per campaign). To statistically compare the proportion of VEMP occurrence, a Z-test was computed.

RESULTS

Experiment 1: Effects of bilateral GVS pulse during gait

This experiment was designed to investigate whether there was a phase dependency on vestibulo-spinal inputs during gait cycles and whether vestibulo-spinal inputs to axial or lower limb muscles were differentially controlled during walking. The subjects maintained their gaze straight ahead with their eyes closed, and GVS created a roll illusion contralateral to the anode, which elicited head displacement ipsilateral to the anode (Fig. 2A). Such lateral displacements were observed in the upper body segments (head, scapula and pelvis) and the stance foot (grounded during GVS but deviated at the following step). By contrast, the swing foot was deviated in the direction opposite to the upper body parts contralateral to the anode. The displacement magnitude in the frontal plane in the more rostral parts was higher (Fig. 2B; head: 6.9 cm (SD .9); scapular girdle: 6.1 cm (SD .8); pelvic girdle: 3.9 cm (SD .6)). The feet were deviated with a magnitude of 2.6 cm (SD .8) in the swing foot and 6.1 cm (SD 1.2) in the stance foot. The opposite directions of deviation between the upper parts of the body and swing foot along with the increased deviation observed in the more cranial parts elicits a body rotation in the frontal plane with an axis located at the hip level.

As expected, we found an effect of the anode side (i.e., polarity) and cycle phase, resulting in a significant interaction among Segment x Polarity x Phase ($F(12,48)=23.6$, $p<0.001$). The post hoc analysis revealed that the magnitude of the deviation of the head, scapular and pelvic girdles did not depend on the cycle phase at which GVS was delivered. By contrast, we found significant differences (Scheffe with $p<0.05$) in the feet displacements according to the cycle phase at which GVS was delivered. More specifically, in the right foot, the GVS effect during the first double stance phase did not differ from the left swing (both loaded phases), and the GVS effect during the second double stance phase did not differ from the right swing (both unloaded phases). However, each loaded phase (first double stance and left swing) significantly differed from each of the unloaded phases (second double stance and right swing). The same findings were observed in the left foot with no difference between the first double stance and left swing (loaded phases), no difference between the second double stance and right swing (unloaded phases), and significant differences between phases originating from each of these two groups (loaded vs. unloaded). This effect was observed in both GVS polarities (anode on the right or left side) but with opposite deviations.

The latency values of the kinematic deviations differed in specific body parts according to the phase (significant Segment x Phase interaction, $F(12,48)=5.3$, $p<0.001$), but the post hoc analysis revealed significant differences in the feet only. When GVS was delivered, a deviation occurred in the grounded foot during the following toe off. Consequently, in both feet, the deviation latencies during the loaded phases (swing of the contralateral foot, 533 ms (SD 127)) were significantly higher than those during the swing phases (214 ms (SD 47)). Similarly, the deviation latencies of the grounded foot were significantly higher than those of the head (203 ms (SD 135)) in the same phase but did not significantly differ from the latencies of the pelvic girdle (343 ms (SD 113)) and scapular girdle (333 ms (SD 105)). Significant differences were not observed among the head, scapular girdle, pelvic girdle and swinging foot deviation latencies.

The muscle activities observed during walking without GVS are consistent with previously observed activities on a treadmill (DeSeze et al., 2008; see Fig. 3 A). The erector spinae at T7 and L4 present a double burst rhythmic activity recorded in the right and left side with one burst after each heel strike. The gastrocnemius only presented one burst per cycle at the end of the stance phase (when the triceps surae is propulsive). To determine the GVS

305 effects, we measured the EMG area and the latency value of the response immediately
306 following GVS. As the full statistical plan was 7 muscle levels x 2 sides x 4 gait phases x 2 GVS
307 polarities, we simplified the model by averaging the right and left muscles at each level with
308 respect to the GVS polarity and loaded foot laterality. For instance, right ES L4 with right anode
309 GVS and left foot loaded was averaged with left ES L4 with left anode GVS and right foot loaded
310 to obtain ES L4 activity with "GVS ipsilateral" and "stance contralateral". This resulted in the
311 statistical plan 7 muscles x 2 GVS polarities (Ipsi/Contra) x 2 phases (Loaded/Unloaded side).

312 Interestingly, we did not observe significant effects of GVS polarity on the VEMP areas
313 of *ES* at the C7 and T7 levels in the *rectus abdominis*, *pectoralis major* and *tibialis anterior*. An
314 effect of the side of the loaded foot was observed in *rectus abdominis* ($F(1,10)=5$, $p<0.05$,
315 Ipsi>Contra) and was near significant at ES C7 ($F(1,10)=4.1$, $p=0.07$, Contra>Ipsi). A significant
316 effect of the GVS polarity was observed in EMG area ES L4 (Fig. 3B upper panel) with higher
317 muscle activities following ipsilateral GVS than contralateral GVS ($F(1,10)=15.1$, $p=0.003$) and
318 no loading phase effect. In *gastrocnemius*, a significant interaction between GVS polarity and
319 the loading phase was observed ($F(1,10)=34.5$, $p<0.001$, Fig. 3B lower panel). The post hoc
320 analysis revealed an effect of GVS polarity (Contra>Ipsi) in the gastrocnemius area only during
321 ipsilateral foot loading.

322 Regarding the VEMP latencies, we compared the onset of the VEMPs elicited by
323 contralateral GVS to ipsilateral GVS (VEMPs with the same latencies but opposite effects on
324 the EMG magnitude). This analysis was performed at the ES T7, L4, Gastrocnemius and TA
325 muscles, where the effects of the opposed GVS were easily identifiable. The two-way ANOVA
326 (4 muscles x 2 phases) showed a main effect of muscle only ($F(3,9)=67$, $p<0.001$) on the VEMP
327 latencies. The post hoc analysis revealed that the erector spinae at T7 and L4 did not have
328 significantly different latencies (34 ms (SD 7) and 41 ms (SD 10), respectively), while these
329 muscle latencies were significantly shorter than the lower muscles latencies at gastrocnemius
330 and TA (140 ms (SD 18) and 173 ms (SD 30), respectively, not different). Altogether, these
331 results indicate that the GVS effect is strongly phase dependent in gastrocnemius but not
332 modulated by the gait cycle in the upper part of the body.

333

334 **Effects of GVS on upright standing subjects**

335 It has been shown that in seated subjects or subjects standing upright while bearing a
336 support, vestibular evoked responses were no longer elicited in the leg muscles (Fitzpatrick et
337 al., 1994). In the present experiment, we investigated whether the same sensory gating of
338 vestibulo-spinal inputs occurred in a similar way in the axial and leg muscles. Therefore, we
339 compared the GVS-induced responses in the absence or presence of a contact with support.
340 A bilateral GVS with the anode on the right (anode back) or left (anode front) mastoid process
341 was delivered with the head turn to the right and occluded vision. The GVS with the anode
342 back induced a backward sway (Fig. 4A) with an activation of the erector spinae and
343 gastrocnemius muscles (Fig. 4BC). The maximum amplitude of the center of pressure during
344 this antero-posterior sway was reduced by head contact (-2.9 mm (SD .9) in freestanding and
345 -.2 mm (SD 1.48) with head contact; N= 9 subjects; Fig. 4A left vs. right panel). The two-way
346 ANOVA revealed a significant interaction between the effects of polarity and condition on the
347 antero-posterior magnitudes of the COP excursions ($F(1,6)=18.3$, $p=0.005$). The forward sway
348 induced by GVS with the anode-front was also reduced (1.4 mm (SD 1.2) in freestanding and
349 1.2 mm (SD 1.41) with head contact), but this effect was lower and not significant. The delay
350 of the occurrence of the maximum sway was not significantly affected by either the polarity
351 or head contact with a mean value of 379 ms (SD 60).

352 Several responses were elicited by GVS in the recorded muscles. As previously reported
353 (Nashner et al. 1974; Britton et al. 1993; Fitzpatrick et al. 1994), GVS with the anode back first
354 elicited a response with a short latency (single arrows, Fig. 4BC left panel) in the erector spinae
355 and gastrocnemius muscles and a medium latency response (double arrow, Fig. 4BC). The
356 short- and medium-latency EMG responses were in opposite direction at the lower limb level
357 only but not in ES. We focused on the medium latency response, which was larger in
358 amplitude, and its direction was correlated with the observed pattern of whole body sway.
359 The comparisons of the VEMP occurrences indicates that the contact condition only
360 influenced the gastrocnemius response. The GVS-elicited VEMPs from the erector spinae (L4
361 level; Fig. 4B) were detected in 78% of the subjects under the freestanding-condition, and this
362 proportion was not significantly reduced to 56% under the head-contact condition ($Z=1$,
363 $p=0.16$). The GVS-elicited VEMPs from the gastrocnemius were detected in 100% of the
364 subjects under the freestanding-condition (Fig. 4B), but this proportion was significantly
365 reduced to 22% of the subjects under the head-contact condition ($Z=3.38$, $p<0.001$).

366 In the erector spinae (L4), the VEMP area was affected by the GVS polarity. As
367 previously described, GVS with the anode back (Fig. 4B) elicited a short latency inhibitory
368 response and a medium latency response of a large amplitude. By contrast, when GVS was
369 delivered with the anode front, the medium latency response was dramatically decreased.
370 The two-way ANOVA revealed a significant main effect of polarity on the erector spinae
371 elicited VEMP area ($F(1,8)=8.5$, $p<0.05$) and no effect of condition or interaction. Interestingly,
372 the same analysis of the VEMPs elicited in the gastrocnemius revealed an interaction between
373 the GVS polarity and contact condition ($F(1,8)=7$, $p<0.05$). The post hoc analysis showed a
374 strong effect of the GVS polarity under the freestanding condition with a large response in the
375 gastrocnemius to the anode back GVS and a marked inhibition with the anode-front GVS (Fig.
376 4C). This effect was drastically and significantly reduced under the head-contact condition
377 with responses representing only 28% of the VEMP areas recorded while freestanding.

378 The VEMP latencies were measured at ES-L4 and the gastrocnemius under the
379 Freestanding condition. The repeated-measures ANOVA revealed significantly shorter
380 latencies in the erector spinae (49 ms (SD 26)) compared with those in the gastrocnemius (89
381 ms (SD 16); $F(1,6)=11.7$, $p<0.05$). The latencies at ES were not affected by the head contact
382 ($F(1,5)=0.26$, $p=0.63$; 51 ms (SD 22) in free standing and 47 ms (SD 35) with head contact).

383 Altogether, these results revealed that incongruent proprioceptive cues had a major
384 effect on the VEMPs in the gastrocnemius but not ES back muscles.

385 **Effects of GVS in modified gravity**

386 To challenge the functioning of the vestibulo-spinal system, we performed
387 experiments in which gravity was modified. Under microgravity, otolithic afferents are lacking
388 because their activation depends on the effects of gravity; hence, the postural adjustments
389 maintaining equilibrium become functionally useless.

390 Figure 5B present the experimental design of the free floating conditions (see
391 Materials and Methods section). The subjects were submitted to GVS during parabolic flights
392 (Fig. 5A) with periods of normal gravity, hyper-gravity (1.8 g) and micro-gravity (0 g). Due to
393 the limited number of available trials under these conditions, GVS was delivered with the
394 anode back only. GVS induced a backward displacement of the upper body in the antero-

395 posterior direction under the normal gravity conditions (Fig. 5C, solid line, sagittal plane),
396 which was increased under the hypergravity condition (dash-dotted line; $F(2,8)=2$, $p=0.19$ with
397 $n=4$ subjects) and disappeared under the microgravity condition (dotted line). Under the
398 normogravity and hypergravity conditions, all subjects expressed VEMPs in ES-L4 and
399 gastrocnemius, whereas under the microgravity condition, 100% of the subjects expressed
400 VEMPs in the left ES-L4, 60% of the subjects expressed VEMPs in the right ES-L4, and no
401 subjects expressed VEMPs in the gastrocnemius (significant decrease, $Z=5.2$, $p<0.001$). We
402 found a significant main effect of gravity on the ES-L4 muscle area (Fig. 6A1; $F(2,8)=6$, $p<0.05$
403 for left ES-L4 and $F(2,8)=5.8$, $p<0.05$ for right ES-L4). The post hoc analysis only revealed a
404 significant difference between the hypergravity and microgravity conditions in the left ES-L4
405 area. We also found a significant main effect of gravity on the gastrocnemius area in the free-
406 floating condition (Fig. 6A2; $F(2,8)=23.8$, $p<0.05$ for left gastrocnemius and $F(2,8)=25$, $p<0.05$
407 for right gastrocnemius). The post hoc analysis revealed that in both sides, the gastrocnemius
408 EMG area was drastically decreased under the microgravity condition (quite null) and
409 enhanced under the hypergravity condition (all p-values <0.05) compared with that under the
410 normogravity condition.

411 Finally, a one-way repeated-measures ANOVA of the latencies at ES-L4 under the free-
412 floating condition did not reveal any significant differences among the latencies at the three
413 levels of gravity (micro-, normo-, and hyper-gravity; $F(2,4)=3.1$, $p=0.15$; Table 2).

414 Under the foot-strapped condition, we tested GVS only in microgravity and
415 normogravity. Measuring the occurrence of VEMPs under the foot-strapped condition also
416 revealed that the VEMP occurrence remained stable at the ES-L4 level (from 86% in
417 normogravity to 75% in microgravity, $Z=0.54$, $p=0.29$ in ES-L4 right; from 100% to 86%, $Z=0.53$,
418 $p=0.29$ in ES-L4 left), while the VEMPs were totally abolished in the gastrocnemius in the
419 absence of gravity (from 100% to 0%, $Z=7.3$ and $p<0.001$ in both side). There was no significant
420 difference in the ES-L4 VEMP area between the normogravity and microgravity conditions
421 (Table 1; $F(1,6)=2.9$, $p=0.14$ in left ES-L4 and $F(1,6)=0.84$, $p=0.39$ in right ES-L4), whereas a
422 main effect of gravity on the gastrocnemius VEMP was observed (left gastrocnemius
423 $F(1,6)=10.3$, $p<0.05$; right gastrocnemius $F(1,6)=6.7$, $p<0.05$).

The repeated-measures ANOVA of the latencies with the condition (free-floating vs. foot-strapped) as a between subjects factor and muscle (ES-L4 vs. gastrocnemius) as the within subjects factor revealed a main effect of muscle ($F(1,8)=37$, $p<0.001$) with latencies at the ES-L4 (67 ms (SD 15)) that were much shorter than the latencies at the gastrocnemius (105 ms (SD 18)). Theses latencies were not significantly affected by the condition (see Table 2). Another two-way ANOVA was performed to analyze the latencies at ES-L4 only with the condition (free-floating vs. foot-strapped) as the between subjects factor and gravity (micro- vs. normo-) as the within subjects factor. Neither gravity nor the condition significantly influenced the latencies ($F(1,6)=5.4$, $p=0.06$).

Finally, we performed a laboratory experiment in which the subjects were suspended in a harness. The aim was to evaluate the role of sensory cues in the gating of gastrocnemius VEMPs with subjects in the upright position, which is comparable to free-floating but with gravitational otolithic activation and spine load. The proportion of subjects in which GVS elicited VEMPs remained the same in the left ES-L4 prior to and during suspension (83%; $Z=0$, $p=0.5$), while there was a non-significant decrease ($Z=0.67$, $p=0.25$) in the right ES-L4 (from 83% to 67%). The VEMP area (Table 1) did not significantly decrease in the ES-L4 ($F(1,5)=-0.4$, $p=0.7$ right side, and $F(1,5)=-0.9$, $p=0.4$ left side). By contrast, the response to GVS completed disappeared in the gastrocnemius (from 100% of the subjects to 0% in the left gastrocnemius, $Z= 3.5$, $p<0.001$; and from 67% to 0% in the right gastrocnemius, $Z=2.4$, $p<0.05$) with a reduction in the VEMP area close to null in the gastrocnemius ($F(1,5)=3.8$, $p<0.05$ right side, and $F(1,5)=2.7$, $p<0.05$ left side). Altogether, the harness condition reproduced the same effects as those observed in micro-gravity with a stable proportion of subjects expressing axial VEMPs in the upright standing and harness conditions despite the gating of VEMPs in the gastrocnemius.

DISCUSSION

We challenged the persistence of vestibular evoked myogenic potentials (VEMPs) in back muscles and leg muscle to determine how these muscles can be experimentally modulated. Our results strongly suggest that a differentiated control mechanism exists between axial and appendicular muscles when an unbalance is detected by vestibular inputs.

454 The finding that with null gravitational information from the otolithic system (microgravity),
455 we still observed persistent GVS elicited responses in axial muscles is particularly interesting.

456 **Functional responses to GVS in upright standing and phase-dependent effects during gait**

457 The significant postural changes induced by GVS in upright standing (Fig. 1) and the
458 mirror response observed when the anodal stimulation was delivered either to the right or
459 left mastoid process (Fig. 3B & 4) validate the reliability of the stimulation protocol. This
460 reliability was also confirmed under the various gravity conditions with a significant increase
461 in the kinematic changes when the postural demand was increased (Fig. 5CII).

462 During gait, the analysis of the lateral displacements following GVS indicates a global
463 translation of the trunk to the anode side, i.e., the side opposite to the detected displacement,
464 which is consistent with previous studies (Ali et al., 2003) and similar to the deviations
465 observed with prolonged GVS (Fitzpatrick et al., 1999; Bent et al, 2000). The higher magnitude
466 displacements in the upper parts of the body and the deviation of the swing foot in the reverse
467 direction correspond to a body rotation in roll (Day et al., 1997; For a review, see Fitzpatrick
468 and Day, 2004; Son et al., 2008) with a rotational axis located at the coxo-femoral articulation.
469 During gait, VEMPs in the gastrocnemius were only recorded in the loaded leg, and the muscle
470 discharge is increased when the loaded leg is ipsilateral to the anode, but the muscle activity
471 is decreased with the contralateral anode. Similar phase effects were observed in the tibialis
472 anterior (but with antagonistic action on the TA and GL; not presented). The phase-
473 dependency reported here is consistent with the phase effects observed in gait kinematic
474 (Bent et al., 2004; Dakin et al., 2013) and lower limb electromyography using stochastic GVS
475 (Blouin et al., 2011) and the role of ground contact forces during unloaded gait (Ivanenko et
476 al., 2002; Sylos-Labini et al., 2014). This modulation of gastrocnemius responses to GVS
477 contrasts with the functional inflexibility of the ES-L4 muscle responses that remained
478 constant along the gait cycle (Fig. 3).

479

480 **Differential gating of vestibular evoked myogenic potentials**

481 One of our most striking observations is the clear dichotomy between the functioning
482 of the vestibulo-spinal pathways impinging on either the axial or leg motoneurons. We

483 observed a systematic suppression of VEMPs in the gastrocnemius when the force output did
484 not contribute to the maintenance of body balance. This finding was observed (1) during the
485 swing phase of the cycle during walking; (2) with head contact in the upright standing position;
486 (3) in the absence of gravity to counteract; and (4) while the body was supported by a hip
487 harness.

488 Experiments performed in modified gravity environments may help provide important
489 insight into the sensorimotor integration of vestibular inputs and confirm that axial and leg
490 muscles are differentially controlled. In microgravity, we reported a complete disappearance
491 of VEMPs in the gastrocnemius muscle, in contrast to a major increase in the VEMP amplitudes
492 in hypergravity to match the increasing destabilizing external forces. This VEMP deletion was
493 not only observed during free-floating but also when cutaneous and proprioceptive feedback
494 was provided through the ankle under the foot-strapped condition. Similarly, when the
495 subjects were sustained in the upright position in a harness (Fig. 6B), i.e., a position similar to
496 that adopted in the free-floating condition but with otolithic and proprioceptive knowledge
497 of the context of normogravity, or stood upright with slight head contact (Fig. 4C), we still
498 observed the deletion of VEMPs in the gastrocnemius. Therefore, the modulation of VEMPs
499 in lower limbs is likely more related to body contact and support from the surroundings than
500 to the postural attitude as observed in seated subjects (Britton et al., 1993; Day et al., 1997).
501 The large decrease in the antero-posterior displacement of the center of pressure observed
502 here (Fig. 4A), which has also been reported by other scholars (Britton et al., 1993; Fitzpatrick
503 et al., 1994), has been interpreted as a gating of the vestibular input on the balance control,
504 which could be dependent on the congruence of sensory feedback (visual, proprioceptive, and
505 vestibular; Luu et al., 2012). Interestingly, when the subjects stood upright with slight head
506 contact, a decrease was observed in the frontward and backward sway (both GVS polarities),
507 demonstrating that this finding could not be explained only by the mechanical impossibility of
508 sway against the forehead contact.

509 In contrast to the above discussion regarding the suppression of GVS-induced activity
510 in the gastrocnemius muscle, a major result of the present study is the persistent responses
511 in ES-L4 following GVS under all tested conditions. This persistence of ES-L4 VEMPs is
512 particularly intriguing under the free-floating conditions in which the subjects were unplugged
513 from their surroundings with no functional requirement of postural adjustments (no

514 constraint of gravity on posture or balance and no visual frame of reference) without any body
515 effectors available for support. The vestibulo-spinal responses observed in our experiments
516 likely originated from the stimulation of the neuroepithelia of the cristae (in the ampula of the
517 semi-circular canals), which was accompanied by concomitant stimulation of the maculae
518 (Fitzpatrick et al., 2004). Thus, in microgravity, the otolithic signal was null, informing of the
519 lack of gravity, and likely became incongruent when GVS occurred. In this context, the
520 persistence of the axial response strongly suggests that the otolithic signal did not interfere
521 with the integration of the semi-circular afferents. Together with the very short latency of the
522 ES VEMP (47 ms versus 89 ms in the gastrocnemius in normal standing), the response of the
523 axial muscles to vestibular inputs is more direct and robust and cannot be modulated by the
524 context.

525 This dichotomy between the axial and leg responses to GVS could have functional
526 significance considering the involvement of the trunk and ankle muscles in postural control.
527 The interrelations between the body and its surrounding can be approached from the
528 following two references values serving to control erect posture (Massion et al, 1998;
529 Ivanenko and Gurfinkel, 2018) that can be dissociated in microgravity: one 'geometrical' value
530 relative to the orientation of the body segment ("posture") and one 'kinetic' value related to
531 the distribution of the body mass with respect to the support area ("equilibrium"). Space flight
532 experiments (Clément et al., 1984; 1988) have shown that the body schema, which is an
533 internal representation of the body geometry, was surprisingly stable in microgravity,
534 although extensive changes were observed in the labyrinthine and proprioceptive inputs. It
535 can be hypothesized that axial VEMPs persisting in microgravity may originate from a process
536 that supports the stability of the body schema. By contrast, Mouchnino et al. (1996) showed
537 that the postural adjustment observed at the ankle during voluntary leg raising disappears in
538 microgravity with an abolition of the shift of the center of mass (CM) toward the supporting
539 limb. The variable VEMP we observed at the lower limb muscles could be related to the kinetic
540 requirement of maintaining the center of pressure inside the polygon of sustentation, which
541 is a constraint that disappears with the loss of gravity.

542

543 **Origin of the gating of VEMPs in the lower limb**

544 Even if the exact mechanisms by which gating may occur remain unclear likely because
545 multiple processes may be involved, it is a ubiquitous property of most vestibular responses.
546 For example, the vestibulo-ocular reflex (VOR) can be suppressed during voluntary gaze
547 behavior directed toward a visual target (Laurutis and Robinson, 1986; Pelisson and Prablanc,
548 1986). Similarly, the vestibulocolic reflex, which stabilizes the head in space by generating a
549 command to move the head in the opposite direction (Colebatch et al., 1994), can be
550 suppressed by voluntary head motion (Ezure and Sasaki, 1978; Goldberg and Cullen, 2011).

551 Regarding the suppression of VEMPs in the leg muscles, several mechanisms can be
552 suggested to explain the gating. If during free floating, the persistence of VEMPs in the lower-
553 limb muscles can be considered behaviorally irrelevant to maintaining balance, under the
554 foot-strapped condition, the VEMPS also disappeared, although there was direct active
555 involvement of the ankle muscles. This finding suggests that gating is partially based on the
556 detection of a gravitational field either by the otolithic system or extravestibular somatic
557 receptors (Mittelstaedt, 1992). However, under the harness or head-contact conditions in
558 normogravity, the detection of a downward gravitational field by upright subjects was not
559 sufficient to elicit VEMPs in the gastrocnemius. Altogether, these results suggest that the
560 incongruence among the vestibular, proprioceptive and cutaneous inputs abolishes the
561 VEMPs in the lower limb muscles. The vestibular responses in the legs could be evoked only
562 when all features of a nominal terrestrial postural task are met as follows: gravity must be
563 detected, segment must be involved in the postural task, and sensorial cues must be
564 congruent.

565 In their detailed study investigating the effects of vestibular stimulation during
566 walking, Iles et al. (2007) reported that gating occurred in the soleus muscle during gait with
567 similar phase-dependency as that observed in the present study, and these authors proposed
568 that gating may occur through interactions with the central pattern generator at the lumbar
569 level. Alternately, these authors also posed the hypothesis that gating could occur at the level
570 of the brain stem. However, if this was the case, the axial and lumbar motoneuron responses
571 could be affected in the same way since it has been recently shown in rodents that the two
572 motoneuronal populations are similarly targeted by the LVST (Kasumacic et al., 2010).

573 **Phylogenetic blueprint of vestibulo-spinal sensorimotor organization**

574 The shift from swimming to upright bipedal locomotion is an outstanding feature of
575 the evolutionary process, and the question of whether any of the underlying neural circuitries
576 and mechanisms responsible for locomotor output production have been preserved during
577 this transitional process remains unanswered. Several studies have previously suggested that
578 during this evolutionary transition, the core features of the spinal cord circuitry of most
579 primitive vertebrates, such as lamprey, have been conserved both in rats (Falgairolle et al.,
580 2007; Beliez et al., 2015) and humans (de Sèze et al., 2008; Ceccato et al., 2009 ; for a review,
581 see Falgairolle et al., 2006; Falgairolle et al., 2013). Nevertheless, the switch to terrestrial
582 modes of locomotion and the emergence of limbs have necessarily increased the complexity
583 of postural and locomotor control mechanisms, and currently, the trunk musculature is
584 required for activity in strict coordination with limb movements during locomotion (Combes
585 et al., 2004). Despite this more complex mode of coordination, the spinal networks
586 responsible for trunk activity, even during bipedal walking, are still based on a bilaterally
587 distributed spinal chain of oscillators as observed in lamprey (Grillner et al., 1995; Grillner and
588 Wallen, 2002) but with the addition of limb CPG circuitry and associated interconnecting
589 pathways. Using an amphibian model, several studies have explored the way in which during
590 metamorphosis, locomotor networks and output transition from a purely trunk CPG (in the
591 tadpole) to a limb CPG (Beyeler et al., 2008; for a review, see Sillar et al., 2008). Therefore, the
592 extent to which the observations in the present study are related to comparable traces of
593 primitive vestibulo-spinal pathways that could have been preserved in mammals is unclear.

594 Two main features of vestibulo-spinal responses may be highlighted in this context.
595 First, the latencies of the vestibulo-spinal responses are on average twice longer in the
596 gastrocnemius compared to those in the ES-L4 muscles (Table 2). Based on the typical
597 conduction velocities reported in several studies (60 and 90 m/s for the lateral and medial
598 vestibulo-spinal tract, respectively; Wilson et al., 1967; Akaike et al., 1973b; Akaike et al.,
599 1973a), the theoretical delays required to recording the onset of muscle responses can be
600 calculated. Assuming a 1 m length (from the head to the lower back) and a minimal conduction
601 velocity of 60 m/s, including several synaptic delays, the vestibular inputs could elicit a
602 response in approximately 30 ms in the ES-L4. In the gastrocnemius, this delay could be
603 increased by up to 40 ms by adding the axonal route (approximately 1 m at 100 m/s) from the
604 lumbar spinal cord to the muscle. Therefore, the dramatic differences between the latencies

605 recorded in the ES-L4 and gastrocnemius cannot be explained by the sole differences in the
606 target distances, suggesting that different pathways and/or mechanisms exist. However, it is
607 unlikely that the differential gating operated on ES-L4 and gastrocnemius is attributable to the
608 involvement of different pathways since the vestibular inputs to lumbar motoneurons are
609 derived solely from the LVST in adult mammals (Wilson and Yoshida, 1969), and a recent
610 studies (Graf, 2007 ; Kasumacic et al., 2010) demonstrated that only LVST establishes
611 connections with both ipsilateral and contralateral thoracic motoneurons. As mentioned
612 above, the possibility has been raised (Iles et al., 2007) that gating could occur at the spinal
613 level. The emergent complexity of the circuitry organization required for hindlimb control
614 could suggest that more complex local circuit interactions occur at the lumbar level. Recent
615 studies have highlighted a major difference in the organization of mammalian neuronal
616 circuits involved in postural and locomotor activities between the axial and lumbar level
617 (Falgairolle et al., 2007; Beliez et al., 2015). Specifically, it has been found that neuronal
618 activity propagates faster in the thoracic segments and that a strong slowdown occurs from
619 the lumbar segments (Cazalets, 2005 ; Falgairolle and Cazalets, 2007). It has been suggested
620 that as lumbar segments are intimately involved in hindlimb control, more complex local
621 circuit interactions could slow the propagation through this region. The same vestibulo-spinal
622 signal processing could occur at the lumbar level, which could explain the longer delay and
623 serve as a basis for the sensory gating of vestibular inputs.

624 According to the phylogenetic perspective, the vestibular system has been present
625 very early in most primitive vertebrates in a definite form sharing many common
626 characteristics with the vestibular system in mammals (Kasumyan, 2004). This high degree of
627 early development is likely related to the challenging situation faced by fishes in their three-
628 dimensional permanently moving natural surroundings in which the sense of equilibrium plays
629 an extremely important role in orientation, especially when vision is not involved. Detailed
630 studies investigating the vestibular control of swimming in lamprey have characterized the
631 commands sent to the spinal cord through reticulospinal neurons (Deliagina et al., 1992 ;
632 Deliagina et al., 2006). This ancestral demand for highly efficient vestibular control could be
633 the source of the strong hard-wired vestibulo-spinal inputs to axial motoneurons with a lower
634 degree of flexibility than late emerging limb motoneurons.

635

CONCLUSION

The results of the studies presented here are all suggestive of the differentiated governance of axial and appendicular segments when body rotation is detected by vestibular inputs. The persistent characteristics of the myogenic adjustments observed in the trunk even in absence of gravity suggest the presence of inflexible reflex wiring functionally efficient to maintain posture. However, the behaviors observed in the experiments during the transient microgravity episodes should be more related to the unconstrained expression of the neural circuitry adapted to terrestrial gravity than the response of adaptable processes to an unusual gravitational field. Multiple testing of postural behaviors in variable gravitational fields (lunar, Martian, etc.) could provide an opportunity to assess the level of the adaptability of these sensorimotor processes in new spatial contexts.

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818 **Figure legends**

819 Figure 1. **Representative kinetic and EMG recordings during GVS-induced perturbations**.
820 Recordings were performed in one subject with the head turned, vision occluded, and anode
821 on the posterior mastoid. A, Backward displacement of the center of pressure. B,
822 Electromyograms from (right) the erector spinae at the T7 and L4 levels, gastrocnemius and
823 tibialis anterior.

824 Figure 2. **Rostro-caudal gradient of GVS-induced perturbation amplitudes during gait**. A,
825 Lateral displacements of the head, scapular girdles, pelvian girdles, and feet following GVS.
826 Traces presenting data averaged across all subjects (N=11). The loaded stance foot following
827 GVS was deviated during the following step, resulting in longer latencies than the swing foot.
828 B, Magnitude of lateral displacements at various segmental levels. There was a decreasing
829 gradient in the displacement magnitude from the head to the pelvic girdle. The swing foot was
830 deviated in the direction opposite to the upper part of the body.

831 Figure 3. **Phase-dependency of GVS-induced perturbations**. A, Averaged rectified EMG of the
832 right and left erector spinae (L4) and gastrocnemius during walking. Two successive
833 normalized cycles (0-100%) are presented. ES muscles present bilateral double burst during
834 each locomotor cycle, and each burst occurred close to the double support phase. Right and
835 left gastrocnemius activity alternated with the burst occurring at the end of the stance period.
836 B, The activity of the ES muscles was increased by GVS with the anode ipsilateral to the muscle
837 and decreased with the anode contralateral to the muscle regardless of the phase of the cycle
838 at which GVS was delivered. By contrast, the gastrocnemius activity was enhanced by the
839 contralateral stimulation and decreased by the ipsilateral stimulation during the stance phase
840 only and not during the swing phase, during which no GVS effect was observed.

841 Figure 4. **Maintenance of vestibulo-spinal reflex in axial muscles in upright standing subjects**.
842 A, During freestanding (left panel), the anteroposterior body sway was dependent on the GVS
843 polarity (positive value = frontward COP displacement). The body sway was reduced close to
844 null when the head slightly touched a support (tight panel, head contact). COP traces were
845 averaged across all subjects (N=9). B, The medium latency response to GVS in the ES muscles
846 was dependent on the GVS polarity and persisted in the absence (left panel) or presence (right
847 panel) of a head contact. C, The medium latency response to GVS in the gastrocnemius muscle
848 was dependent on the GVS polarity and virtually abolished in the presence (right panel) of a
849 head contact.

850 Figure 5. **Experimental conditions during parabolic flight.** A, Recordings from the plane
851 altimeter (dashed line) and the accelerometer (black line, axis perpendicular to the plane
852 ground) during one parabola. Each microgravity period (22 s) was flanked by two hypergravity
853 periods (20 s), and the parabolas were separated by a steady flight period (>90 s). B, The
854 subjects stayed upright with their vision occluded and head turned. The distended tether
855 prevented the extreme excursion of the subject in microgravity. C, Displacements of the upper
856 parts of the body following GVS with the anode on the posterior mastoid in (I) the lateral,
857 vertical and sagittal plane of the head during steady flight and (II) the sagittal plane during
858 steady flight (continuous line), microgravity (dotted line) and hyper gravity (dashed line) for
859 the head, the scapular and the pelvian girdle.

860 Figure 6. **Maintenance of vestibulo-spinal reflexes in axial muscles with decreasing postural**
861 **constraints.** A, During upright standing, VEMPs (rectified EMG synchronized to the GVS start
862 and averaged across the subjects) were elected by GVS (anode on the posterior mastoid
863 process) from the erector-spinae L4 (left panels) and gastrocnemius (right panels) muscles. In

microgravity, VEMPs were no longer observed in the gastrocnemius but were still present in the erector spinae. B, Under laboratory conditions, the VEMPs elicited by GVS from the erector-spinae L4 (left panels) and gastrocnemius (right panels) muscles were observed during freestanding in both the ES and gastrocnemius muscle but disappeared from the gastrocnemius muscles when the subjects were suspended upright in a harness.

Table 1. VEMP area under various conditions. Under the static conditions (modified gravity, harness, and head contact), the areas were normalized by the VEMPs observed under the adjoining control condition (i.e., 100% = VEMP area in free upright standing in normogravity). For the VEMPs during gait, the areas are expressed as a percent of the median activity measured during the gait cycles without GVS. Values represent the means ± SD.

Table 2. Averaged latencies of VEMPs measured in all experiments. Non-applicable (*"NA"*) is assigned when VEMPs were not observed under the corresponding condition. Values represent the means ± SD.

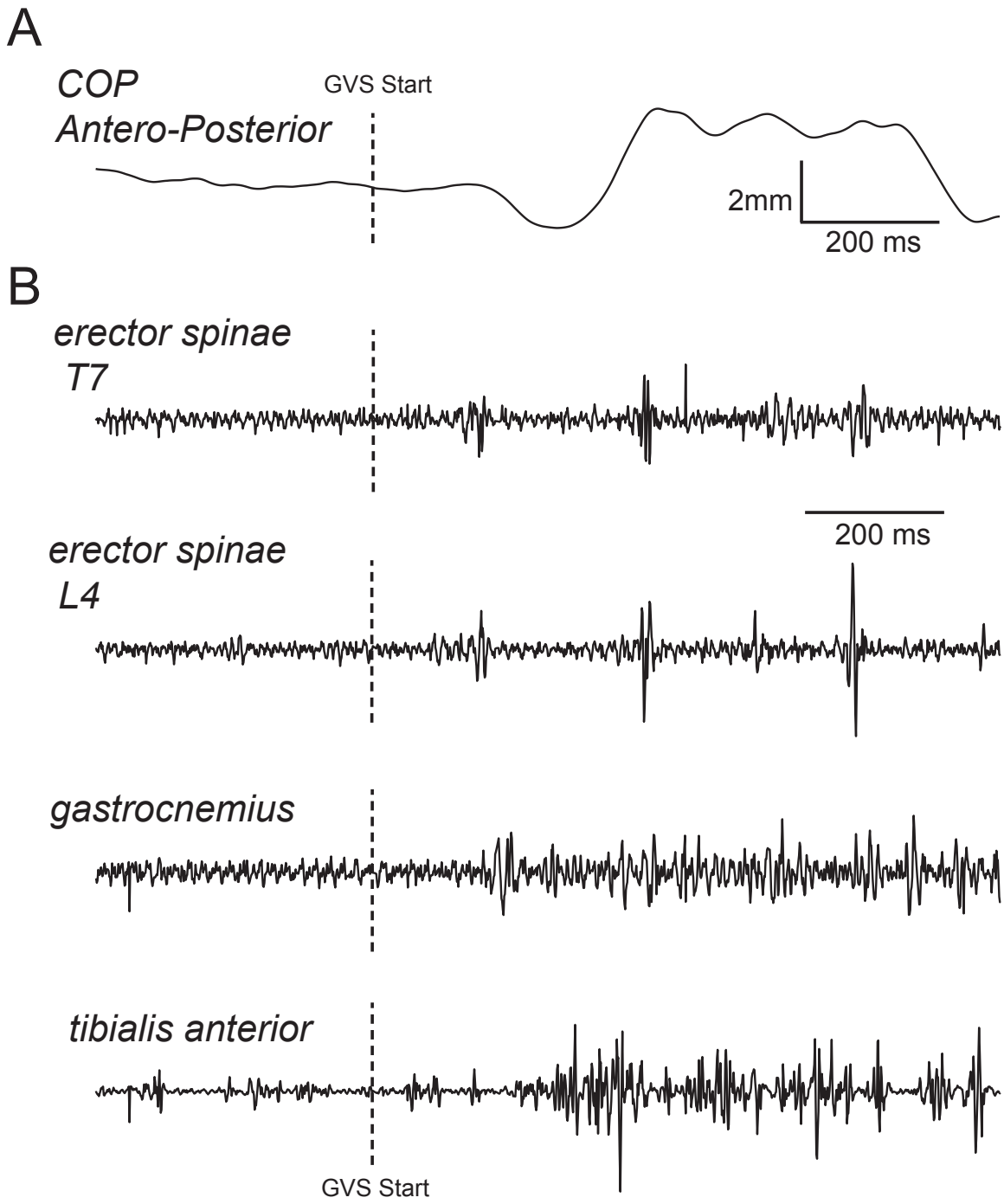

A
COP
Antero-Posterior
GVS Start
2mm
200 ms
B
erector spinae
T7
200 ms
erector spinae
L4
gastrocnemius
tibialis anterior
GVS Start

Figure 1

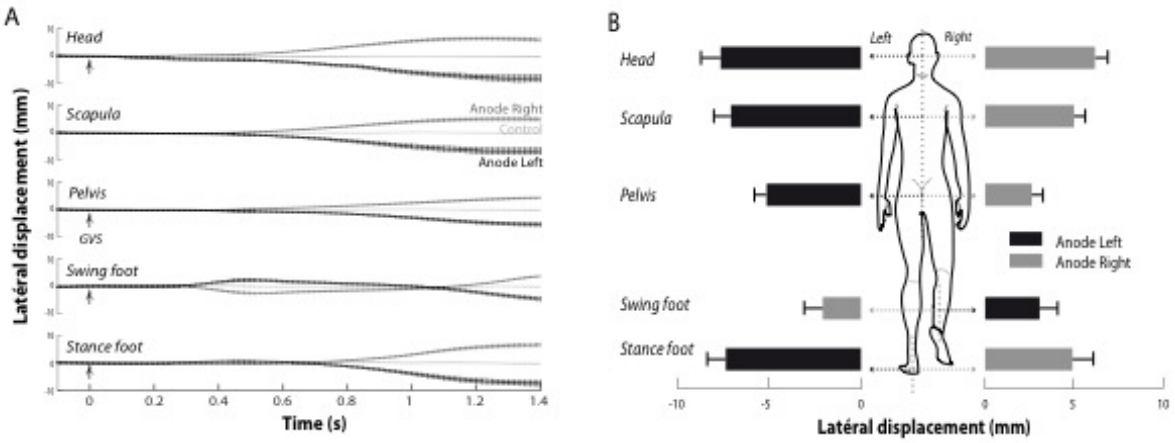


Figure 2

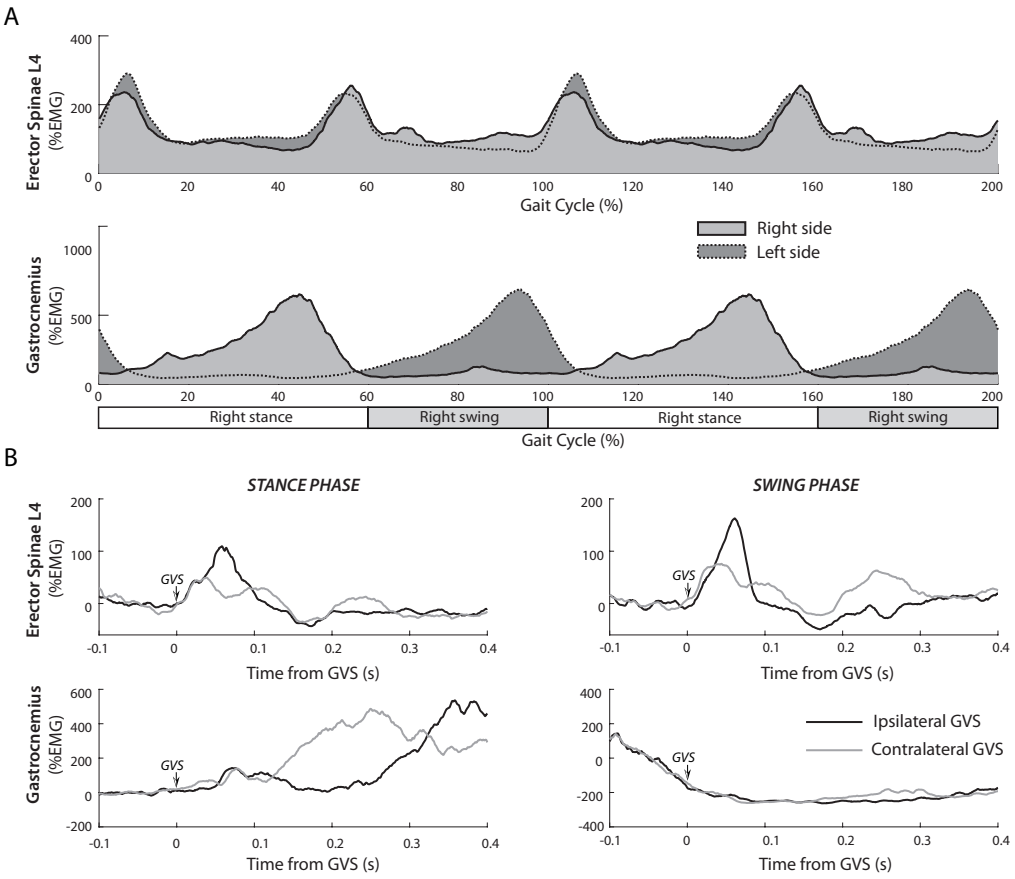


Figure 3

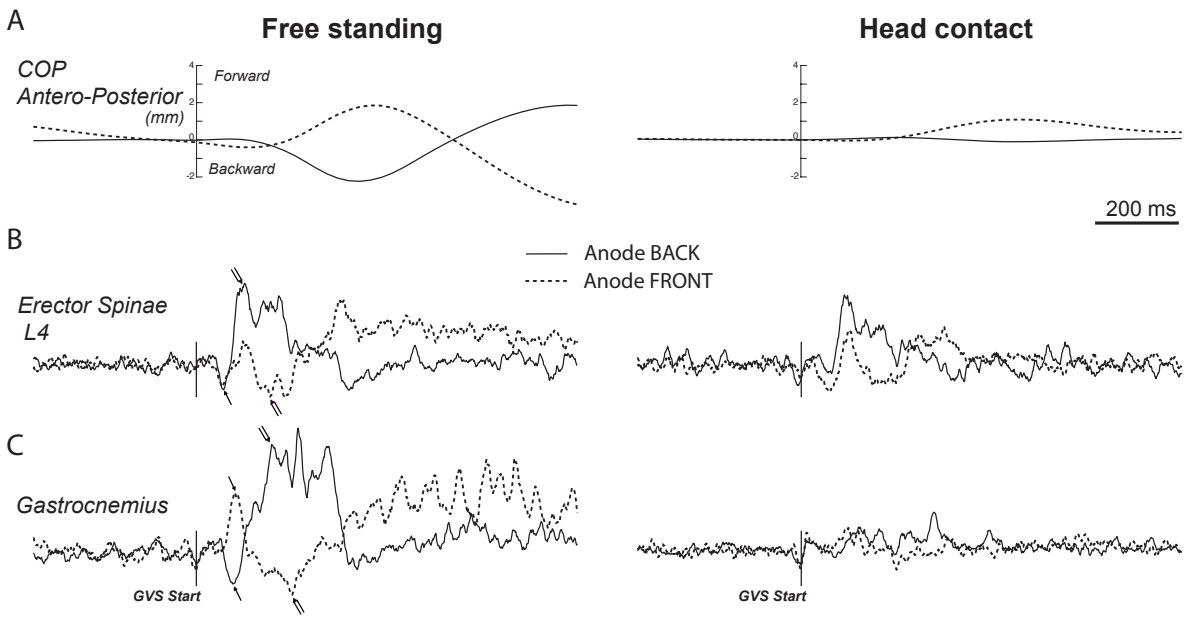
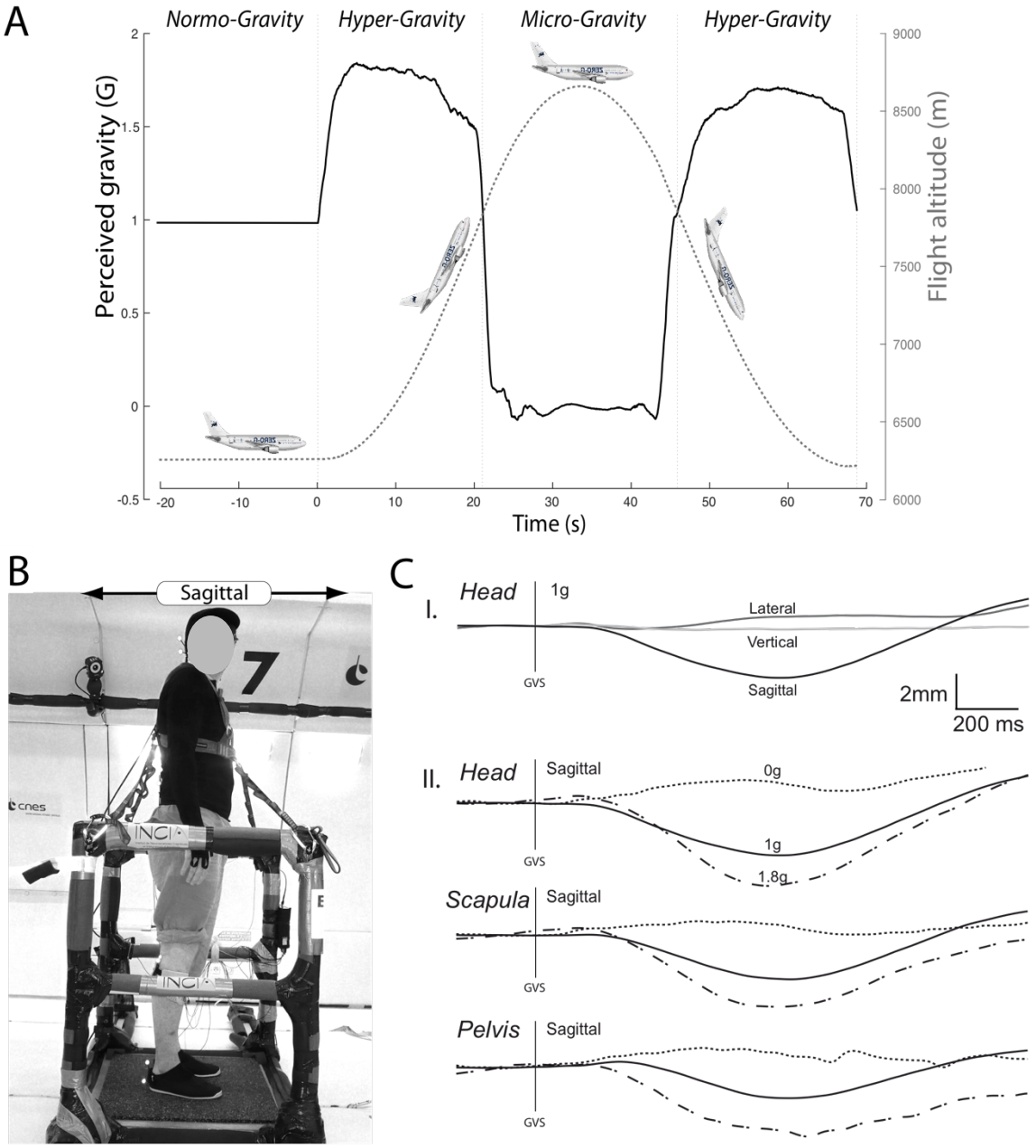

A
Free standing
Head contact
COP
Antero-Posterior
(mm)
Forward
Backward
200 ms
B
Anode BACK
Anode FRONT
Erector Spinae
L4
C
Gastrocnemius
GVS Start
GVS Start

Figure 4



890

891 **Figure 5**

892

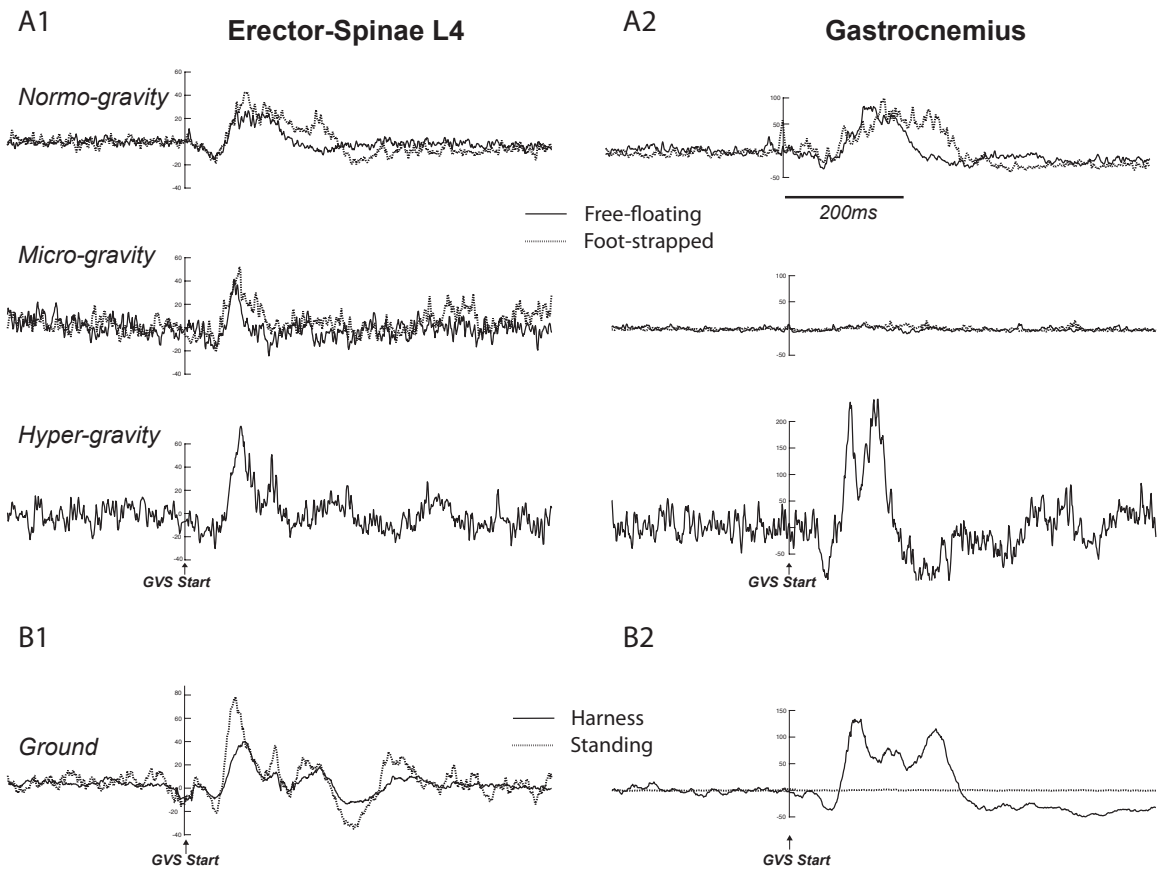

A1
Erector-Spinae L4
A2
Gastrocnemius
Normo-gravity
Micro-gravity
Hyper-gravity
Free-floating
Foot-strapped
200ms
GVS Start
B1
B2
Ground
Harness
Standing

Figure 6

VEMPs areas (% of normal standing ± SD)	Parabolic Flights			Ground		VEMPs areas (% of no GVS ± SD)	Gait			
	Hypergravity	Microgravity		Harness	Standing with Head Contact		Load Ipsilateral		Load Controlateral	
	Free floating	Free floating	Foot strap				Anode Ipsi	Anode Contra	Anode Ipsi	Anode Contra
ES-L4	232 ±123	105 ±114	82 ±42	138 ±117	97 ±102	**ES-L4**	106 ±37	83 ±33	119 ±35	92 ±22
Gastrocnemius	251 ±157	-1 ±19	20 ±30	2 ±6	28 ±15	**Gastrocnemius**	96 ±55	201 ±99	48 ±38	55 ±33

Table 1

VEMP Latencies (ms)		Condition	ES-L4	Gastrocnemius
Parabolic Flights	**Normogravity**	*Free floating*	72 ±13	108 ±15
		Foot strap	61 ±16	101 ±20
	Hypergravity	*Free floating*	62 ±7	84 ±11
	Microgravity	*Free floating*	57 ±6	*NA*
		Foot strap	61 ±10	*NA*
Harness		*Sustained*	65 ±14	*NA*
Standing		*Free standing*	47 ±35	89 ±16
		Head Contact	51 ±22	*NA*
Gait		*Appui Ipsi*	41 ±10	136 ±14
		Appui Contro	42 ±11	144 ±20
			ES-T7	**Tibialis Anterior**
		Appui Ipsi	36 ±7	161 ±27
		Appui Contro	33 ±8	185 ±28
KINEMATIC		**Body part**	**Latencies (ms)**	
Gait		*Head*	203 ±135	
		Scapular girdle	333 ±105	
		Pelvic girdle	343 ±113	
		Swing foot	214 ±47	
		Stance foot	533 ±127	

Table 2