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 upright subjects. 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.

SIGNIFICANCE STATEMENT

We seek to address the degree to which the underlying neural circuitry and mechanisms involved in trunk muscle control during locomotion, have been preserved in human. To this end, we challenged the persistence of vestibular-evoked responses in trunk muscles using galvanic vestibular stimulation, in conditions where leg muscle responses were expected to be modulated (walking, upright standing, free-floating subjects during parabolic flight). We found that vestibulo-motor responses persisted in trunk muscles whatever the behavioral conditions, whereas the lower limb responses were flexibly modulated. These results suggest a phylogenetically conserved blueprint of sensorimotor organization, with strongly hard-wired vestibulo-spinal inputs to axial motoneurons and a higher degree of flexibility for the late emerging limb motoneurons.

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. 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

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

114 **Electromyographic recordings and analysis**

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

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

133 For each stimulation, a 4 s time window was defined on both sides of the GVS onset (2
134 s before and 2 s after). For each subject, the EMGs were subsequently synchronized and
135 averaged for each GVS polarity and condition and normalized by the activity measured before
136 the occurrence of GVS (tonic activity during normal standing = 100%). The detection threshold
137 to identifying VEMPs during the 300 ms following the GVS start was two standard deviations
138 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

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

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

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

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

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

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

202 Nine subjects participated in this experiment (5 females and 4 males, 25.3 [±4] years
203 old). We measured the effects of GVS on upright standing subjects under the following two
204 conditions: (1) "freestanding" in which the subjects had to stay upright with their head turned
205 to the right and their eyes closed and (2) "head contact" in which the subjects remained in the
206 same position but with their head slightly in contact with a wall mounted on wheels allowing
207 for precise proprioceptive feedback regarding body sway but could not be used as a firm
208 support. Each subject was submitted to bipolar GVS with the anodal stimulation randomly set
209 on the left or right mastoid process. Each condition included 20 trials, and each trial included
210 4 GVS with randomized polarity and an unpredictable delay (>5 s). The condition occurrence
211 was randomized throughout the test session. Each subject experienced 160 GVS (2 conditions
212 x 20 trials x 4 stimulations).

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

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

221 Twelve subjects were tested in the upright standing position with their heads turned
222 to the right, anode on the posterior mastoid process, and vision occluded by a mask. GVS
223 occurred during normogravity (4 stimulations during each steady flight period between the
224 parabolas), the first hyper-gravity period (n=4), and micro-gravity (n=4), resulting in a total of
225 180 GVS. All GVS were delivered at the same polarity to trigger VEMPs in the gastrocnemius

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

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

250 *Kinematics*

251 We placed three reflective markers on each of the following segments: head, scapular
252 girdle, and pelvic girdle. The 3D data were captured by 5 cameras (Optitrack s250e) at 250 Hz.
253 The EMG data were synchronized and averaged to obtain one sample synchronized to the GVS
254 start per subject, segment, Gravity and condition. Based on the averaged data, we manually
255 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

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

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

332 Regarding the VEMP latencies, we compared the onset of the VEMPs elicited by
333 contralateral GVS to ipsilateral GVS (VEMPs with the same latencies but opposite effects on
334 the EMG magnitude). This analysis was performed at the ES T7, L4, Gastrocnemius and TA
335 muscles, where the effects of the opposed GVS were easily identifiable. The two-way ANOVA
336 (4 muscles x 2 phases) showed a main effect of muscle only ($F(3,9)=67$, $p<0.001$) on the VEMP
337 latencies. The post hoc analysis revealed that the erector spinae at T7 and L4 did not have
338 significantly different latencies (34 ms (SD 7) and 41 ms (SD 10), respectively), while these
339 muscle latencies were significantly shorter than the lower muscles latencies at gastrocnemius
340 and TA (140 ms (SD 18) and 173 ms (SD 30), respectively, not different). Altogether, these
341 results indicate that the GVS effect is strongly phase dependent in gastrocnemius but not
342 modulated by the gait cycle in the upper part of the body.

343

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

345 It has been shown that in seated subjects or subjects standing upright while bearing a
346 support, vestibular evoked responses were no longer elicited in the leg muscles (Fitzpatrick et
347 al., 1994). In the present experiment, we investigated whether the same sensory gating of
348 vestibulo-spinal inputs occurred in a similar way in the axial and leg muscles. Therefore, we
349 compared the GVS-induced responses in the absence or presence of a contact with support.
350 A bilateral GVS with the anode on the right (anode back) or left (anode front) mastoid process
351 was delivered with the head turn to the right and occluded vision. The GVS with the anode
352 back induced a backward sway (Fig. 4A) with an activation of the erector spinae and
353 gastrocnemius muscles (Fig. 4BC). The maximum amplitude of the center of pressure during
354 this antero-posterior sway was reduced by head contact (-2.9 mm (SD .9) in freestanding and
355 -.2 mm (SD 1.48) with head contact; N= 9 subjects; Fig. 4A left vs. right panel). The two-way
356 ANOVA revealed a significant interaction between the effects of polarity and condition on the
357 antero-posterior magnitudes of the COP excursions ($F(1,6)=18.3$, $p=0.005$). The forward sway
358 induced by GVS with the anode-front was also reduced (1.4 mm (SD 1.2) in freestanding and
359 1.2 mm (SD 1.41) with head contact), but this effect was lower and not significant. The delay
360 of the occurrence of the maximum sway was not significantly affected by either the polarity
361 or head contact with a mean value of 379 ms (SD 60).

362 Several responses were elicited by GVS in the recorded muscles. As previously reported
363 (Nashner et al. 1974; Britton et al. 1993; Fitzpatrick et al. 1994), GVS with the anode back first
364 elicited a response with a short latency (single arrows, Fig. 4BC left panel) in the erector spinae
365 and gastrocnemius muscles and a medium latency response (double arrow, Fig. 4BC). The
366 short- and medium-latency EMG responses were in opposite direction at the lower limb level
367 only but not in ES. We focused on the medium latency response, which was larger in
368 amplitude, and its direction was correlated with the observed pattern of whole body sway.
369 The comparisons of the VEMP occurrences indicates that the contact condition only
370 influenced the gastrocnemius response. The GVS-elicited VEMPs from the erector spinae (L4
371 level; Fig. 4B) were detected in 78% of the subjects under the freestanding-condition, and this
372 proportion was not significantly reduced to 56% under the head-contact condition ($Z=1$,
373 $p=0.16$). The GVS-elicited VEMPs from the gastrocnemius were detected in 100% of the
374 subjects under the freestanding-condition (Fig. 4B), but this proportion was significantly
375 reduced to 22% of the subjects under the head-contact condition ($Z=3.38$, $p<0.001$).

376 In the erector spinae (L4), the VEMP area was affected by the GVS polarity. As
377 previously described, GVS with the anode back (Fig. 4B) elicited a short latency inhibitory
378 response and a medium latency response of a large amplitude. By contrast, when GVS was
379 delivered with the anode front, the medium latency response was dramatically decreased.
380 The two-way ANOVA revealed a significant main effect of polarity on the erector spinae
381 elicited VEMP area ($F(1,8)=8.5$, $p<0.05$) and no effect of condition or interaction. Interestingly,
382 the same analysis of the VEMPs elicited in the gastrocnemius revealed an interaction between
383 the GVS polarity and contact condition ($F(1,8)=7$, $p<0.05$). The post hoc analysis showed a
384 strong effect of the GVS polarity under the freestanding condition with a large response in the
385 gastrocnemius to the anode back GVS and a marked inhibition with the anode-front GVS (Fig.
386 4C). This effect was drastically and significantly reduced under the head-contact condition
387 with responses representing only 28% of the VEMP areas recorded while freestanding.

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

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

395

396 **Effects of GVS in modified gravity**

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

401 Figure 5B present the experimental design of the free floating conditions (see
402 Materials and Methods section). The subjects were submitted to GVS during parabolic flights
403 (Fig. 5A) with periods of normal gravity, hyper-gravity (1.8 g) and micro-gravity (0 g). Due to
404 the limited number of available trials under these conditions, GVS was delivered with the

405 anode back only. GVS induced a backward displacement of the upper body in the antero-
406 posterior direction under the normal gravity conditions (Fig. 5C, solid line, sagittal plane),
407 which was increased under the hypergravity condition (dash-dotted line; $F(2,8)=2$, $p=0.19$ with
408 $n=4$ subjects) and disappeared under the microgravity condition (dotted line). Under the
409 normogravity and hypergravity conditions, all subjects expressed VEMPs in ES-L4 and
410 gastrocnemius, whereas under the microgravity condition, 100% of the subjects expressed
411 VEMPs in the left ES-L4, 60% of the subjects expressed VEMPs in the right ES-L4, and no
412 subjects expressed VEMPs in the gastrocnemius (significant decrease, $Z=5.2$, $p<0.001$). We
413 found a significant main effect of gravity on the ES-L4 muscle area (Fig. 6A1; $F(2,8)=6$, $p<0.05$
414 for left ES-L4 and $F(2,8)=5.8$, $p<0.05$ for right ES-L4). The post hoc analysis only revealed a
415 significant difference between the hypergravity and microgravity conditions in the left ES-L4
416 area. We also found a significant main effect of gravity on the gastrocnemius area in the free-
417 floating condition (Fig. 6A2; $F(2,8)=23.8$, $p<0.05$ for left gastrocnemius and $F(2,8)=25$, $p<0.05$
418 for right gastrocnemius). The post hoc analysis revealed that in both sides, the gastrocnemius
419 EMG area was drastically decreased under the microgravity condition (quite null) and
420 enhanced under the hypergravity condition (all p-values <0.05) compared with that under the
421 normogravity condition.

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

425 Under the foot-strapped condition, we tested GVS only in microgravity and
426 normogravity. Measuring the occurrence of VEMPs under the foot-strapped condition also
427 revealed that the VEMP occurrence remained stable at the ES-L4 level (from 86% in
428 normogravity to 75% in microgravity, $Z=0.54$, $p=0.29$ in ES-L4 right; from 100% to 86%, $Z=0.53$,
429 $p=0.29$ in ES-L4 left), while the VEMPs were totally abolished in the gastrocnemius in the
430 absence of gravity (from 100% to 0%, $Z=7.3$ and $p<0.001$ in both side). There was no significant
431 difference in the ES-L4 VEMP area between the normogravity and microgravity conditions
432 (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
433 main effect of gravity on the gastrocnemius VEMP was observed (left gastrocnemius
434 $F(1,6)=10.3$, $p<0.05$; 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

Our results strongly suggest that a differentiated control mechanism exists between axial and appendicular muscles when an unbalance is detected by vestibular inputs. The finding that with null gravitational information from the otolithic system (microgravity), we still observed persistent GVS elicited responses in axial muscles is particularly interesting.

465

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

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

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

489

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

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

493 observed a systematic suppression of VEMPs in the gastrocnemius when the force output did
494 not contribute to the maintenance of body balance.

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

514 In contrast to the above discussion, a major result of the present study is the persistent
515 responses in ES-L4 following GVS under all tested conditions. This persistence is particularly
516 intriguing under the free-floating conditions in which the subjects were unplugged from their
517 surroundings with no functional requirement of postural adjustments. Moreover, in
518 microgravity the otolithic signal was null, informing of the lack of gravity. In this context, the
519 persistence of the axial response strongly suggests that the otolithic signal did not interfere
520 with the integration of the semi-circular afferents. Together with the very short latency of the
521 ES VEMP (47 ms versus 89 ms in the gastrocnemius in normal standing), the response of the
522 axial muscles to vestibular inputs is more direct and robust and cannot be modulated by the
523 context.

524

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

526 Even if the exact mechanisms by which gating may occur remain unclear likely because
527 multiple processes may be involved, it is a ubiquitous property of most vestibular responses.
528 For example, the vestibulo-ocular reflex (VOR) can be suppressed during voluntary gaze
529 behavior directed toward a visual target (Laurutis and Robinson, 1986; Pelisson and Prablanc,
530 1986). Similarly, the vestibulocolic reflex, which stabilizes the head in space by generating a
531 command to move the head in the opposite direction (Colebatch et al., 1994), can be
532 suppressed by voluntary head motion (Ezure and Sasaki, 1978; Goldberg and Cullen, 2011).

533 If during free floating, the persistence of VEMPs in the lower-limb muscles can be
534 considered behaviorally irrelevant to maintaining balance, under the foot-strapped condition,
535 the VEMPS also disappeared, although there was direct active involvement of the ankle
536 muscles. This finding suggests that gating is partially based on the detection of a gravitational
537 field either by the otolithic system or extravestibular somatic receptors (Mittelstaedt, 1992).
538 However, under the harness or head-contact conditions in normogravity, the detection of a
539 downward gravitational field by upright subjects was not sufficient to elicit VEMPs in the
540 gastrocnemius. Altogether, these results suggest that the incongruence among the vestibular,
541 proprioceptive and cutaneous inputs abolishes the VEMPs in the lower limb muscles. The
542 vestibular responses in the legs could be evoked only when all features of a nominal terrestrial
543 postural task are met as follows: gravity must be detected, segment must be involved in the
544 postural task, and sensorial cues must be congruent.

545 In their detailed study investigating the effects of vestibular stimulation during
546 walking, Iles et al. (2007) reported that gating occurred in the soleus muscle during gait with
547 similar phase-dependency as that observed in the present study, and these authors proposed
548 that gating may occur through interactions with the central pattern generator at the lumbar
549 level. Alternately, these authors also posed the hypothesis that gating could occur at the level
550 of the brain stem. However, if this was the case, the axial and lumbar motoneuron responses
551 could be affected in the same way since it has been recently shown in rodents that the two
552 motoneuronal populations are similarly targeted by the LVST (Kasumacic et al., 2010). This is
553 the only pathway that conveys vestibular input to lumbar motoneurons in adult mammals

554 (Wilson and Yoshida, 1969) with connections to both ipsilateral and contralateral thoracic
555 motoneurons (Graf, 2007). We therefore conclude that gating may occur at the lumbar level
556 for hindlimb control, supported by the complex neuronal circuit interactions involved in
557 postural and locomotor activities at the lumbar level (Falgairolle et al., 2007; Beliez et al.,
558 2015). This is in coherence with the dramatic differences observed between the latencies in
559 the ES-L4 and the gastrocnemius in our experiments, that cannot be explained by the sole
560 differences in the target distances.

561

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

563 The shift from swimming to upright bipedal locomotion is an outstanding feature of
564 the evolutionary process, and the question of whether any of the underlying neural circuitries
565 and mechanisms responsible for locomotor output production have been preserved during
566 this transitional process remains unanswered. Several studies have previously suggested that
567 during this evolutionary transition, the core features of the spinal cord circuitry of most
568 primitive vertebrates, such as lamprey, have been conserved both in rats (Falgairolle et al.,
569 2013) and humans (de Sèze et al., 2008; Ceccato et al., 2009). According to this phylogenetic
570 perspective, the vestibular system has been present very early in most primitive vertebrates
571 in a definite form sharing many common characteristics with the vestibular system in
572 mammals (Kasumyan, 2004). This ancestral demand for highly efficient vestibular control
573 could be the source of the strong hard-wired vestibulo-spinal inputs to axial motoneurons,
574 with a lower degree of flexibility than late emerging limb motoneurons. The switch to
575 terrestrial modes of locomotion and the emergence of limbs have necessarily increased the
576 complexity of postural and locomotor control mechanisms, and currently, the trunk
577 musculature is required for activity in strict coordination with limb movements during
578 locomotion (Combes et al., 2004).

579

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688 **Figure legends**

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

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

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

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

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

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

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

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

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

747

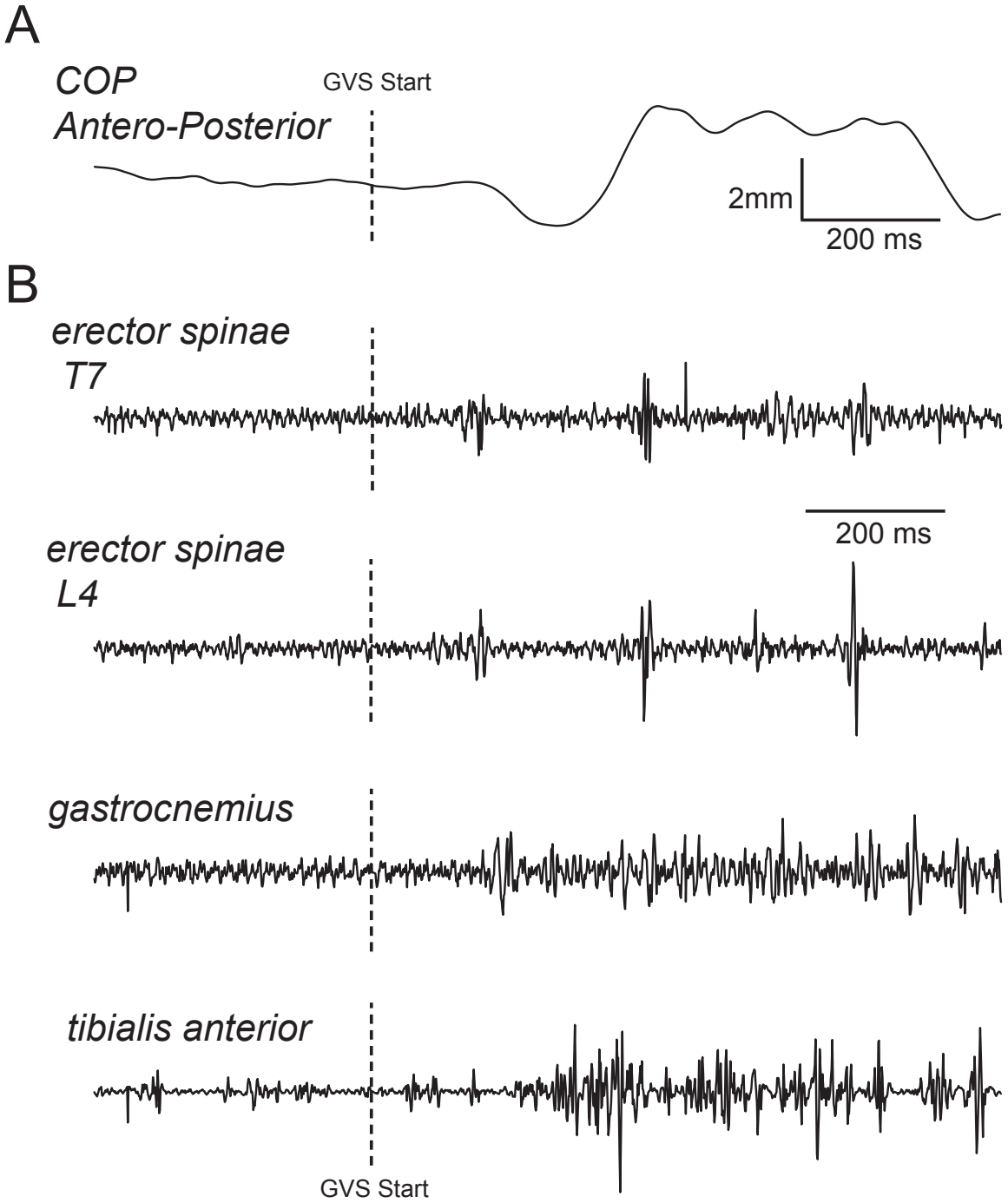
A
COP
Antero-Posterior
GVS Start
2mm
200 ms
B
erector spinae
T7
200 ms
erector spinae
L4
gastrocnemius
tibialis anterior
GVS Start

Figure 1

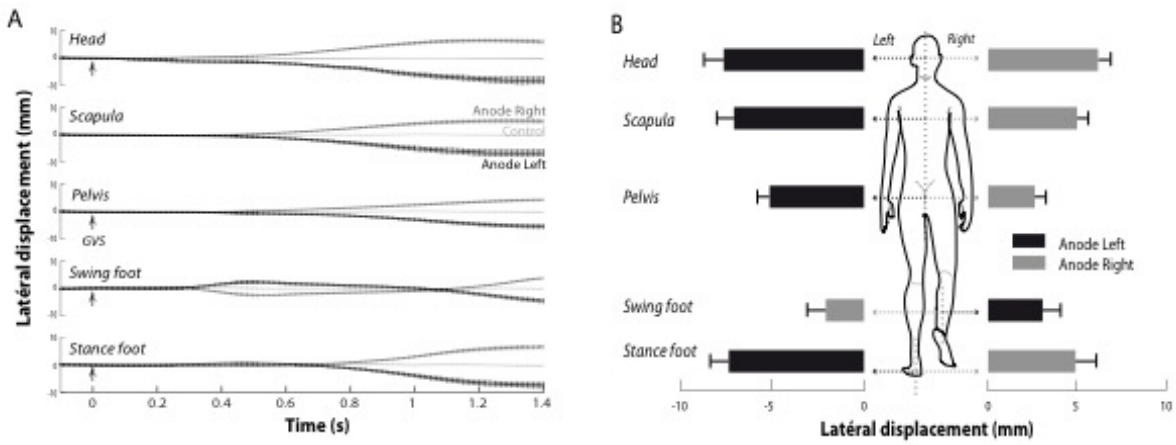

Figure 2

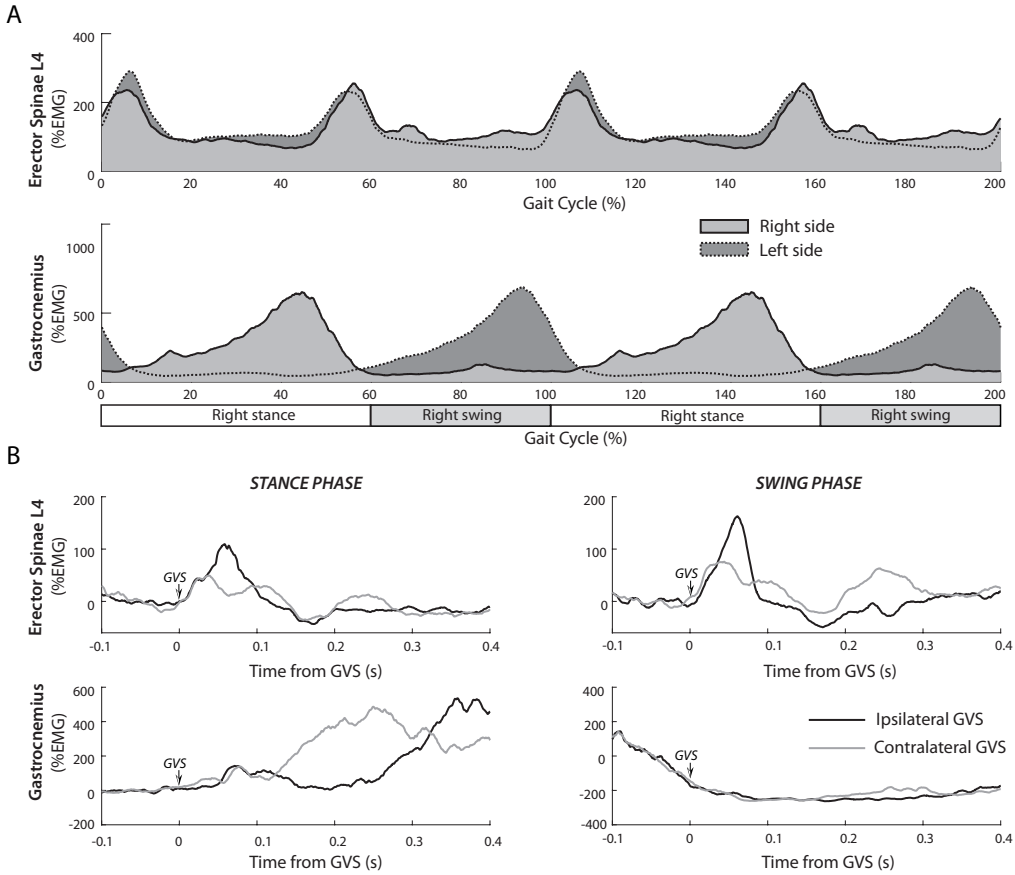

Figure 3

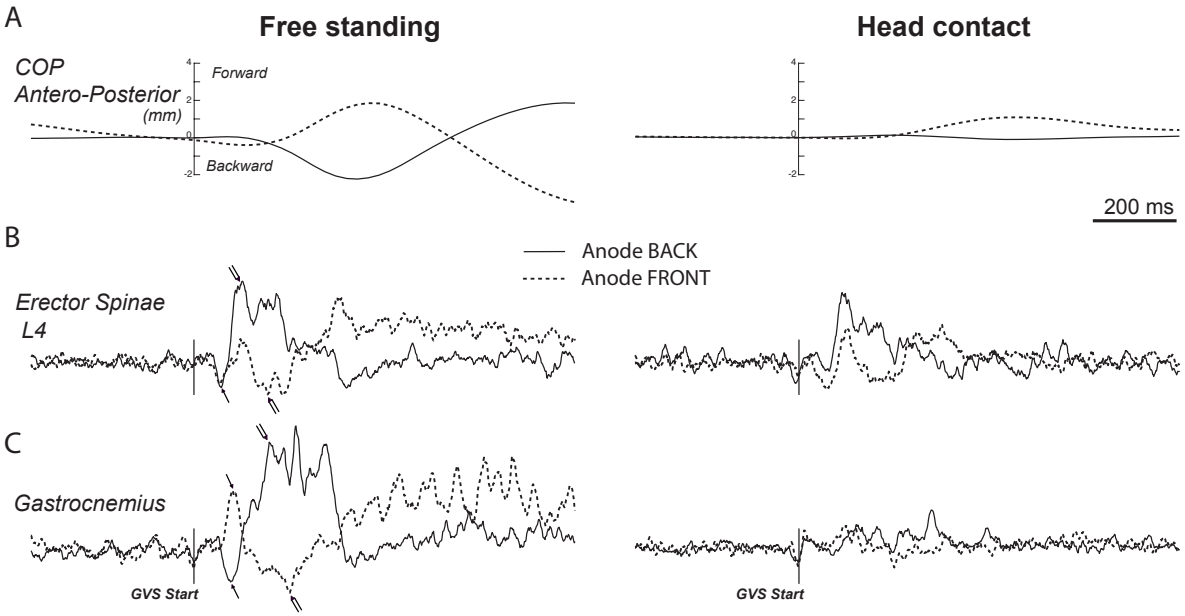
A
Free standing
Head contact
COP
Antero-Posterior
(mm)
Forward
Backward
4
2
0
-2
200 ms
B
Anode BACK
Anode FRONT
Erector Spinae
L4
C
Gastrocnemius
GVS Start
GVS Start

Figure 4

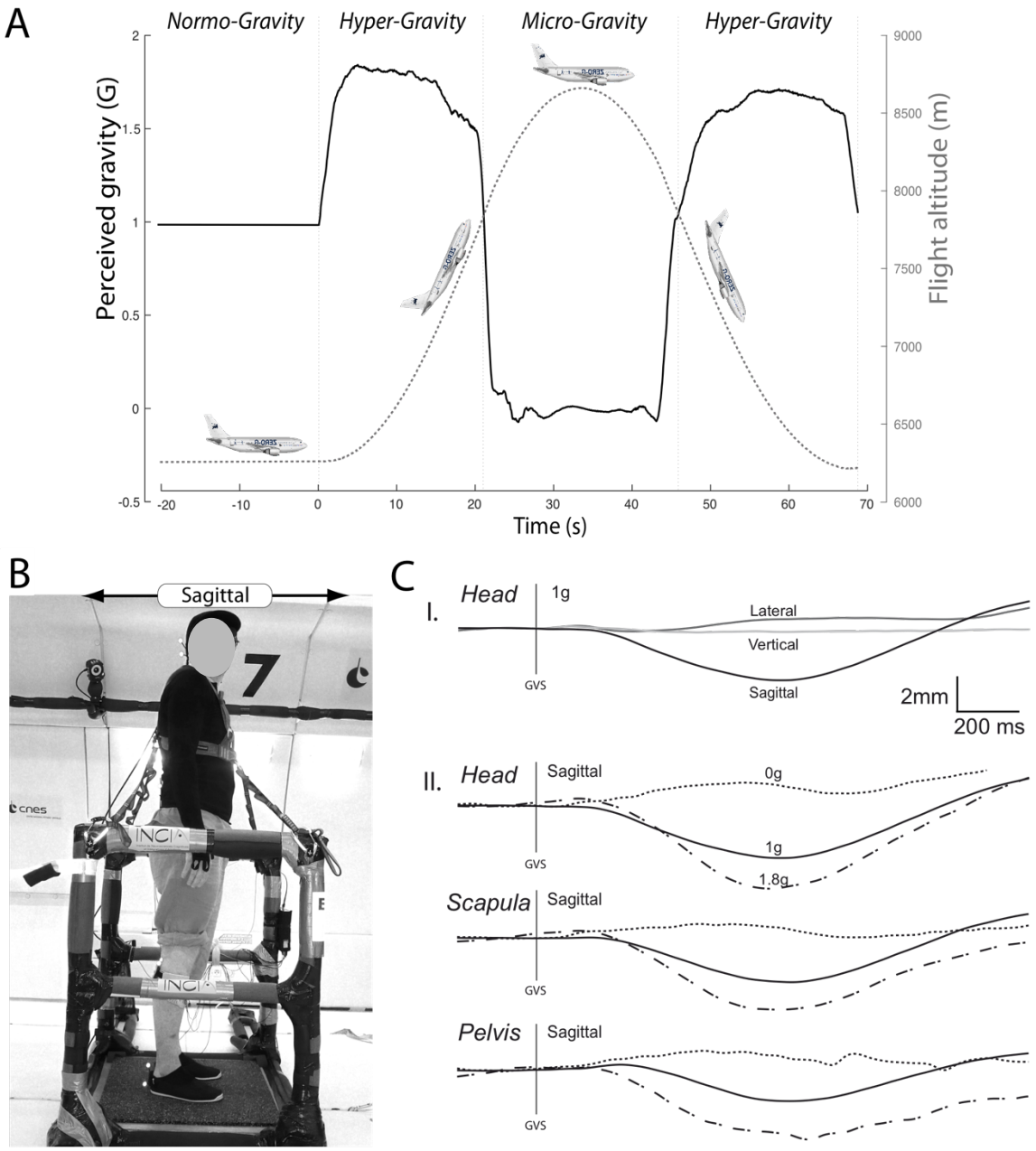
A
Normo-Gravity
Hyper-Gravity
Micro-Gravity
Hyper-Gravity
Perceived gravity (G)
Flight altitude (m)
Time (s)
B
Sagittal
C
I.
Head
1g
Lateral
Vertical
Sagittal
GVS
2mm
200 ms
II.
Head
Sagittal
0g
1g
1.8g
Scapula
Pelvis

Figure 5

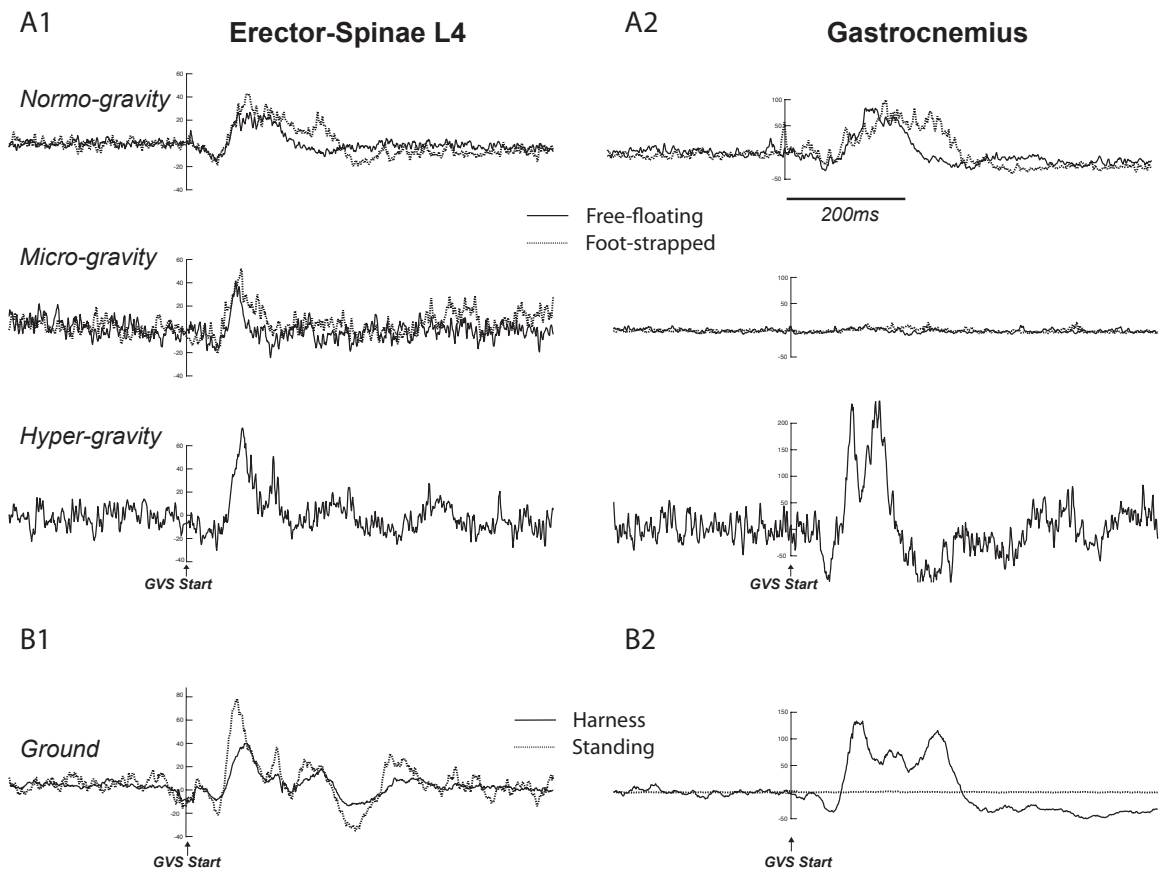
A1
Erector-Spinae L4
A2
Gastrocnemius
Normo-gravity
Micro-gravity
Hyper-gravity
Free-floating
Foot-strapped
200ms
GVS Start
GVS Start
B1
B2
Ground
Harness
Standing
GVS Start
GVS Start

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