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Christopher J. Dakin, Billy L. Luu, Kees van den Doel, John Timothy Inglis and Jean-Sébastien Blouin

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## Short-duration galvanic vestibular stimulation evokes prolonged balance responses

Gregory Martin Lee Son,<sup>1</sup> Jean-Sébastien Blouin,<sup>1,2</sup> and John Timothy Inglis<sup>1,2,3</sup>

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**Lee Son GM, Blouin J-S, Inglis JT.** Short-duration galvanic vestibular stimulation evokes prolonged balance responses. *J Appl Physiol* 105: 1210–1217, 2008. First published July 31, 2008; doi:10.1152/jappphysiol.01398.2006.—The application of galvanic vestibular stimulation (GVS) evokes distinct responses in lower limb muscles involved in the control of balance. The purpose of this study was to investigate the balance and lower limb muscle responses to short-duration GVS and to determine whether these responses are modulated by small changes in center of gravity (CoG) and baseline muscle activity occurring during quiet standing. Twelve subjects stood quietly on a force plate with their feet together and were instructed to look straight ahead. One thousand twenty-four GVS stimuli (4 mA, 20-ms pulses) were delivered bilaterally to the mastoid processes in a bipolar, binaural configuration. Bilateral surface electromyography (EMG) from soleus (Sol) and tibialis anterior (TA) and ground reaction forces were recorded. EMG and force responses were trigger averaged at the onset of the GVS pulse. Short-duration GVS applied during quiet standing with the head facing forward evoked characteristic balance responses and biphasic modulation of all muscles with the same polarity for ipsilateral Sol and TA. The amplitude of the GVS-evoked muscle responses was modulated by both the estimated position of the subject's CoG and the background activation of the recorded muscle. Muscle-dependent modulations of the GVS-evoked muscle responses were observed: the Sol responses decreased, while the TA responses increased when the CoG position shifted toward the heels. The well-defined balance responses evoked by short-duration GVS are important to acknowledge when studying the vestibulo-motor responses in healthy subjects and patient populations.

vestibulo-motor responses; electromyography; center of pressure

THE CONTRIBUTIONS OF VESTIBULAR information in the control of human balance are still being debated. Visual and somatosensory inputs provide the dominant sources of afferent information during stance, while the vestibular system is thought to have a less important role (30). Galvanic vestibular stimulation (GVS), a technique used to probe the vestibular system, has gained attention from researchers studying human balance (5, 6, 8, 9, 14, 15, 26, 29, 36, 37; for review see Ref. 11). GVS alters the firing rates of all vestibular afferents with a preference toward the irregular afferents (12), such that the anode decreases and the cathode increases afferent firing rates (13). In standing humans, binaural, bipolar GVS applied for a long duration (1–2 s) elicits a well-defined biphasic muscle response (4, 9) and a multiphasic center of pressure (CoP) response often identified by lateral sway and tilt toward the side of the anode (8, 21, 28). Short-duration GVS (20–50 ms) have also been used to evoke vestibulomotor responses in lower and

upper limb muscles engaged in balance (4, 40). Such stimuli have been thought to evoke motor responses with minimal or no balance response, but it remains to be determined whether such brief GVS pulses specifically evoke vestibulomotor responses or if they evoke a concomitant balance response. The primary aim of the present study was to quantify the muscle and balance responses associated with brief 20-ms GVS pulses.

Muscle and whole body responses elicited by GVS during quiet standing have been mostly described, regardless of the body and CoP position (8, 38, 39). One notable exception, however, is a study by Marsden et al. (23), who showed that asymmetric stance alters vestibular-evoked postural responses. When leaning over one of the lower limbs, the GVS-evoked lateral ground reaction force of the loaded leg increases, while that of the unloaded leg decreases (23). Following the assumption that loading is associated with a change in center of gravity (CoG) position, we would expect small changes in the GVS-evoked ground reaction forces during natural sway associated with a balancing act. Since the GVS-evoked muscle and balance responses are likely coupled to each other (4, 9, 26), we expect the vestibular-evoked muscle responses to vary during natural sway. Variations in muscle activity following short-duration GVS stimuli are small. To observe GVS-evoked motor responses in standing humans, electrical muscle activity is averaged over a large number of stimuli delivered at different body positions that occur due to natural body oscillations. To date, this type of analysis has limited the exploration of dynamic modulations of vestibular-evoked responses as a function of body position in quiet stance. The secondary purpose of this study was to assess the modulations in vestibulomotor responses during quiet standing using short-duration GVS.

We hypothesized that 1) short-duration (20-ms) GVS pulses evoke well-defined balance responses, and 2) modulations of the muscle responses to short-duration GVS will be observed as subjects swayed away from their central standing position. Electromyographic (EMG) responses in the soleus (Sol) and tibialis anterior (TA) muscles and balance responses (measured by CoP) were recorded. To investigate vestibulo-motor response modulations during natural sway, the muscle responses were analyzed based on the estimated position of the CoG. The GVS-evoked muscle responses were first analyzed based on background EMG, because changes in CoG position can be associated with changes in lower limb muscle activity. This initial analysis revealed a modulation of the vestibular reflexes based on background muscle activity. In subsequent analyses,

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background EMG was used as a cofactor in the statistical analysis to determine the unique contribution of CoG position on the amplitude modulation of the vestibular-evoked muscle responses. Our results supported the hypotheses that 1) brief galvanic vestibular pulses evoke balance responses, and 2) vestibulomotor responses are independently modulated by CoG position during quiet standing in humans.

## MATERIALS AND METHODS

**Subjects.** Twelve healthy subjects (6 men, 6 women) between the ages of 21 and 32 yr, with no history of neurological disease or injury, participated in the experiment. The experimental protocol was explained, and the subjects gave their written, informed consent to participate. The procedures conformed to the standards of the Declaration of Helsinki and were approved by the University of British Columbia's clinical research ethics board.

**Stimulus.** Short-duration GVS was delivered using a bipolar, binaural configuration. Two carbon-rubber stimulating electrodes (9 cm<sup>2</sup>) were attached to the mastoid processes and secured with an elastic headband. Output signals were sent from a computer through a 1401-micro interface (Cambridge Electronics Design, Cambridge, UK), which delivered a square-wave pulse through a constant-current analog stimulus isolation unit (model 2200 Analog Stimulus Isolator, AM Systems, Carlsborg, WA), which generated an output current of 4 mA. The duration of each pulse was 20 ms and was delivered with a randomized interstimulus interval between 800 and 1,300 ms.

**Protocol.** Subjects were instructed to stand quietly with their heads facing forward and their eyes open. To control for head pitch angle (5, 7, 10), subjects were asked to maintain their head position by looking straight ahead. They stood on a force plate (Bertec 4060-80, Bertec, Columbus, OH) with their feet 1–2 cm apart (measured at the medial malleolus). During each trial, subjects were asked to keep their arms at their sides and minimize extraneous body movements. Subjects performed four trials and were exposed to 256 GVS perturbations in each trial (128 anode right/cathode left: anode right configuration; 128 anode left/cathode right: anode left configuration); the presentation of stimulus polarity was randomized in the trial sequence. Between trials, sufficient rest periods were provided to prevent the possibility of muscle fatigue. The total count of stimuli each subject received over the experiment was 1,024 GVS pulses (512 for each electrode configuration).

**EMG and analysis.** Surface EMGs were measured bilaterally from Sol and TA muscles. Self-adhesive Ag-AgCl surface electrodes (Soft-E H59P, Kendall-LTP, Chicopee, MA) were placed on the skin along the length of the specified muscle with an interelectrode distance of 12 mm. EMG was amplified and bandpass filter from 30 to 1,000 Hz (Grass P511, Grass-Telefactor), sent to an analog-to-digital converter (Micro 1401, Cambridge Electronic Design), and digitized at 5 kHz. The digitized signal was analyzed offline using full-wave rectification and integration with a 10-ms time constant with Matlab 6.5 software (Mathworks, Natick, MA). GVS-evoked muscle and posture responses were trigger averaged to the onset of the GVS pulse. EMG responses were quantified using peak-to-peak amplitudes, response onset latencies, and peak latencies. Response onset latencies were determined using a log-likelihood-ratio algorithm (32, 33) and then confirmed visually. CoP was determined from the ground reaction forces collected from the force plate and digitized using the same analog-to-digital converter as the EMG signals. Computation of the anteroposterior (AP) and mediolateral (ML) CoP was calculated from the forces and moments in the *x*-, *y*-, and *z*-axes recorded from the force plate. The forces were filtered using a fourth-order, low-pass, dual-pass Butterworth filter with a cutoff frequency of 20 Hz. Whole body CoG was estimated using a gravity line model, as described by Zatsiorsky and Duarte (42) and was visually inspected to ensure validity. CoP- and CoG-evoked responses were quantified using

displacements of individual peaks, onset latencies, and peak latencies. Displacements of individual peaks were determined as the displacement between the peak and the mean position of the CoG (averaged from –50 to 0 ms before GVS onset).

GVS-evoked muscle responses were first analyzed to determine whether background EMG influenced the GVS-evoked muscle responses. Background muscle activity was quantified by integrating the rectified EMG (iEMG) from 50 ms prestimulation to the onset of the GVS perturbation. Five hundred twelve GVS-evoked muscle responses (per GVS electrode configuration) were ranked into an array based on the magnitude of the iEMG. The 60 muscle responses when the iEMGs were the smallest were determined as the responses with minimal activity (iEMG<sub>min</sub>). Likewise, the 60 muscle responses when the iEMGs were median and largest were classified respectively as the responses with median and maximal activity (iEMG<sub>med</sub> and iEMG<sub>max</sub>).

The main analysis investigated amplitude modulations in the GVS-evoked muscle responses based on the position of the CoG. Position of the CoG was estimated from the force plate, and five CoG positions were determined: center, left, right, front, and back. Five hundred twelve GVS-evoked muscle responses (per GVS electrode configuration) were sorted into arrays for the AP and the ML axes based on the position of the CoG. EMG responses segregated based on the AP axis were analyzed independently of those segregated based on the ML axis. The 60 muscle responses when the CoG positions were the furthest left were determined as the responses in the left position, and vice versa for the right position. The 60 muscle responses when the CoG positions were the furthest forward were determined as the responses in the forward position, and vice versa for the backward position. The 60 muscle responses when the CoG positions were median in the ML and AP axes were determined as the responses in the center position. Since our initial analysis showed covariation between background EMG and amplitude of the GVS-evoked muscles responses, background muscle activity was used as a covariate in the statistical analysis. For each subject, an averaged background iEMG (–50 to 0 ms before the GVS perturbation onset) was computed for each CoG position of interest.

**Control experiment.** The balance responses observed following short-duration GVS pulses lasted ~3 s after the onset of the pulse. Since the interstimulus interval of the initial protocol was shorter than the time required for the CoP and CoG responses to return to equilibrium, it was important to perform a control experiment with longer interstimulus interval to avoid the potential confounder of the balance response being influenced by the next GVS pulse. Five additional subjects were tested on a different day. They stood on a force plate (Bertec 4060-80; Bertec) with their feet 1–2 cm apart (measured at the medial malleolus). Subjects were exposed to 4-mA, 20-ms GVS pulses presented with a random interstimulus interval of 4–5 s. During each trial, subjects were asked to keep their arms at their sides and minimize extraneous body movements. Subjects performed two trials and were exposed to 80 GVS perturbations in each trial (40 anode right/cathode left: anode right configuration; 40 anode left/cathode right: anode left configuration); the presentation of stimulus polarity was randomized in the trial sequence. Only the ground reaction forces were measured for this control experiment. The GVS-evoked CoP and CoG responses were quantified using displacements of individual peaks and peak latencies. Displacements of individual peaks were determined as the displacement between the peak and the mean position of the CoG (averaged from –50 to 0 ms before GVS onset).

**Statistical analysis.** Descriptive statistics were performed for the following dependent variables of the balance and muscle responses to GVS: peak amplitudes for CoP and CoG displacements, peak-to-peak amplitudes for muscle responses, response onset latencies, and peak latencies. To compare the amplitude and timing of the CoP and CoM responses evoked by short-duration GVS pulses with different interstimulus intervals, independent *t*-tests were used. For the GVS-evoked muscle responses sorted by background EMG, independent two-way

(GVS polarity  $\times$  iEMG) repeated-measures analyses of variance were used for each muscle to assess peak-to-peak amplitude modulations attributed to GVS configuration and background muscle activity. For the GVS-evoked muscle responses sorted by CoG position, two-way (GVS polarity  $\times$  CoG position) repeated-measures analyses of covariance were used to assess peak-to-peak amplitude differences between GVS configuration and CoG position using background iEMG as the covariate. Independent repeated-measures analyses of covariance were performed for each muscle and for the AP and ML axes. Post hoc decomposition of main effects and interactions was performed using Tukey's honestly significant difference tests. All statistical analyses were performed using Statistica 6.0 (Statsoft, Tulsa, OK) and SPSS 15.0 (SPSS, Chicago, IL) software; statistical significance was  $P \leq 0.05$ .

## RESULTS

Short-duration GVS perturbations did not induce observable EMG or whole body responses from individual stimuli, but, when averaged, biphasic EMG responses in the Sol and TA muscles and distinct CoP and CoG postural responses were present (Fig. 1). The peak-to-peak amplitudes, onset and peak latencies of the EMG, and postural (CoP and CoG) responses between the anode right and anode left GVS conditions were

not statistically different from each other, and the values were combined ( $P > 0.05$ ).

The averaged CoP responses evoked by short-duration GVS pulses were triphasic, with the first and third peaks toward the side of the anode, and the second peak toward the cathode. Peak displacements were small, with an averaged CoP excursion of 0.26 (SD 0.21), 0.66 (SD 0.48), and 1.89 mm (SD 1.44) from the averaged neutral position. The onset and peak latencies of the three CoP peaks occurred at 70 (SD 7) and 140 (SD 22), 208 (SD 36) and 375 (SD 43), and 554 (SD 72) and 1,247 ms (SD 289) following the GVS onset, for peaks 1, 2, and 3, respectively. Unexpectedly, we observed monophasic CoG responses to the short-duration GVS pulses with a single deviation toward the side of the anode. The averaged CoG displacement evoked by the GVS was 0.80 mm (SD 0.58) from the averaged neutral position. The onset and peak latency of the single GVS-evoked CoG deviation occurred at 221 (SD 48) and 1,218 ms (SD 300), while the CoG response returned to baseline  $\sim 3$  s after the short-duration GVS pulse onset (Fig. 2).

The GVS anode right (cathode left) configuration yielded an initial decrease followed by an increase in EMG activity for the left Sol and TA and an increase for the right Sol and TA (opposite EMG responses for the GVS anode left-cathode right configuration). The mean onset latencies were 61 (SD 8) and 61 ms (SD 9) for the left and right Sol and 58 (SD 8) and 60 ms (SD 8) for the left and right TA, respectively. The onset latencies of the second response of opposite polarity for left and right Sol were 94 (SD 9) and 96 ms (SD 8), while the mean onset latencies for the second responses of left and right TA were 98 (SD 11) and 96 ms (SD 7), respectively. The peak latencies of the biphasic responses were 96 (SD 38) and 144 (SD 28), 83 (SD 24) and 142 (SD 22), 82 (SD 17) and 142 (SD 34), and 80 (SD 26) and 130 (SD 37) ms for the left Sol, right Sol, left TA, and right TA, respectively.

The interstimulus interval (0.8–1.3 s) was shorter than the evoked CoG response (peak at 1.2 s; duration  $\sim 3$  s). Hence, the profile of the CoG-evoked response by short-duration GVS pulses (20 ms) in the present study could have been influenced by the subsequent GVS pulse. The control experiment with longer interstimulus intervals (4–5 s) confirmed that the CoP and CoG responses evoked by short-duration GVS pulses were prolonged, albeit small. Peak CoP excursions were, on average, 0.10 (SD 0.12), 0.46 (SD 0.29), and 1.45 mm (SD 1.46) from the averaged neutral position for peaks 1, 2, and 3, respectively. Latencies of the three CoP peaks occurred at 122 (SD 15), 476 (SD 83), and 1,454 ms (SD 432) following the GVS onset. Peak CoG displacement evoked by the GVS was, on average, 0.93 mm (SD 1.09) from the averaged neutral position and occurred 1,515 ms (SD 708) after the short-duration GVS pulse (the CoG response returned to baseline  $\sim 3$  s after the GVS pulse onset). The spatial and temporal characteristics of the balance responses were similar, irrespective of the interstimulus interval used (multiple  $t$ -tests:  $P$  values  $> 0.05$ ; only the latency of the second CoP peak occurred later with longer interstimulus intervals:  $P < 0.05$ ). This validates the use of shorter interstimulus intervals in the present study for the subsequent analyses.

**Muscle responses sorted by iEMG.** When the GVS-evoked muscle responses were sorted based on the magnitude of background EMG, the peak-to-peak amplitude of the reflexes elicited in Sol and TA were modulated (significant main effect

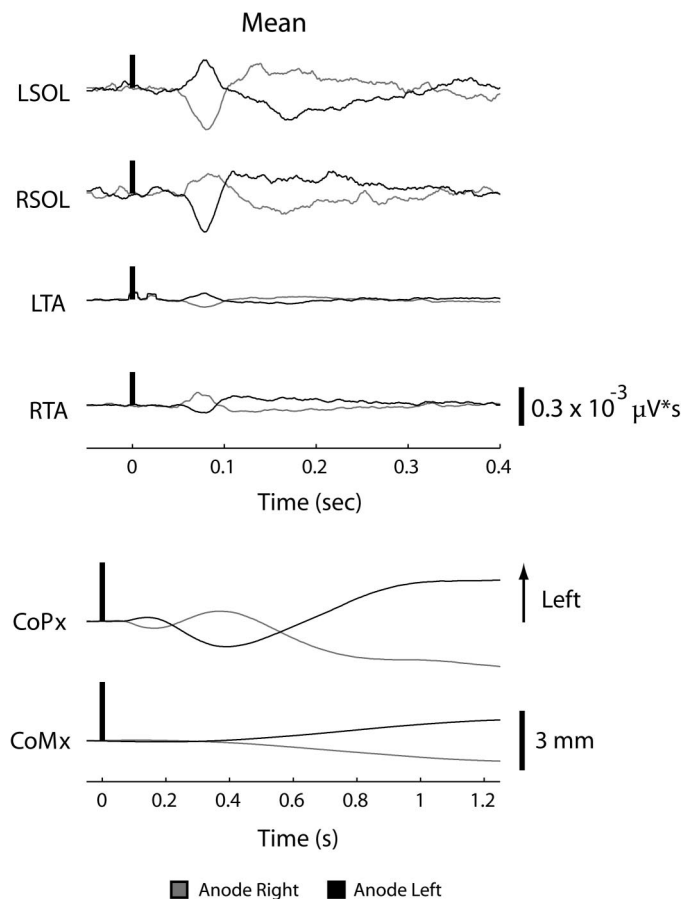


Fig. 1. Mean ( $n = 512$ ) electromyographic (EMG) responses from the left soleus (LSol), right soleus (RSol), left tibialis anterior (LTA), and right tibialis anterior (RTA) muscles; center of pressure in the mediolateral axis (CoPx), and estimated center of gravity in the mediolateral axis (CoGx) from a single subject. The vertical solid bar represents the galvanic vestibular stimulation (GVS). All EMG responses have been artificially aligned to zero. Note: the time axes for the EMG and CoP/CoG responses are different.



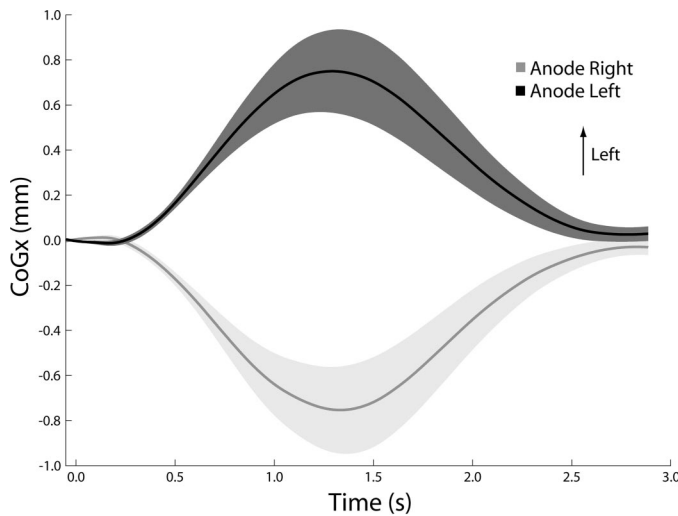


Fig. 2. Mean CoGx averaged across subjects. The shaded areas represent 1 SE above and below the average. Both CoG responses have been artificially aligned to zero.

for all muscles, multiple  $P < 0.05$ ; Fig. 3A, Table 1). The magnitude of Sol and TA reflexes increased when background EMG increased from  $iEMG_{\min}$  to  $iEMG_{\text{med}}$  to  $iEMG_{\max}$  (Fig. 3B). Post hoc tests revealed that the peak-to-peak amplitude for  $iEMG_{\min}$  was smaller than  $iEMG_{\max}$  for all muscles ( $P < 0.05$ ), and  $iEMG_{\text{med}}$  was smaller than  $iEMG_{\max}$  for right Sol and bilateral TA ( $P < 0.05$ ).

**Muscle responses sorted by CoG (with background iEMG as covariate).** Oscillations of the estimated projection of CoG altered the peak-to-peak amplitude of the GVS-evoked muscle responses (Fig. 4A; Table 2). In the AP axis, background EMG was significantly associated with the peak-to-peak amplitude of the muscle responses for the right Sol ( $F = 10.20$ ,  $P < 0.05$ ) and the right TA ( $F = 4.36$ ,  $P < 0.05$ ). Independent of the modulations associated with background EMG, anterior CoG positions increased reflex amplitude in the left and right Sol ( $F = 12.24$ ,  $P < 0.05$ ;  $F = 14.21$ ,  $P < 0.05$ , respectively), but decreased reflex amplitude in left and right TA ( $F = 5.88$ ,  $P < 0.05$ ;  $F = 10.12$ ,  $P < 0.05$ , respectively) (Fig. 4B). On average, the magnitudes of positional shifts of the CoG (related to natural sway) were 13.2 (SD 4.7) and 12.6 mm (SD 4.4) for anterior and posterior displacements, respectively, from a relative center position.

In the ML axis, background EMG was not significantly associated with the peak-to-peak reflex amplitude (multiple  $P > 0.05$ ). In contrast, right shifts in CoG position increased reflex amplitude in right TA, while left CoG positional shifts decreased reflex amplitude in this muscle ( $F = 8.08$ ,  $P < 0.05$ ; Fig. 4A) [the opposite was observed for left TA ( $F = 3.02$ ,  $P = 0.057$ ); Fig. 4B]. On average, the magnitudes of positional shifts of the CoG (related to natural sway) were 8.1 (SD 3.0) and 8.4 mm (SD 4.7) for right and left displacements, respectively, from a relative center position.

## DISCUSSION

The aims of the present experiment were to examine the balance responses evoked by short-duration GVS, as well as the modulations of the muscle responses by the body oscillations occurring as subjects maintain balance. The present

results showed that 1) short-duration GVS applied to standing volunteers evoked well-defined, prolonged balance responses, and 2) the amplitude of the GVS-evoked muscle responses was modulated by both the background activation of the recorded muscle and the estimated position of the subjects' CoG. These two main findings support our initial hypotheses and are discussed further in the following text.

**Prolonged balance responses evoked by short-duration GVS.** The first important finding of the present experiment was the prolonged biomechanical responses generated by short-duration GVS pulses (20 ms). The short-duration GVS stimuli used in the present study evoked well-defined triphasic CoP and monophasic CoG responses.

The onset latencies of the first and third CoP components occurred at 70 and 554 ms and were directed toward the anode. The second CoP component occurred 208 ms after the onset of

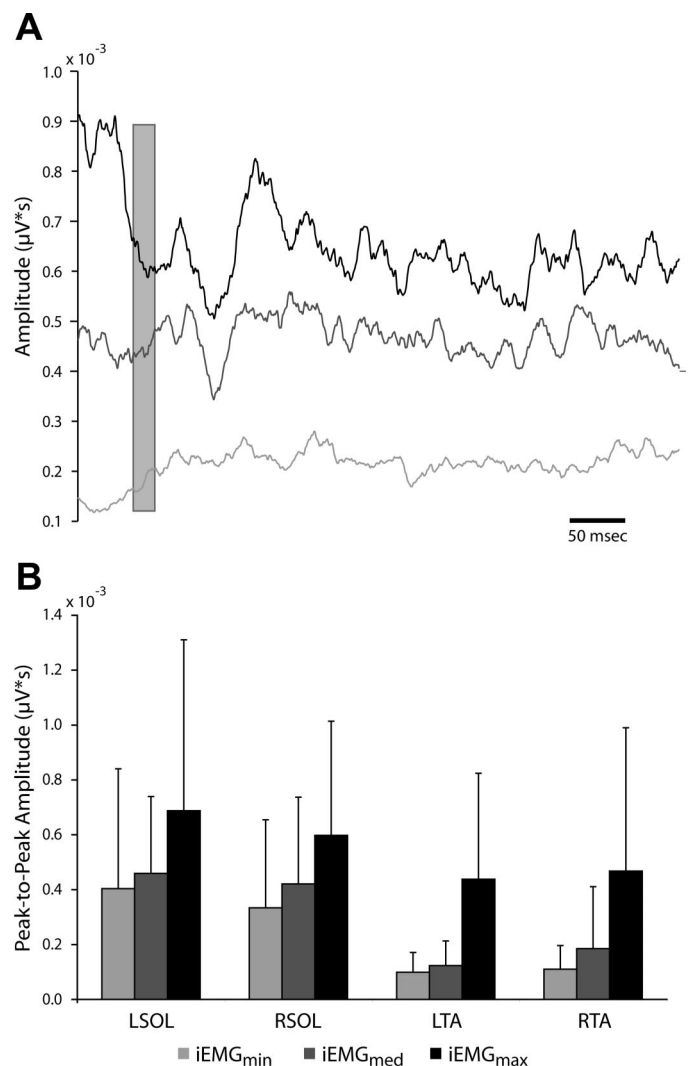


Fig. 3. A: mean EMG responses ( $n = 60$  per condition) of the LTA that are categorized by background muscle activity from a single subject. The shaded gray bar represents the GVS stimulation. The light gray trace represents minimal background muscle activity ( $iEMG_{\min}$ ), the dark gray trace represents median muscle activity ( $iEMG_{\text{med}}$ ), and the black trace represents maximal background muscle activity ( $iEMG_{\max}$ ). B: grand mean ( $n = 12$ ) of the peak-to-peak amplitudes from all four muscles for all subjects specified by iEMG. The vertical lines represent 1 SD away from the mean value.

Table 1. Peak-to-peak amplitudes from GVS-evoked muscle responses sorted by background muscle activity

	LSol	RSol	LTA	RTA
iEMG <sub>min</sub>	0.00040 (0.00044)	0.00033 (0.00032)	0.00010 (0.00007)	0.00011 (0.00009)
iEMG <sub>med</sub>	0.00046 (0.00028)	0.00042 (0.00032)	0.00012 (0.00009)	0.00019 (0.00023)
iEMG <sub>max</sub>	0.00069 (0.00062)	0.00060 (0.00042)	0.00044 (0.00039)	0.00047 (0.00052)

Values are mean (SD) peak-to-peak amplitudes (in  $\mu V \cdot s$ ) from the galvanic vestibular stimulation (GVS)-evoked responses in the left soleus (LSol), right soleus (RSol), left tibialis anterior (LTA), and right tibialis anterior (RTA) sorted by background muscle activity. iEMG<sub>min</sub>, iEMG<sub>med</sub>, iEMG<sub>max</sub>: minimal, median, and maximal integrated electromyography, respectively. GVS anode left and GVS anode right conditions have been combined to calculate the mean values (SD).

the GVS stimulus and was directed toward the cathode. Previous authors observed biphasic CoP responses using long-duration GVS pulses ( $>1$ -s stimuli), with the larger, second response directed toward the anode (8, 24). The polarity and timing of the first and second CoP components observed by these authors correspond to the characteristics of the second and third CoP components observed here. This might suggest that the first CoP component could have been present but too small to be observed in these previous studies. Indeed, Njio-kiktjen and Folkerts (27) reported triphasic CoP responses to

long-duration GVS stimuli but mentioned that the first component was not always present.

In addition to the observed CoP responses, a prolonged monophasic CoG response was evoked by short-duration GVS pulses: it peaked at  $\sim 1$  s after the GVS pulse and lasted  $\sim 3$  s. Hence, the CoG-evoked response by short-duration GVS was longer than the interstimulus intervals used in the current protocol (0.8–1.3 s). As showed by the control experiment, these short interstimulus intervals did not influence the amplitude or duration of the balance responses observed, probably

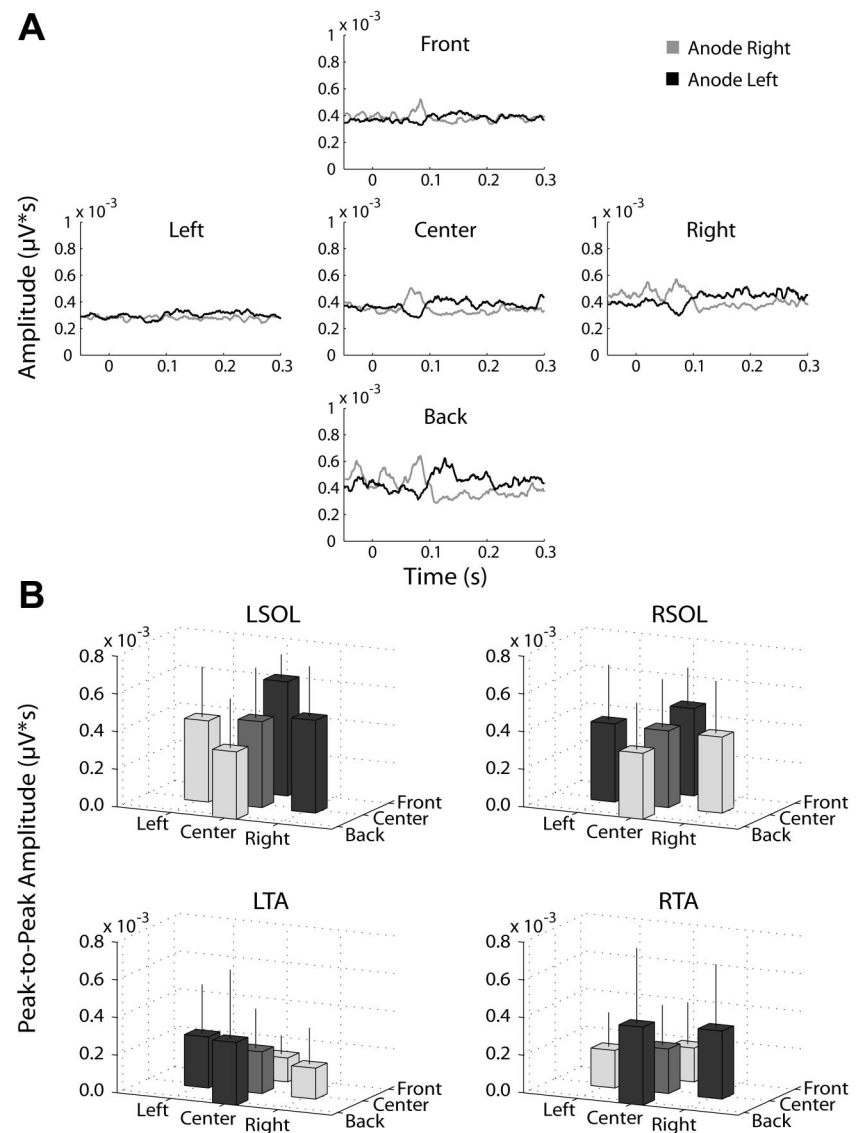


Fig. 4. A: mean GVS-evoked EMG responses ( $n = 60$  per condition) of the RTA sorted by CoG position from a single subject. Time zero on the horizontal axis represents the onset of the GVS stimulation. Note that the modulation of the GVS-evoked muscle responses when the CoG position shifted along the mediolateral axis was relatively independent of the amplitude of background EMG (see RESULTS). B: grand mean ( $n = 12$ ) of the peak-to-peak amplitudes from all four muscles for all subjects in the specified CoG positions. The vertical lines represent 1 SD away from the mean value. The three shades of gray represent the CoG positions with the smallest (lightest) to largest (darkest) peak-to-peak amplitudes. Note that reflex amplitude modulation is partly explained by changes in background EMG activity (mainly for the antero-posterior axis; see RESULTS).

Table 2. Peak-to-peak amplitudes from GVS-evoked muscle responses sorted by center of gravity position

	LSol	RSol	LTA	RTA
Back	0.00036 (0.00027)	0.00035 (0.00025)	0.00033 (0.00037)	0.00041 (0.00041)
Center	0.00046 (0.00030)	0.00043 (0.00026)	0.00015 (0.00012)	0.00025 (0.00026)
Front	0.00061 (0.00028)	0.00046 (0.00024)	0.00013 (0.00008)	0.00018 (0.00015)
Left	0.00043 (0.00027)	0.00041 (0.00030)	0.00027 (0.00026)	0.00020 (0.00019)
Center	0.00046 (0.00027)	0.00041 (0.00026)	0.00022 (0.00021)	0.00024 (0.00022)
Right	0.00049 (0.00027)	0.00040 (0.00028)	0.00016 (0.00020)	0.00036 (0.00034)

Values are mean (SD) peak-to-peak amplitudes ( $\mu\text{V} \cdot \text{s}$ ) from the GVS-evoked responses in the LSol, RSol, LTA, and RTA sorted by center of gravity position. GVS anode left and GVS anode right conditions have been combined to calculate the mean values (SD).

because of the random presentation of the polarity of the vestibular stimuli. The monophasic CoG response contrasted with the triphasic CoP response. This is likely a consequence of the CoG containing mostly the low frequencies of the CoP signal and the short duration of the initial CoP oscillations. Brief (20 ms) vestibular stimuli evoked prolonged balance responses, despite it being impossible to identify these responses visually following individual pulses. Prolonged motor responses following brief GVS pulses have been observed for the human eye system (2). Vestibuloocular reflexes evoked by a 100-ms GVS pulse peaked  $\sim 100$  ms after the onset of the pulse, but GVS-evoked eye movements lasted over 1 s (2).

Although well-defined, robust, and prolonged, the CoP and CoG responses evoked by 20-ms, 4-mA GVS pulses were small (late anode CoP component: 1.7 mm; CoG response: 0.8 mm) compared with the sway responses evoked by 4,000-ms, 0.7-mA stimuli [late-anode CoP component: 20–25 mm from the neutral position (8)]. In fact, the balance responses evoked by brief vestibular stimuli are hidden within the normal oscillations occurring while subjects maintain balance. Despite their small amplitude, it is important to acknowledge that short-duration GVS pulses do not only elicit vestibulo-motor responses, but also evoke associated balance responses. Hence, such stimulation protocol is not suitable to distinguish the vestibulo-motor responses from the balance responses in healthy or patient population, nor does it help in understanding how, or if, these two components of the GVS-evoked response are linked. Stochastic vestibular stimulation may be better suited to achieve these objectives, but this remains to be properly examined (6, 22).

*Biphasic vestibulo-motor responses evoked by short-duration GVS.* We observed biphasic responses in bilateral Sol and TA muscles to short-duration GVS stimuli when the subjects were looking forward. Previous authors have reported biphasic EMG responses in the Sol muscle with the subjects' heads turned to the side (1, 4, 39, 40). The short duration of the stimuli did not influence the temporal characteristics of the vestibulo-motor responses; we observed muscular responses similar to those previously described for prolonged and brief stimuli. This suggests that brief vestibular stimuli (20 ms) only evoke a muscular response at the onset of the stimulus. The initial facilitation or inhibition of muscle activity (depending on the electrode configuration) was observed  $\sim 60$  ms after the onset of the GVS perturbation, with a change in polarity occurring  $\sim 35$  ms later. In addition, opposite muscle response polarities were seen between bilateral muscles, which supports previous observations in Sol, gastrocnemius, and hip abductors with the head facing forward (8). The coactivation of Sol and TA to binaural, bipolar vestibular stimuli when the head is

forward is difficult to explain with respect to the direction of the balance response. The main line of action of these muscles is in the AP direction, whereas the direction of the balance response to the vestibular stimulus used here is in the ML direction. It is possible that coactivation of the Sol and TA is required to maintain AP stability but allow the whole body to sway in the ML direction in response to vestibular stimuli with the head forward. However, the possible association between the muscle and balance responses requires further investigation.

*Modulations of the GVS-evoked muscle responses.* During natural upright stance, we observed that background muscle activity influenced the amplitude of the vestibulo-motor response. The peak-to-peak amplitude of the Sol and TA reflexes increased when the vestibular stimulus was delivered at moments of larger background EMG activity in the respective muscles. These observations are in accordance with general reflex scalability with background activity (25, 40) and with previous reports instructing subjects to lean forward when recording the reflexes in the Sol (4, 31, 38, 39) or to stand on an inclined surface for the TA muscles (9). Another possible explanation for these observations is the nonuniform projection of the vestibular volley to lower limb motor units. In the cat, electrical stimulation of Deiters' nucleus preferentially influenced type FF motoneurons of the triceps surae ( $2.6\times$  greater input) compared with type S motoneurons (41). The results from the present study could suggest that higher threshold motor units recruited during times of larger background muscle activity could be influenced to a greater extent by the descending vestibular volley than the lower threshold motor units (16, 20).

Vestibulo-motor responses were also modulated by shifts in the position of the CoG occurring during upright stance. AP shifts in CoG position for all four muscles and ML shifts in CoG position for the TA muscles generated changes in the magnitude of the GVS-evoked response. Modulations with CoG position in the AP axis were expected for the Sol and TA muscles due to the muscles' main line of action in the AP axis. Additionally, modulations with the CoG position in the ML axis could be explained by the small ML component in the line of action of TA.

Modulations of the GVS-evoked muscle responses (independent of background EMG) in the AP and ML directions could be consistent with small modulations in vestibulomotor responses due to posture-dependent gating of balance responses (34). A likely source of vestibular modulations is the interaction between the somatosensory afferents from the lower limbs activated by the balance task and the GVS-evoked vestibular volleys. Supporting this view, Marsden et al. (23, 24) showed that changes in limb loading accomplished through asymmetric



stance alters the lateral ground reaction forces elicited by GVS perturbations. These authors argued that somatosensory receptors (from skin, muscle, tendon, or joint) could have contributed to the load-related changes in the GVS-evoked responses. Another observation worth mentioning is the load-induced reduction in the amplitude of the GVS-evoked muscle responses in Sol reported by Iles and Pisini (14). Although the exact neural pathways responsible for these modulations remain unclear, Ia presynaptic and Ib inhibitory pathways could be potential candidates, since the descending GVS-evoked vestibular drive is suspected to interact with them (14, 16–18) and that H reflexes are dynamically modulated during quiet stance (35). Another possible source of vestibulomotor response modulation is a relative change in the weighting of vestibular information based on the position of the CoG. Modulation in weighting of vestibular information has been demonstrated in locomotion for humans, and it seems likely that the same phenomenon could occur in quiet standing (3). More eccentric CoG positions are associated with eccentric head positions with respect to the base of support, which could lead to larger or smaller central weighting of vestibular information.

In the present study, we used a single-force plate to estimate movements of the center of mass. Although this technique is appropriate and gives a good estimate of CoG position (19, 42), it assumes that the body sways similarly to an inverted pendulum. This assumption could be violated when subjects are exposed to unnatural external perturbations, such as GVS. The modulations of the GVS-evoked muscle responses in the ML direction suggest that load is an important factor and would require dual plates to adequately quantify load in future studies. The present study only investigated the influence of CoG position on the vestibulomotor responses, but it is possible that CoG velocity and acceleration also contribute to the organization of the vestibulomotor responses. Furthermore, other techniques, such as coherence and stochastic vestibular stimulation (6), may provide a better estimate of loading effects, independent of background EMG due to the normalization of the output responses by each of the inputs.

The results from the present study have shown the possibility to evoke balance and muscle responses in both the Sol and TA in standing humans looking straight ahead using short-duration GVS. We have further shown that vestibulo-motor responses are modulated, depending on the position of the subjects' CoG during quiet stance. Since balance responses may influence motor output, the presence of a prolonged balance response to short-duration vestibular stimuli is important to recognize when using this technique to elicit vestibulomotor responses in healthy individuals and various patient populations.

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