The purpose of this study was to investigate whether application of bipolar galvanic vestibular stimulation (GVS) would influence the common modulation of motor unit discharge rate in bilateral soleus muscles during quiet standing. Soleus motor unit activity was recorded with fine wire electrodes in each leg. Subjects stood, with eyes closed, on two adjacent force platforms to record postural sway with the head facing straight ahead, turned to right, or turned left. Subjects also swayed voluntarily without GVS to the same position as evoked during the GVS. There was no difference in the common drive to bilateral soleus motoneurons during quiet standing and voluntary sway tasks. Common drive was significantly lower during right cathode GVS with the head straight or turned to the right. These results demonstrate that manipulation of vestibular afferent input influences the common modulation of bilateral soleus motor unit pairs during quiet standing.

Keywords: common drive, motor unit, muscle, posture, galvanic vestibular stimulation, human

The control of standing posture requires the integration of feedback from visual, somatosensory, and vestibular systems, with coordinated activation of postural musculature to maintain an upright stance. The control of quiet standing is predominantly a task that requires bilateral activation of the ankle plantarflexors (Winter et al., 1993). For instance, Gatev et al. (1999) and Masani et al. (2003) have shown that the ankle plantarflexors were highly correlated to an anterior-posterior (AP) directional sway during quiet standing. Of this musculature, it is believed that the soleus muscle plays a dominant role in adjusting the anterior-posterior center of pressure (AP-COP) because the gastrocnemius has been shown to be less active in humans in quiet standing (Duyssens et al., 1991).

In keeping with the important role of soleus in maintaining quiet stance, Mochizuki and colleagues (2005, 2006, 2007) performed a series of studies to investigate the control of motor units in the soleus muscles of both legs. While
synchronization of motor units was low between soleus muscles of each leg in standing tasks (Mochizuki, Ivanova & Garland, 2005), common drive was evident (Mochizuki et al., 2006; Mochizuki, Ivanova & Garland, 2007). ‘Common drive’ is a term describing when the firing rates of concurrently active motor units tend to modulate in unison (De Luca et al., 1982; De Luca & Erim, 1994; Semmler & Nordstrom, 1998) and is thought to reflect common inputs to the motoneuron pool. Common drive to motoneurons may provide a level of simplification in the organization of the inputs to the motoneuron pool; that is, common inputs rather than separate command signals may control the motor unit discharge rate (De Luca & Erim, 1994).

The source of the common inputs to motor units in the right and left soleus muscles during standing is not completely understood. Descending corticospinal inputs are one possibility but this is less likely a source of input in the lower extremity where the corticospinal projections are weaker than in the upper extremity (Brouwer & Ashby, 1990). Furthermore, Mochizuki, Ivanova & Garland (2007) found that common drive was less when subjects swayed voluntarily as opposed to natural sway, suggesting that voluntary corticospinal projections were not a strong source of common input.

One source of common input to soleus muscles during standing that has not been investigated hitherto is vestibular input. Motoneurons of the soleus muscle receive input from the vestibulospinal tract (Grillner, Hongo & Lund, 1970). Shinoda et al. (1986) found that several axons originating in the lateral vestibulospinal tract of the cat project unilaterally and bilaterally to soleus motoneurons. Therefore, in the current study, we sought to investigate whether manipulation of vestibular afferent inputs using galvanic vestibular stimulation (GVS) would influence the common modulation of motor unit discharge bilaterally during quiet standing.

Bipolar GVS slightly increases the discharge rate of vestibular afferents on the side of the cathode and decreases it on the side of the anode (Goldberg, Smith & Fernandez, 1984). Studies on humans during standing have demonstrated that bipolar GVS induces a postural sway toward the side of the anode to compensate for a false perception of sway to the side of the cathode (Wardman, Taylor & Fitzpatrick, 2003; Fitzpatrick & Day, 2004). In the current study, bipolar GVS was used to activate the vestibular afferents to test the hypothesis that altering the vestibular afferent firing would change the common modulation of motor units in the soleus muscle.

Methods

Subjects

Ten subjects (9 males and 1 female; age 26.6 ± 5.6 yr), all right-hand dominant, with no known neuromuscular disorders participated in this study after providing informed written consent. Not all subjects performed all the conditions. The Research Ethics Board for Health Sciences Research Involving Human Subjects at The University of Western Ontario approved this study.

Experimental Protocol

Galvanic vestibular stimulation was applied with silver-silver chloride electrodes (Ag-AgCl; 18 mm diameter) with gel-infused pads that were affixed to the skin
over the mastoid processes. The GVS passes a direct current of approximately 1 mA between the mastoid processes. The stimulation was delivered with a Grass S88 constant voltage electrical stimulator in continuous mode at a voltage of 400 V equipped with a stimulus isolation unit SIU5 and a constant current unit CCU1 (Grass Medical Instruments, Quincy, MA). The latter was used to convert the voltage to constant current and to control the polarity and intensity of the stimulation. When the cathode was placed on the left mastoid and the anode on the right mastoid, this was called a left cathode GVS. When the polarity was reversed, it was called a right cathode GVS. Subjects sway toward the anode to counteract the false representation of sway induced by activation of the vestibular afferents on the cathodal side. Therefore, the polarity of the stimulation determines the direction that the subjects tend to sway.

Subjects stood with their feet shoulder width apart on adjacent AMTI OR6–6-1000 (Advanced Mechanical Technology, Watertown, MA) force platforms. For the duration of the experiments, subjects stood with their arms hanging loosely at their side. The position of the arms was not changed throughout the experiment.

There were three stimulation conditions, all performed with the eyes closed.

**Condition A.** Five subjects performed the following standing tasks: 1) quiet standing with head straight for 1.5 min; 2) standing with head turned to the right for 1.5 min (prestimulation); 3) standing with head turned right and right cathode GVS turned on for 40 s; 4) standing with head turned to the right for 40 s with no stimulation (poststimulation). The last two tasks were repeated three times. The right cathode GVS with head turned to the right resulted in predominantly anterior postural sway. At the end (Task 5), subjects were asked to voluntarily sway forward slowly until they reached a body posture that corresponded to the average AP-COP position seen during the stimulation task (based on verbal instruction) and they maintained this position for one minute. This voluntary static forward sway task was performed to determine if the change in the common drive was related solely to the change in AP-COP position produced during the stimulation or was influenced by the GVS itself.

**Condition B.** Six subjects repeated the above tasks (including the voluntary sway) with the head turned to the left with and without left cathode GVS.

**Condition C.** Seven subjects performed the following standing tasks with their head straight: 1) quiet standing with no stimulation for 1.5 min; 2) standing with either right cathode GVS or left cathode GVS for 40 s (Tasks 2 and 4). The stimulation was repeated three times for each polarity and the order of polarity was selected at random. Following each bout of stimulation, subjects stood quietly without stimulation for 40 s (Tasks 3 and 5).

The order of the conditions (A, B, C) was randomized for each subject. Two subjects performed all three conditions and eight subjects did not. The reason for including the head turned conditions was to ensure that an anterior sway is caused by GVS, because the soleus motor units control the AP sway. Predominantly medial-lateral sway was caused by GVS with the head straight.

**Data Acquisition**

**Electromyography.** Surface electromyographic (EMG) electrodes were placed on the midline of the soleus (Sol) ~2 cm distal to the belly of the gastrocnemius,
on gastrocnemius medialis (GM) muscle belly, and tibialis anterior (TA) belly ~5 cm distal to the tibial tuberosity. The surface EMG was recorded using bipolar Ag-AgCl electrodes (8 mm diam, 20-mm interelectrode distance). The EMG signals were amplified, filtered (10–1,000 Hz), sampled at 2,500 Hz, and saved for off-line analysis.

Single motor unit potentials were recorded intramuscularly using three 50 μm stainless steel fine wires (California Fine Wire, Grover Beach, CA) in a bipolar configuration. The wires were fastened together at the tip using ethyl cyanoacrylate adhesive and then passed through a disposable 25-gauge, 2-cm-long hypodermic needle (Becton Dickinson). Cutting the tips of the three wires exposed the terminal ends. Three wires allowed for the possibility of three different bipolar electrode configurations. A small hook at the terminal end of the fine wire electrode held the electrode in place after the needle was removed. All wire electrodes and hypodermic needles were autoclaved (AMSCO Autoclave) for 45 min at 120 °C before use.

Two fine wire electrodes were inserted in each leg at approximately 15 cm superior to the lateral malleolus in the lateral side of each soleus muscle. Before any recording, the position of the electrodes was adjusted, as necessary, to record single motor unit activity on both channels. Once the best electrode positions were found, the electrodes were not moved again and testing began. During these experiments, normally one motor unit could be analyzed per electrode; therefore, one motor unit pair was analyzed typically in each experiment. The intramuscular EMG signals were amplified, filtered (10–10,000Hz), sampled at 25,000Hz and saved for off-line analysis.

**Force Platform Measures.** Three signals from each force platform, moments of the forces in sagittal (Mx) and frontal (My) planes and the vertical ground reaction force (Fz) were sampled at 500 Hz. Calculation of the AP-COP was performed on-line to determine the AP-COP position during the stimulation in Conditions A and B. The average AP-COP position during the stimulation tasks was provided to the subjects verbally during the voluntary sway task.

**Data Analysis**

All signals were digitized on-line using a 16-bit acquisition system (Power 1401 with Spike2 software, Cambridge Electronic Design, Cambridge, UK) and stored on a computer for off-line analysis.

**Common Drive.** Single motor units were categorized off-line using a template-matching algorithm (Spike2, version 6.03, Cambridge Electronic Design) that classified motor units according to their amplitude and shape. Manual inspection of the motor unit action potential train followed the automatic classification to ensure accuracy by removing any action potentials that could not be identified with absolute certainty.

The motor unit spike trains were divided into 5–10 s epochs, in which the interspike intervals (ISIs) within the epochs were between 50 ms and 2 × mean ISI (calculated over 20 s of data). If a section of the data within an epoch did not meet these criteria, the entire epoch for both legs was discarded and the next 5–10 s epoch immediately after the discarded section was assessed. ISIs below the lower limit (<50 ms) were considered to result potentially from misclassified spikes,
while the upper limit of $2 \times \text{mean ISI}$ was used as a way of controlling for missed spikes or derecruitment of the motor unit (Andreassen & Rosenfalck, 1980). This process was necessary because any gaps or extra spikes cause erroneous deviations in the instantaneous firing rate.

The common drive analysis was implemented using Spike2. The motor unit action potential train was converted to a continuous signal representing the smoothed firing rate of the motor unit using “event-to-waveform” built-in function. This was completed by applying a built-in 600 ms wide symmetrical raised cosine bell function sampled at 1,000 Hz to each classified action potential, centered to its firing time. A representation of the firing rate over the duration of the epoch was produced by the series of interpolated raised cosine bells. The resulting signals were high-pass filtered with a $-3$ dB low-frequency cutoff of 0.75 Hz before cross correlation.

The common drive for bilateral motor unit pairs was calculated using the built-in “waveform correlation” function for epochs that met the aforementioned criteria. The waveform correlation function was used to correlate the smoothed firing rate of the motor units, one from the left and other from right leg. The common drive coefficient was determined by taking the maximal value of the function lying within $\pm 50$ ms of time $= 0$ ms. The reported common drive value for each motor unit pair was the average of all epochs in that Condition. The number of epochs used for each average common drive value ranged from 3 to 12. The length of the epoch had no influence on the common drive coefficient, as illustrated by the Pearson correlation coefficient of $r = -0.03 \pm 0.15$ between the length of the epoch and the common drive coefficient.

**Center of Pressure.** The center of pressure displacement in the AP direction was calculated using the vertical ground reaction force (Fz) and the moment of force in the sagittal plane (Mx) as measured by the force platforms such that $\text{AP-COP} = \frac{\text{Mx}}{\text{Fz}}$. The change in the position of AP-COP during stimulation and voluntary sway conditions was computed in the following way. The average AP-COP displacement was determined for each epoch with common drive values. The baseline position of the AP-COP was subtracted from the AP-COP for each epoch in the stimulation and voluntary tasks to establish the change. The baseline was determined by averaging AP-COP displacement in the epochs preceding each stimulation task. If there were fewer than 4 epochs before the stimulations, then the AP-COP was averaged over 20 s before the stimulation. The AP-COP target position for voluntary sway was determined by averaging the AP-COP positions for all three stimulation tasks in the condition. These measurements were only taken for Conditions A and B because they produced a predominantly AP sway.

The standard deviation of the COP was calculated for tasks with no stimulation (10–20 s periods) and during the time periods when the stimulation was turned on and the intensity gradually increased (ON period) and when the stimulation intensity was gradually decreased and turned off (OFF period). The variability of COP was used to determine if the stimulation caused an imbalance to quiet standing because the GVS could not be calibrated directly.

**Surface EMG.** The root mean square (RMS) of the surface EMG was measured for all tasks in 30s epochs. For tasks that lasted 1.5 min (quiet standing with head straight and head turned, and voluntary tasks), three epochs at the beginning,
middle and end of the task were averaged. For the stimulation and poststimulation
tasks, measurement began 5 s after the ON/OFF of GVS and the 3 repetitions were
averaged. The RMS EMG from the quiet standing with head straight task was used
to normalize all subsequent tasks in the experiment.

**Statistical Analysis**

Statistical analysis was performed using SPSS for Windows v. 13.0 (SPSS, Chicago,
IL). The Shapiro-Wilk normality test was used to determine whether the common
drive coefficients, motor unit discharge rate, AP-COP data and RMS EMG were
normally distributed. The common drive coefficient data did not meet the normality
requirements to use parametric statistics. Therefore, Kruskal-Wallis H tests were
used to determine whether the common drive coefficient differed among stimula-
tion and no stimulation tasks in the three conditions. When these differences were
significant, post hoc Mann-Whitney \( U \) tests were used to ascertain which tasks
differed significantly from prestimulation. Two-way ANOVAs were performed to
evaluate the differences in motor unit firing rate, with tasks and legs as factors, for
each condition. Two-way repeated-measures ANOVAs (factors, leg and stimula-
tion (pre, ON/OFF) as the repeated factor) were used to evaluate the difference
in the standard deviation of the COP in the AP (all conditions) and medial-lateral
(condition C) directions between prestimulation and ON/OFF stimulation periods,
as well as to compare the AP-COP displacement change in stimulation and volun-
tary tasks. A series of one-way ANOVAs was used to determine any differences
in RMS EMG across muscles for each task; when no significant differences were
found, one-way repeated-measures ANOVA was used to compare the pooled RMS
EMG across tasks. Tukey’s post hoc tests were used when there was a significant
task effect. Normally distributed data are presented as mean ± SD (SD); for not
normally distributed data, a median and interquartile range was used. \( p ≤ .05 \) was
used as the requirement for statistical significance.

**Results**

**Firing Rate of Motor Units**

The firing rate of motor units and the number of motor units in each condition (A,
head right; B, head left; C, head straight) and task are presented in Table 1. There
was no difference in the firing rate of motor units between legs in all conditions
(Condition A: \( p = .31 \); Condition B: \( p = .72 \); Condition C: \( p = .25 \)). Galvanic ves-
tibular stimulation also had no significant effect on the firing rates of the motor
units, as there was no difference across tasks in all conditions (Condition A: \( p =
.62 \); Condition B: \( p = .94 \); Condition C: \( p = .63 \)). In several cases, a motor unit pair
was present in two or all three conditions. In addition, a motor unit pair within a
condition may not have been present in all the tasks.

**GVS and Common Drive**

In Conditions A and B, the cathode was positioned posteriorly to ensure anterior
sway. Figure 1 illustrates the motor unit discharge and the changes in com-
mon drive during right cathode GVS in Condition A in a representative subject. In
Condition A, a significant change in common drive was evident with right cathode GVS ($p = .05$). Post hoc analysis revealed that, in comparison with prestimulation values, the common drive coefficient was significantly different during right cathode GVS ($p = .03$) but not during poststimulation ($p = .41$) or voluntary sway ($p = .39$) tasks (Figure 2a). The lower common drive with right cathode GVS cannot be explained by an order effect because the common drive after the stimulation returned to the prestimulation level. In Condition B (head turned left), there was no significant change in the common drive across tasks ($p = .85$; Figure 2a). These findings revealed that simply turning the head, or voluntarily holding a slight static forward posture did not affect the common drive.

In Condition C, during quiet standing with the head straight, the common drive coefficient decreased significantly from prestimulation levels ($p = .02$) only with the application of right cathode GVS (Figure 2b). The common drive in the poststimulation task did not return completely to the prestimulation level and remained slightly lower ($p = .048$). Similar to Condition B with the head turned left, there was no significant change in the common drive from left cathode GVS across tasks ($p = .68$; Figure 2b).

**Table 1 Motor Unit Firing Rate for All Tasks and Conditions**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Task</th>
<th>Firing Rate (Hz)</th>
<th>Number of MUs</th>
<th>MU pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Right MU</td>
<td>Left MU</td>
<td></td>
</tr>
<tr>
<td>A 1. Head Straight</td>
<td>8.5 ± 1.6</td>
<td>7.4 ± 1.7</td>
<td>11</td>
<td>8</td>
</tr>
<tr>
<td>Head 2. Prestim</td>
<td>7.6 ± 1.1</td>
<td>7.4 ± 0.9</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>Right 3. Right stim</td>
<td>8.2 ± 1.3</td>
<td>7.5 ± 0.7</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td>4. Post right stim</td>
<td>8.3 ± 1.3</td>
<td>7.3 ± 0.6</td>
<td>12</td>
<td>7</td>
</tr>
<tr>
<td>5. Voluntary sway</td>
<td>7.6 ± 0.3</td>
<td>7.3 ± 1.1</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>B 1. Head Straight</td>
<td>7.6 ± 2.1</td>
<td>7.7 ± 1.7</td>
<td>16</td>
<td>10</td>
</tr>
<tr>
<td>Head 2. Prestim</td>
<td>7.5 ± 2.0</td>
<td>7.7 ± 0.9</td>
<td>16</td>
<td>11</td>
</tr>
<tr>
<td>Left 3. Left stim</td>
<td>7.8 ± 2.0</td>
<td>7.9 ± 1.4</td>
<td>17</td>
<td>12</td>
</tr>
<tr>
<td>4. Post left stim</td>
<td>7.6 ± 1.9</td>
<td>7.5 ± 1.7</td>
<td>17</td>
<td>12</td>
</tr>
<tr>
<td>5. Voluntary sway</td>
<td>7.0 ± 1.8</td>
<td>7.4 ± 2.8</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>C 1. Prestim</td>
<td>8.9 ± 2.3</td>
<td>7.7 ± 0.9</td>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td>Head 2. Right stim</td>
<td>8.2 ± 2.4</td>
<td>7.8 ± 1.0</td>
<td>19</td>
<td>12</td>
</tr>
<tr>
<td>Straight 3. Post right stim</td>
<td>8.2 ± 21.3</td>
<td>7.7 ± 1.0</td>
<td>17</td>
<td>11</td>
</tr>
<tr>
<td>4. Left stim</td>
<td>8.6 ± 2.1</td>
<td>7.9 ± 1.0</td>
<td>20</td>
<td>11</td>
</tr>
<tr>
<td>5. Post left stim</td>
<td>9.4 ± 1.9</td>
<td>8.4 ± 1.3</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>8.6 ± 2.1</td>
<td>7.9 ± 1.0</td>
<td>45</td>
</tr>
</tbody>
</table>

Values presented as means ± SD
Vestibular Inputs and Common Modulation of Bilateral MUs

Figure 1 — Representative data of the effect of right cathode GVS on the common modulations in firing rate of two motor units with the head turned right. Five second epochs from a prestimulation (left) and stimulation (right) task are shown. Recordings of two single motor units (MU), followed in both tasks are presented in the top two rows. MU 1 (black tracings) was recorded from the right soleus muscle. MU 2 (gray tracings) was recorded from the left soleus muscle. Smoothed firing rate of both MUs is in the bottom row. Insets: cross-correlation functions for the prestimulation ($\rho = 0.68$) and stimulation ($\rho = 0.44$) periods.

Center of Pressure and Surface EMG

The galvanic vestibular stimulation produced an anterior sway in both Conditions A and B that was matched with the voluntary sway. There was no significant difference in the AP COP displacement in Task 5 of Condition A (right leg, $0.67 \pm 0.86$ cm; left leg, $0.78 \pm 0.37$ cm) compared with the COP displacements of Task 3 in matching experiments (right leg, $0.64 \pm 0.60$ cm; left leg, $0.76 \pm 0.39$ cm) (leg: $p = .49$; task: $p = .92$). In Condition B, the AP COP displacements also matched the displacements during stimulation task (right leg: $0.99 \pm 0.72$ cm vs. $0.93 \pm 0.53$ cm for voluntary and stimulation, respectively; left leg: $1.09 \pm 0.70$ cm vs. $1.10 \pm 0.42$ cm for voluntary and stimulation, respectively; leg: $p = .24$; task: $p = .85$).

To measure the effectiveness of the galvanic vestibular stimulation, the variability of the COP excursions during ON/OFF periods was compared with that in prestimulation periods (Table 2). There was no effect of leg on the variability of the AP COP in any condition (Condition A: $p = .42$; Condition B: $p = .92$; Condition C: $p = .3$). The standard deviation of the AP COP was increased in all Conditions during the ON/OFF periods (Condition A: $p = .001$; Condition B: $p = .004$; Condition C (right GVS): $p = .009$; Condition C (left GVS): $p = .002$). In addition, in Condition C (head straight), the standard deviation of the medial-lateral COP was increased during the ON/OFF (right GVS: $p = .008$; left GVS: $p = .01$; Table 2).
Figure 2 — Effect of bipolar galvanic vestibular stimulation on common drive with head turned left and right (A) and during head straight tasks (B). A. Common drive coefficients for head left (open circles) and head right (black circles) conditions are presented in the pre-stimulation, stimulation, poststimulation and voluntary tasks. B. Common drive coefficients are presented prestimulation, during stimulation and poststimulation for left cathode (open circles) and right cathode (black circles) GVS. * significantly different from prestimulation. Data are presented as median and interquartile range.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Task</th>
<th>Anterior-posterior</th>
<th>Medial-lateral</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Right Leg</td>
<td>Left Leg</td>
</tr>
<tr>
<td>A. Head Right</td>
<td>Prestim</td>
<td>0.43 ± 0.12</td>
<td>0.49 ± 0.13</td>
</tr>
<tr>
<td></td>
<td>ON/OFF stim</td>
<td>0.68 ± 0.10*</td>
<td>0.71 ± 0.10*</td>
</tr>
<tr>
<td>B. Head Left</td>
<td>Prestim</td>
<td>0.50 ± 0.08</td>
<td>0.50 ± 0.12</td>
</tr>
<tr>
<td></td>
<td>ON/OFF stim</td>
<td>0.80 ± 0.33*</td>
<td>0.79 ± 0.22*</td>
</tr>
<tr>
<td>C. Head Straight</td>
<td>Prestim</td>
<td>0.40 ± 0.14</td>
<td>0.50 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>Right GVS ON/OFF</td>
<td>0.73 ± 0.37*</td>
<td>0.80 ± 0.23*</td>
</tr>
<tr>
<td></td>
<td>Left GVS ON/OFF</td>
<td>0.64 ± 0.25*</td>
<td>0.79 ± 0.29*</td>
</tr>
</tbody>
</table>

Values presented as means ± SD
* significantly different from Prestim; P < 0.05
Another measure of effectiveness of the GVS was evident in the surface EMG of the ankle plantarflexors. There was minimal activation of TA muscles, therefore only the activity of Sol and GM bilaterally was analyzed. Because Sol and GM behaved similarly (one-way ANOVA P values ranged from 0.2 to 0.8), Sol and GM were pooled. In conditions A and B when an anterior sway was evoked, the RMS EMG increased on average by $17 \pm 21\%$ ($p = .02$) and $16 \pm 38\%$ ($p = .02$) during stimulation and voluntary tasks, respectively as compared with quiet standing with head turned. In condition C when a medial-lateral sway was evoked, poststimulation RMS EMG was on average only $4 \pm 7\%$ and $5 \pm 10\%$ higher than prestimulation values, for right cathode GVS and left cathode GVS, respectively ($p = .54$).

Figure 3 illustrates representative data on the change in AP-COP after the stimulation was turned ON and the intensity of the stimulus was gradually increased (between the dashed lines). EMG activity from the gastrocnemius medialis and soleus increased when the AP-COP moved forward. The increase in ankle plantarflexor activity may have served to limit the forward sway induced by the stimulation.

**Discussion**

The results of this study demonstrated that the strength of common modulation of bilateral motor unit pairs was reduced with right cathode GVS, regardless of whether the head was straight or turned to the right. The common modulation of bilateral motor unit firing rates was not influenced by the voluntary sway task.
Although speculative, this study may illustrate a form of vestibular asymmetry in vestibular afferent inputs to the soleus muscles in each leg during standing tasks.

**Vestibular Afferent Input Contribution to Common Drive of Bilateral Soleus Motor Units**

A decrease in the common drive was observed by manipulating the vestibular afferent inputs. The vestibulospinal tract provides excitation to extensor motoneurons in the lumbosacral region of the spinal cord innervating ankle plantarflexor muscles (Grillner, Hongo & Lund, 1970) and bilateral projections from the lateral vestibular nuclei to soleus motoneurons have been observed in the cat (Shinoda, Ohgaki & Futami, 1986). Unilateral caloric stimulation of the vestibular apparatus in humans was shown to produce bilateral triceps surae EMG responses (Mano et al., 1976). These descending bilateral projections may influence the bilateral common modulations in motor unit discharge in the soleus muscle. The reduction in common drive was only evident during right cathode GVS tasks with the head straight and turned right (Figure 2). This raises the possibility of vestibular asymmetry.

The stepping test, first created by Unterberger in 1938 and later modified by Fukuda (1959), was developed as a clinical test aimed at examining vestibulospinal disturbances in patients suffering from unilateral vestibular dysfunction. The angle of rotation was measured following stepping in the same position with eyes closed. In healthy humans, the Fukuda stepping test had a smaller deviation compared with patients (Fukuda, 1959; Reiss & Reiss, 1997b). This deviation was believed to represent the nondominant vestibular side (Previc & Saucedo, 1992; Reiss & Reiss, 1997a; Reiss & Reiss, 1997b). This dominance may be due to the asymmetry in the otolithic system that could originate from the fetal position and according to Previc & Saucedo (1992), was suggested as the main cause of directional deviation. As a follow-up measure, the Fukuda stepping test was conducted in six of the ten participants in the study. Three of the six subjects showed deviation toward the left and the other three deviated toward the right, giving inconclusive results about the role of vestibular dominance in common drive. However, Bonanni & Newton (1998) tested the reliability of the Fukuda stepping test and yielded moderate test-retest reliabilities, below 0.70. Therefore, the Fukuda stepping test may not have been a reliable measure for the purposes of our study.

The unilateral centrifugation test, proposed by Wetzig et al. (1990) is the most current technique used to assess sensitivity and dominance of the utricle. To determine dominance from one or the other utricle, an imbalance in the afferent firing rate should give rise to ocular counter rotation and otolith ocular reflex (Wuyts et al., 2007). Evidence in subjects with normal vestibular function has shown individual asymmetries between right and left otolith afferent signals (Clarke & Engelhorn, 1998; Helling et al., 2006; Wuyts et al., 2007). In addition, Vesterhauge & Kildegaard (1977) indicated that left sided vestibular hypofunction is a normal phenomenon shown in the electronystagmography using caloric excitation. Therefore, it was possible that a left-sided vestibular hypofunction was unable to compensate for the decrease in afferent firing rate during right cathode GVS resulting in a decrease of common modulation in bilateral soleus motor units.

A more recent study by Dieterich et al. (2003) used warm water caloric stimulation while the metabolic activity of the brain was recorded using positron
emission tomography. They demonstrated a right vestibular dominance in the right
cortical hemisphere in right-handed subjects and left vestibular dominance in the
left-handed subjects in the left cortical hemisphere. This finding strengthens the
idea of right vestibular dominance or left-sided vestibular hypofunction playing a
role in the reduced common drive with right GVS in the current study. Although
left-hand dominant subjects did not take part in this study, a decrease in common
drive with left GVS would be predicted.

Common Drive and Postural Sway Profile

Subjects standing quietly demonstrated that the AP modulations of the COP are
similar between both legs (Winter et al., 1993). Mochizuki, Ivanova & Garland (2007)
showed that the common drive coefficient was affected by the position of AP-COP.
The authors found the common drive to be higher during an anterior sway and lower
during a posterior sway. In that study, the AP-COP change was ~2 cm, twice that
of the change (~1 cm) observed in the current study. As a result, when subjects
voluntarily maintained the same AP-COP position as the one induced by the GVS,
the common drive coefficients remained similar to those seen during quiet standing
before and after stimulation. These results suggest that the reduction in common
drive found during right cathode GVS was not solely a function of sway position.

The current study adds to the body of knowledge underlying the common
modulation of motor units during standing. Previously, studies have indicated that
proprioceptive inputs contribute to common drive in the soleus muscles (Mochizuki
et al., 2006). In addition, descending inputs may also contribute to the common
drive of motor units for motor control (Marsden et al., 1999; De Luca & Erim,
2002). The present findings demonstrate that manipulation of the vestibular affer-
ent input influences the common drive of soleus motor unit pairs during standing.

Conclusion

These findings illustrate that manipulating vestibular afferent inputs during standing
influences the common modulation of firing rates of soleus motor unit pairs from
the left and right leg. Although speculative, decreases in the common drive to motor
unit pairs during right cathode GVS may be explained by vestibular dominance.
The significance of these findings provides us with a greater understanding of the
control of motor unit common modulation in standing and strengthens the idea that
common drive has a central nervous system component.

References

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