Subthreshold Vestibular Reflex Effects in Seated Humans Can Contribute to Soleus Activation When Combined With Cutaneous Inputs

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The integration of vestibular and somatosensory information for the control of lower limb musculature remains elusive. To determine whether a subthreshold vestibular input influences the cutaneous evoked response, the isometric EMG activity in the posturally inactive soleus muscles of 13 healthy, seated subjects was collected. Vestibular afferents were activated using galvanic vestibular stimulation (GVS; 1.8–2.5mA, 500ms), while percutaneous electrical stimulation was delivered to the distal tibial nerve (11ms train of 3 × 1.0 ms pulses, 200Hz) to activate foot sole skin afferents. GVS elicited responses in soleus both independently and when combined with cutaneous stimulation. The responses to the combined sensory input showed an interaction between the two sensory modalities to influence muscle activation. Of note is the presence of significant muscle modulation in the combined condition, where subthreshold vestibular inputs altered the outcome of the cutaneous reflex response. This finding has implications for individuals with sensory deficiency. In the case of an absent or deficient sensory modality, balance protective reflexes to maintain postural equilibrium may be enhanced with targeted sensory augmentation.

Keywords: vestibular, somatosensory, sensory integration, human

Vestibular and cutaneous inputs contribute to the ability of bipeds to maintain body orientation, verticality and balance (Horak, Shupert, Dietz & Horstmann, 1994; Pozzo, Levik & Berthoz, 1995; Bent, Inglis & McFadyen, 2002; Day, Severac-Cauquil, Bartolomei, Pastor & Lyon, 1997; Day & Cole, 2002; Lund & Broberg, 1983; Roll, Kavounoudias & Roll, 2002; Magnusson, Enbom, Johansson & Pyykko, 1990). It is well recognized that the vestibular system facilitates orientation of the body in space through integration with somatosensory input (Horak, Shupert, Dietz & Horstmann, 1994; Pozzo, Levik & Berthoz, 1995). Independently, vestibular (Kennedy & Inglis 2001), and cutaneous (Fallon, Bent, McNulty, & Macefield, 2005; Aniss, Gandevia, & Burke, 1992; Zehr, Collins & Chua, 2001) input both have the ability to modulate the excitability of the lower limb motoneuron (MN)
pool in humans. However, to date, there is limited research (Szturm, Ireland & Jell, 1987) examining how the signals from vestibular and somatosensory systems interact to produce an integrated postural response. Advances were made in 2003, when Marsden and colleagues observed changes in the galvanic vestibular stimulation (GVS) evoked postural response during body loading and unloading. GVS is a current applied to the eighth cranial nerve that alters the firing of peripheral vestibular afferents (Goldberg, Smith & Fernandez, 1984) and generates a measurable electromyographic (EMG) response in the soleus muscle characterized by a short latency (SL) inhibitory and medium latency (ML) excitatory response (Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993; Fitzpatrick, Burke, & Gandevia, 1994; Nashner, & Wolfson, 1974, Welgampola & Colebatch, 2001; Welgampola & Colebatch, 2005). Marsden et al. (2003) observed an enhanced postural response to binaural GVS in the head forward position following increased mechanical loading of the foot, although it remains elusive what receptors specifically facilitated this response.

In the current study, GVS was delivered in the seated position. Notably, for a GVS vestibular reflexive response to be elicited in the lower limb, muscles must be actively engaged in balance. When subjects are seated, this response is significantly reduced or disappears completely (Day, Severac Cauquil, Bartolomei, Pastor & Lyon, 1997; Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993). The seated paradigm can therefore provide the opportunity to use a stimulation level that has a subthreshold influence on the MN pool, which is important when investigating sensory interactions. It is clear that vestibular input maintains an influence in a seated position as with the absence of proprioceptive feedback GVS can evoke a large postural response in sitting (Day and Cole 2002).

Similar to the GVS responses, SL and ML reflexive responses can be observed after electrically stimulating cutaneous afferents of the foot sole over the distal tibial nerve (Zehr, Collins & Chua, 2001, Fung & Barbeau, 1994). With this reflex, muscles need only be isometrically contracted to 15% maximum voluntary contraction (MVC; similar to quiet stance), not posturally engaged, to evoke a response (Burke, Dickson, & Skuse, 1991).

The aim of the current study was to observe the interaction of cutaneous and vestibular input to determine their combined potential in modulation of MN pool excitability. Specifically, we wanted to determine if a subthreshold vestibular contribution could manifest a reflex response if combined with supra threshold cutaneous input to the MN pool. We hypothesized that cutaneous information from the foot sole would enable the vestibular contribution to become apparent in lower limb muscles. The presence of an interaction in the current manuscript highlights the role of cutaneous input in support of vestibular driven balance protective mechanisms.

Methods

Subject Preparation

Thirteen healthy subjects (8 female, 5 male, average age 24.1 ± 2.0 years) provided written consent. Ethics were obtained from the University of Guelph Research Ethics Board, which complied with the declaration of Helsinki.
Subjects were seated with their head facing forward and eyes closed. Hip, knee and ankle angles were maintained at 145°, with respect to the more proximal segment. Subjects maintained an isometric plantar flexion (20% MVC) against a flat surface to create tonic activity of the soleus akin to that seen in standing (Fung & Barbeau, 1994). Frequent rest periods were provided to prevent muscle fatigue and to ensure consistent background muscle activation.

**Vestibular Stimulation**

Bipolar, binaural GVS (500ms square wave pulse, 3xthreshold) was delivered through Ag/AgCl electrodes placed on the skin over the two mastoid processes; the Cathode was placed ipsilateral to the right soleus muscle. GVS was delivered using a constant current linear isolated stimulator (World Precision Instruments A395, Sarasota, FL), controlled by Spike 2 (Version 6; Cambridge Electronic Design, Cambridge UK). The stimulus level for all subjects was on average 2.02mA ± 0.06. This stimulus level was chosen based on a level three times individual threshold (during standing). Threshold (range 0.6–0.8mA) was determined as the level when a just noticeable movement of the head was detected. Threshold level is often accompanied with a sensation of “disorientation” reported by the participant (Bent, McFadyen, French Merkley, Kennedy & Inglis, 2000). This level of stimulation (3×threshold) reflects levels known to evoke both reflex responses in standing, as well as modulate the MN pool in a prone position (Kennedy & Inglis, 2001) and is therefore sufficient to influence the MN pool in the current study. Due to the sitting posture it is expected that independent vestibular reflex responses in soleus will be below a level that is measurable via EMG (Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993). To reflect this, the vestibular contribution is referred to as “subthreshold”.

**Cutaneous Stimulation**

Percutaneous stimulation (11ms train of 3 × 1.0 ms pulses; 200Hz) was delivered to the skin over the distal tibial nerve of the right leg (below medial malleolus) using stainless steel electrodes (5mm diameter) spaced 2cm apart (S88× Grass stimulator, Grass SIU-C constant current unit; Astro-Med, RI, USA). Stimulation intensity was set at two times radiating threshold (2×RT). RT represents the stimulation level that evokes a clear radiating parasthesia into the cutaneous area that is represented by the medial plantar nerve (i.e., the heel and sole of the foot toward the toes) (Zehr, Stein & Komiyama, 1998).

Subjects participated in a total of 180 randomized trials consisting of 3 different conditions: GVS Only (Cathode ipsilateral to right leg), Cutaneous Only (right leg), and GVS+Cutaneous (combined). Spike 2 software was used to monitor contraction levels (20% MVC). Trials where EMG was outside of the 20% (± 5%) were excluded (less than 3% of trials). MVC was calculated as the peak EMG activation over 50ms averaged across three maximal efforts.

For all subjects, GVS was delivered 55ms before cutaneous stimulation to ensure input from vestibular and cutaneous sources reached the lower limb motoneuron pool at the same time (Kennedy & Inglis, 2001; Fung & Barbeau, 1994). Although the determination of individual response latencies (and therefore unique interstimulus-intervals) would increase the observation of a combined reflex response, it would have increased the total number of trials by 60%, increasing the confounds of fatigue and habituation.
Data Collection

EMG data were collected bilaterally for both soleus (Sol) and tibialis anterior (TA) using surface electrodes (Ag-AgCl bipolar electrodes, Kendall LTP, Chicopee, MA). Right leg EMG data were used to evaluate the effects of stimulation on the motoneuron pool. EMG signals were differentially amplified (gain 500, band pass 10–1000Hz, AMT-8 Bortec Biomedical Ltd, Calgary, Canada) and digitally sampled at 2000Hz (Model 1401 DAQ system, CED, Cambridge UK). EMG data were rectified and smoothed using a moving average filter with a 5ms-sliding window. This is a common analysis method to prevent the cutaneous stimulus artifact from being averaged into the response (Zehr, Stein & Komiyama, 1998). Sixty sweeps of EMG activity were spike trigger averaged (STA; 50ms pre and 250ms post stimulus) to the onset of GVS for each subject. In trials containing no GVS, EMG activity was STA to the onset of cutaneous stimulation. To compare responses in trials both containing and lacking GVS, all EMG traces were aligned to where the onset of GVS did, or would, occur (if delivered). To achieve this 55 ms was added to all “cutaneous only” trials (Figure 1).

Analysis and Statistics

Vestibular reflex responses occur within the range 40–70ms (SL) and 90–130ms (ML) (Fitzpatrick, Burke & Gandevia, 1994; Nashner & Wolfson 1974; Cathers, Day & Fitzpatrick, 2005). Based on these latencies our vestibular reflex responses to GVS were identified as short (a decrease in activity beginning at 40–70ms), and medium (an increase in activity beginning at 70–130ms). Anything beyond 130 ms was not considered a ML GVS response. Cutaneous reflex responses were defined

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**Figure 1** — Schematic depicting the relative onsets of the i) GVS pulse ii) cutaneous pulse, as well as the expected response to iii) cutaneous stimulation and iv) cathodal GVS.
using 3 epochs (Fallon, Bent, McNulty, & Macefield, 2005; Zehr, Collins & Chua, 2001), two of which fell into time categories that coincided with the GVS response. Responses greater than 130ms were classified as long latency. EMG activity was considered “significant” if the trace fell outside (greater or less than) 2SD about the mean background EMG activity, within the mentioned expected latencies (relative to GVS onset), for a duration of at least 20ms (Di Fabio 1987). The mean background EMG activity (15–20%) was calculated over 50ms before stimulation onset, using STA. Latency data were calculated from stimulation onset to when the EMG response surpassed 2SD. These values are reported with respect to the onset of GVS. Amplitude was calculated as a percent change from background EMG.

Results

Ten of the thirteen subjects responded to at least one of the 3 test conditions (cutaneous only, GVS only, GVS/cutaneous combined). A vestibular-cutaneous interaction was evident in six of these ten subjects demonstrating the importance of a combined input in the generation of lower limb muscle activation. The nature of the combined response varied and is explained further below.

Response to Independent Stimuli

In 10 subjects, significant EMG responses were evoked in soleus after the cutaneous stimulation was delivered to the distal tibial nerve (Figure 2A). The EMG response consisted of two components; SL inhibition (average onset latency and magnitude; 58.2ms (±2.8), 13.2% MVC [±10.7]), followed by ML facilitation (average onset latency and magnitude; 87.5ms [±12.8], 21.9% MVC [±10.9]). The characteristics of these reflex responses corroborate the findings from past literature (Aniss, Gandevia, & Burke, 1992; Burke, Dickson & Skuse, 1991).

Contrary to reports in the literature to date, GVS (Avg: 2.02mA, 500ms) was able to elicit reflexive activity in 2 subjects in the soleus muscle ipsilateral to the Cathode (during 20% MVC isometric contraction; Figure 2B). For both subjects the EMG activity was classified as ML facilitatory (average onset of 113.5 ms ± 6.36, amplitude 5.0% [±0.424] of MVC [above background EMG]).

Response to Combined Vestibular and Cutaneous Stimulation

While all ten subjects elicited a response, it is notable that in six subjects the interaction of vestibular and cutaneous input resulted in an altered response during the combined stimuli. Subjects are further categorized below to facilitate an understanding of what may be contributing to the combined response.

Of the ten subjects, only two showed an initial response to the “GVS only” stimulation, which has not been demonstrated previously in sitting (Day, Severac Cauquil, Bartolomei, Pastor & Lyon, 1997; Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993), but has been shown in the prone position (Kennedy and Inglis 2001). In these two individuals, the combined response could be classified as a “summation” of the independent reflexes based on single stimulation trial profiles (Table 1A). Both the onset latencies and the amplitudes of the individual
Figure 2 — Sample EMG response from one representative subject to A) cutaneous stimulation demonstrating short latency (SL) inhibitory, and medium latency (ML) facilitatory components. The two lines about the baseline represent two standard deviations (SD) about the mean of the full wave rectified and smoothed EMG. Responses which surpassed these lines for at least 20ms were considered “significant”. Please note that the stimulus artifact has been removed to highlight the responses of interest. B) Sample EMG responses from one subject showing ML facilitation to cathodal Galvanic vestibular stimulation. A significant response is seen at 118ms, based on the response surpassing two standard deviations above the background EMG. The reflex is categorized as ML based on onset criteria (>70ms and <130ms).
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stimuli support a summation of sensory sources in the combined response. These data suggest an alignment of these two reflex responses whereby the ML excitatory cathode response (113.5 ± 6.36 ms) aligns with the ML excitatory cutaneous response (129.5 ± 0.7 ms) to produce the combined response. Notably, these two subjects had lower GVS thresholds and therefore a lower stimulus magnitude, which is known to contribute to a delayed onset of the GVS ML response (Ali, Rowen, & Iles, 2003).

Four subjects demonstrated what we termed a “facilitation” effect, where the influence of a subthreshold vestibular contribution (no overt response to individual GVS stimuli) was able to contribute to the overall response in the presence of skin input. In these subjects, SL inhibitory cutaneous responses appear to be abolished by the presence of a subthreshold ML excitatory vestibular contribution (Table 2, gray columns). These two reflex responses, the SL skin and ML vestibular align when one considers the timing of the SL cutaneous and “projected” subthreshold ML vestibular responses relative to the respective stimuli (Figure 3); both occur at an approximate latency of 100–115 ms (relative to GVS onset).

Table 1  A) Onset latency and amplitude for two test subjects in response to cathode only, skin only, and combined cathode/skin conditions. These subjects appeared to demonstrate summation effects of independent stimuli in the paired condition with respect to amplitude. B) Subject data for four subjects whose onset and amplitude in the combined GVS/skin condition were comparable to the onset and amplitude in the cutaneous only response. These data suggest that in these subjects, the vestibular input was considerably subthreshold. Note all onset latencies are reported relative to the onset of GVS (which occurs 55 ms before skin stimulation). Latencies in brackets in B are relative to cutaneous stimulation.

<table>
<thead>
<tr>
<th>A Summation</th>
<th>Onset latency (ms)</th>
<th>Amplitude (%MVC)</th>
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<tr>
<td>Subject</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>GVS only</td>
<td>109 ms</td>
<td>118 ms</td>
</tr>
<tr>
<td>Cutaneous only</td>
<td>129 ms</td>
<td>130 ms</td>
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<tr>
<td>Combined</td>
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<tr>
<th>B No Change</th>
<th>Onset latency (ms)</th>
<th>Amplitude (%MVC)</th>
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<tr>
<td>Subject</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Cutaneous only</td>
<td>133 ms</td>
<td>134 ms</td>
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<td></td>
<td>(78 ms)</td>
<td>(7 ms)</td>
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<tr>
<td>Combined</td>
<td>130 ms</td>
<td>131 ms</td>
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Table 2  Subject data from the four subjects demonstrating the “facilitation” effect, where subthreshold vestibular contributions were able to influence the response through the presence of skin input. The SL cutaneous response appears to be abolished (light gray) by the presence of a subthreshold ML vestibular contribution. All latencies are reported relative to the onset of the GVS stimulation (i.e. where GVS would have occurred in the cutaneous only trials and where it did occur in the combined trials). NB. Subject six did not demonstrate a ML response to the cutaneous input.

<table>
<thead>
<tr>
<th>Subject 3</th>
<th>Subject 4</th>
<th>Subject 5</th>
<th>Subject 6</th>
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<tr>
<td>SL</td>
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<tr>
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<td>(ms)</td>
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<td>132</td>
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<td>(%MVC)</td>
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<td>38.4</td>
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Finally, the remaining four subjects of the ten demonstrated a combined “GVS/cutaneous” response that did not differ from the “cutaneous only” response in these subjects. In these subjects the vestibular input was likely considerably subthreshold and unable to alter the excitability of the MN pool (Table 1B). A one sample student t test indicated that the difference between these two conditions (cutaneous only vs. combined cutaneous/GVS) for onset and amplitude was not significantly different from zero ($p > .05$).

**Discussion**

The current objective was to determine whether the combined influences of vestibular and cutaneous input resulted in a unified reflex response. We observed that when combined with cutaneous input the subthreshold vestibular contribution was able to impact the reflex response in the soleus muscle. Despite a large vestibular input ($3\times$ threshold), the seated position has conventionally shown a lack of muscular response (Day, Severac Cauquil, Bartolomei, Pastor & Lyon, 1997; Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993). The current work has highlighted the potential impact of this subthreshold vestibular input by combining it with another sensory source; cutaneous. The implications of the findings are that, in a sensory deficient state, combined sensory sources may be necessary to excite the motor neuron pool and generate an appropriate balance recovery response.
Figure 3 — Data from one subject showing A) the “Projected” EMG response to cathodal GVS stimulation along with actual data from the cutaneous only stimulation and B) data from the paired GVS/cutaneous condition. In this subject, the cutaneous stimulation appears to “enable” the contribution of the subthreshold vestibular response to become apparent. The result is an abolishment of the SL skin response.* Note the persistence of the ML cutaneous response.

Independent Stimuli

GVS can evoke EMG responses in the soleus muscle during a variety of postural tasks (Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993; Nashner & Wolfson, 1974), however, when subjects are braced (Fitzpatrick, Burke & Gandevia, 1994) or seated (Day, Severac Cauquil, Bartolomei, Pastor & Lyon, 1997; Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993), these responses are reduced or absent. Collectively, this has been interpreted to indicate that muscles must be posturally active for a vestibularly driven reflexive response to be seen in soleus EMG. In the current study we observed that vestibular stimulation alone elicited a reflexive response in posturally inactive muscles in two subjects.
The significant GVS response in two seated subjects may have resulted from an instability generated by the task (Welgampola & Colebatch, 2001). To achieve and maintain a 20% isometric contraction these two subjects may have engaged their lower segments to aid in postural stability, thereby increasing the weighting of vestibular input (Day and Cole 2002). Importantly the remaining eight subjects demonstrated the expected subthreshold response to the “GVS only” stimulation.

**Combined Responses**

Six subjects demonstrated an *altered* response when vestibular and cutaneous inputs were combined. The combined responses were manifested differently across subjects likely due to differences in onset latency and duration of the individual reflex responses (see below). Based on the presence, or absence, of an initial GVS response, the combined reflex could be identified as summative (*n* = 2), or facilitatory (*n* = 4).

For subjects showing the summation response, the initial GVS response occurred in the latter range of the ML time frame for classification (113.5 ± 6.36), and we propose that this reflex response was aligned with the ML cutaneous response, which was observed early in the latency range for cutaneous classification (74.5 ± 0.7ms or 129.5 from GVS onset). Of note, both of these subjects had GVS thresholds at or below 0.5mA). These low thresholds (increased vestibular weighting) may explain the emergence of a reflex response to the “GVS only” condition while sitting. Low intensities of GVS amplitude have also been shown to increase ML onset times (Ali, Rowen & Iles, 2003) leading to the temporal opportunity for a summation response. Both the magnitude and onset latencies of the individual and combined responses strongly argue in support of a summation response (see Table 1). The literature supports the idea of sensory integration; two independent sources of information resulting in a summed response (Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993; Welgampola & Colebatch, 2001; Hlavacka, Krizkova & Horak, 1995; Kavounoudias, Roll & Roll, 2001). Support for linear summation of vestibular and somatosensory inputs specifically, is provided by investigations into the perception of verticality, such that postural shifts correspond in magnitude to the theoretical sum of the effects measured using isolated sensory inputs (Hlavacka, Krizkova & Horak, 1995). More recent research also demonstrates a linear summation of vestibular and skin inputs through changes in the H-reflex amplitude (Lowrey & Bent, 2009). Therefore, it is perhaps not surprising that this type of interaction was observed in the current study when an initial GVS response was observed in soleus.

The most prominent effect we observed in the current study was evidence of an interaction between cutaneous and vestibular contributions where no independent vestibular responses were evoked initially. In these trials the subthreshold vestibular reflex had an influence on the outcome of the final reflex response. In fact, the subthreshold vestibular response does not become apparent *until* it is combined with the cutaneous reflex response. This “enabling” of the vestibular contribution through a cutaneous input highlights an important integrative resource for lower limb muscle modulation and the potential for the vestibular input to ultimately influence a postural response. To date, there has been a paucity of information on combined contributions from the cutaneous and vestibular systems. Earlier work by Marsden and colleagues (2003), attempted to delve into the interaction between load receptors and vestibular
contribution. Although these authors showed that an increased body load corresponded to augmented vestibular responses, they could not establish which of these load sensors; cutaneous or golgi tendon organs were involved. Here, we have demonstrated that not only is there a combined response of these two sensory sources (cutaneous and vestibular), but that cutaneous receptors specifically, have the ability to modulate, and potentially facilitate a vestibular contribution.

We recognize that since our subjects were tested in a seated paradigm, application to postural control is not as apparent. What we have demonstrated here is the ability for the interaction to exist between these sensory modalities, although we cannot say where this interaction occurs based on our current data. In application, these findings are of particular importance when vestibular contribution is reduced (through physiological changes with aging or pathology; Welgampola & Colebatch, 2005) relevant cutaneous input may compensate for this deficiency. One strategy to obtain adequate cutaneous input is to implement rehabilitation devices targeted at the augmentation of skin input; increased ridge support (Maki, Perry, Norrie & McIlroy, 1999) or using vibrating insoles (Priplata, Niemi, Harry, Lipsitz & Collins, 2003). In elderly populations, these types of devices can significantly reduce sway, improving overall balance control (Maki, Perry, Norrie & McIlroy, 1999). The current study suggests that these augmentations in cutaneous input may contribute twofold to positive balance outcomes; first, through primary contributions directly enhancing cutaneous input, and second through indirect facilitation of the vestibular response.

**Limitations**

While we believe we have demonstrated a novel and important sensory interaction between skin and vestibular reflexes related to the control of upright balance, we recognize the limitations herein. The variable results across participants, while they don’t detract from the overall conclusions, do provide insight into the biological differences that exist within the population. The range of responses to the combined stimulation; summation, facilitation or combined response are likely due to individual difference in sensory weighting as well as inherent differences in conduction velocity, which were not systematically measured, or controlled. Threshold levels of GVS were established in the standing position (Bent et al. 2000), and therefore the level of stimulation may not transfer linearly to the sitting position for all participants based on individual sensory weighting. This would give rise to greater subthreshold levels in some than in others and the resultant variable combined responses. Notably, with our participants divided into smaller subgroups, statistical strength became limited.

Given these limitations, we recognize that our findings necessitate caution, but also recognize the important contribution that the work has made to understanding sensory interactions in this context.

In conclusion, the current work has been able to demonstrate the presence of an interaction between cutaneous input and vestibular input for the modulation of muscles used in the generation of balance protective reflexes. Specifically, subthreshold vestibular contributions can benefit from the presence of cutaneous input sources.
Acknowledgments

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References


