

The altered vestibular-evoked myogenic and whole-body postural responses in old men during standing



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ABSTRACT

Age-related decrements within the sensorimotor system may lead to alterations and impairments in postural control, but a link to a vestibular mechanism is unclear. The purpose of the present study was to determine whether vestibular control of standing balance is altered with adult aging. Eight old (~77 years) and eight young (~26 years) men stood without aids on a commercially available force plate with their head turned to the right, arms relaxed at their sides and eyes closed while receiving stochastic vestibular stimuli (0–25 Hz, root mean square amplitude = 0.85 mA). Surface electromyography signals were sampled from the left soleus, medial gastrocnemius and tibialis anterior. Whole-body balance, as measured by the anteroposterior forces and muscle responses, was quantified using frequency (coherence and gain functions) and time (cumulant density function) domain correlations with the vestibular stimuli. Old men exhibited a compressed frequency response of the vestibular reflex with a greater relative gain at lower frequencies for the plantar flexors and anteroposterior forces than young. In the time domain, the peak amplitude of the short latency response was 45–64% lower for the plantar flexors and anteroposterior forces ($p \leq 0.05$) in the old than young, but not for the tibialis anterior ($p = 0.21$). The old men had a 190% and 31% larger medium latency response for only the tibialis anterior and anteroposterior forces, respectively, than young ($p \leq 0.01$). A strong correlation between the tibialis anterior and the force response was also detected ($r = 0.80$, $p < 0.01$). In conclusion, net vestibular-evoked muscle responses led to smaller short and larger medium latency peak amplitudes in anteroposterior forces for the old. The present results likely resulted from a compressed and lower operational frequency range of the vestibular reflexes and the activation of additional muscles (tibialis anterior) to maintain standing balance.

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1. Introduction

Maintaining standing balance is a critical component of tasks of daily living that is often compromised with healthy adult aging (Shaffer and Harrison, 2007; Ishiyama, 2009). For example, old adults are more unstable (Abrahamová and Hlavacka, 2008; Baudry et al., 2012; Kouzaki and Masani, 2012) and require greater corticospinal activity to stand (Baudry et al., 2014) than younger adults. As a result, old adults exhibit increased plantar flexor activation and greater co-activation of the antagonistic dorsiflexors (Baudry et al., 2012, 2014; Benjuya et al., 2004; Laughton et al., 2003) than young, which may stem from age-related alterations in

the vestibular, proprioceptive and visual systems (Lord and Menz, 2000; Lord et al., 1991; Shaffer and Harrison, 2007). Vestibular impairment may be a critical factor for imbalance and falls (Pothula et al., 2004) since hair cell loss and degeneration of vestibular afferent pathways are both consequences of natural adult aging (Ishiyama, 2009). The involvement of the somatosensory and visual systems in elderly balance deterioration is well-documented (Abrahamová and Hlavacka, 2008; Lord and Menz, 2000; Sundermier et al., 1996), but the involvement of the vestibular system with age-related balance impairments has been evaluated only through the exclusion of other sensory systems. For example, the contribution of the vestibular control of balance is often speculated based on postural tests of sway with altered visual (e.g., blindfolded) and proprioceptive cues (e.g., standing on foam). Thus, the effect of adult aging on the vestibular control of balance is still not well-understood.

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Galvanic vestibular stimulation (GVS) and stochastic vestibular stimulation (SVS) are valuable tools for investigating the role of vestibular information in the control of standing balance (Britton et al., 1993; Dakin et al., 2007; Fitzpatrick and Day, 2004). Low amplitude currents applied over the mastoids modulate the firing rate of the underlying vestibular afferents (Goldberg et al., 1984) and produce compensatory myogenic responses and whole-body movements to maintain upright posture (Dakin et al., 2007; Day et al., 1997; Fitzpatrick et al., 1994; Luu et al., 2012). In the lower limb, muscle responses exhibit a biphasic pattern consisting of two distinct peaks of short (~60 ms) and medium (~110 ms) latencies (Britton et al., 1993; Fitzpatrick et al., 1994; Lee Son et al., 2008; Nashner and Wolfson, 1974; Welgampola and Colebatch, 2002). Details of the physiological mechanisms have yet to be determined, but reports have suggested that the short and medium latency components may originate from different sources (Britton et al., 1993; Cathers et al., 2005; Dakin et al., 2007, 2010; Mian et al., 2010; Welgampola and Colebatch, 2002). Welgampola and Colebatch (2002) reported that the peak amplitude of the short latency response was smaller in old adults, but the medium latency response was similar when compared with young controls. However, that study focused solely on a single muscle group, the soleus, using traditional GVS. It is unknown whether the observed age-related alterations observed for the soleus are indicative of altered vestibular responses at the whole-body level during the maintenance of upright balance. Measuring forces applied to the whole-body would offer valuable information regarding the net result of all muscles involved in the vestibular postural response (Mian and Day, 2009; Pastor et al., 1993).

Vestibular reflexes induced via SVS are represented in the lower limb musculature over a bandwidth of 0–20 Hz (Dakin et al., 2007; Forbes et al., 2013), which corresponds to the dynamic range of the vestibular system (Armand and Minor, 2002; Huterer and Cullen, 2002). With healthy adult aging, whole muscle contractile properties are slower (Dalton et al., 2009, 2014), motor unit firing rates are lower (Dalton et al., 2009, 2010; Rubinstein and Kamen, 2005) and inherent motor neuron properties are altered (Kalmar et al., 2009; Piotrkiewicz et al., 2007), but these age-related declines cannot be generalized to all muscles and their constitutive motor neurons (Dalton et al., 2008, 2009; Deschenes et al., 2010; Ishihara et al., 1987; Moran et al., 2005). Further, high-frequency sound and vibrotactile detection thresholds are increased with adult aging (Wells et al., 2003; Willott, 1984). These results suggest a shift towards slower and lower physiological frequencies in the motor and various sensory systems with adult aging. It is reasonable to postulate that the operational frequency range of the vestibulo-motor system would also shift towards a lower compressed bandwidth in old when compared with young adults. Furthermore, disparate age-related alterations within the neuromuscular system combined with increased muscle activity during quiet standing may alter the representation of the vestibular reflex in the various muscles. Hence, the summation of these responses may reflect an altered vestibular control of balance at the whole-body level in old men compared with young.

The purpose here was to evaluate the effect of adult aging on how an isolated vestibular error signal is transmitted to the muscles controlling the ankle and the corresponding summation of these reflexes at the whole-body level using frequency (coherence and gain) and time (cumulant density) approaches. We hypothesized that the frequency bandwidth over which vestibular reflexes are represented at the muscle and whole-body levels would compress and shift towards lower operating frequencies. Although the vestibulo-myogenic response represents a summation of a broad bandwidth of frequencies in young adults (Dakin et al., 2011), it seems that the short latency response is shaped primarily by higher frequencies (>10 Hz); whereas the medium latency likely reflects lower frequencies (Dakin et al., 2007, 2010). Consequently, we hypothesized the short latency vestibular response would be smaller in the old men; whereas the later response

(medium latency) would be maintained or larger for the old men than the young.

2. Materials and methods

2.1. Participants

Eight old (aged: 76.5 ± 6.3 years; mass: 78.5 ± 12.6 kg; height: 173.8 ± 5.1 cm) and eight young (aged: 26.3 ± 3.6 years; mass: 82.1 ± 13.9 kg; height: 179.9 ± 7.4 cm) healthy men with no known history of neurological diseases or injuries volunteered for the study. Participants were given written and oral details of the experiment and granted written and oral informed consent prior to participation. All procedures conformed to the standards of the Declaration of Helsinki and were approved by the local university's research ethics board.

2.2. Vestibular stimuli

A continuous randomly varying current, in both amplitude and frequency, was applied binaurally to the mastoid processes in a bipolar configuration. The SVS signal essentially is filtered white noise that is scaled to a desired peak to peak amplitude (Dakin et al., 2007). SVS allows for the characterization of whole-body postural and muscle responses in both the frequency and time domains (Dakin et al., 2007; Mian et al., 2010; Reynolds, 2010). Carbon rubber electrodes (9 cm^2), coated in Spectra 360 electrode gel (Parker Laboratories, Fairfield, USA), were positioned over the mastoid processes with Durapore tape (3M Canada, London, Canada) and an elastic headband. Vestibular stimuli were generated on a PC computer using Spike2 software (Cambridge Electronics Design, Cambridge, UK) and sent to an isolated bipolar constant current stimulator (input range: ± 10 V, output range: ± 10 mA; DS5, Digitimer Ltd., Welwyn Garden City, UK) via an analog output of a Power 1401 (Cambridge Electronics Design, Cambridge, UK). Once the SVS signal was generated, each subject was exposed to the same waveform for every trial to ensure that frequency bands were identical among subjects. To ensure a significant vestibular reflex (Dakin et al., 2010, 2011), the SVS signals were delivered using a 0–25 Hz bandwidth with a peak to peak amplitude of ± 1.5 mA (RMS = 0.85 mA) for three 60-s trials. Stochastic vestibular stimuli containing similar RMS amplitudes and frequency bandwidth have been shown to evoke a postural reflex (Dakin et al., 2007; Forbes et al., 2013; Luu et al., 2012). Adequate rest (approximately 1 min) was given between exposures to prevent fatigue.

2.3. Experimental set-up

Participants stood upright with their medial malleoli ~10 cm apart on a force plate (Model 9287a, Kistler Instrument Corp., Amherst, USA). Participants stood relaxed while blindfolded and kept their arms at their sides and head rotated to the right, 90° (Fig. 1A). A laser pointer was secured above the left ear and oriented to Reid's plane, which passes bilaterally through the inferior orbital margin and the external acoustic meatus. The head was tilted $\sim 18^\circ$ upward from the horizontal. Because of the well-documented relationship between head yaw angle and the direction of the vestibular-evoked postural response and the orientation of the GVS vector that results from the presumed stimulation of all vestibular afferents (Cathers et al., 2005; Day and Fitzpatrick, 2005; Lund and Broberg, 1983; Mian and Day, 2009; Pastor et al., 1993), the postural response to the electrical vestibular stimulation was aligned primarily with the anteroposterior (AP) rotations about the ankles. This set-up maximized the vestibular-evoked reflex in line with the action of the ankle plantar flexors and dorsiflexors. Thus, for the purposes of this study we only tested time and frequency correlations with the SVS

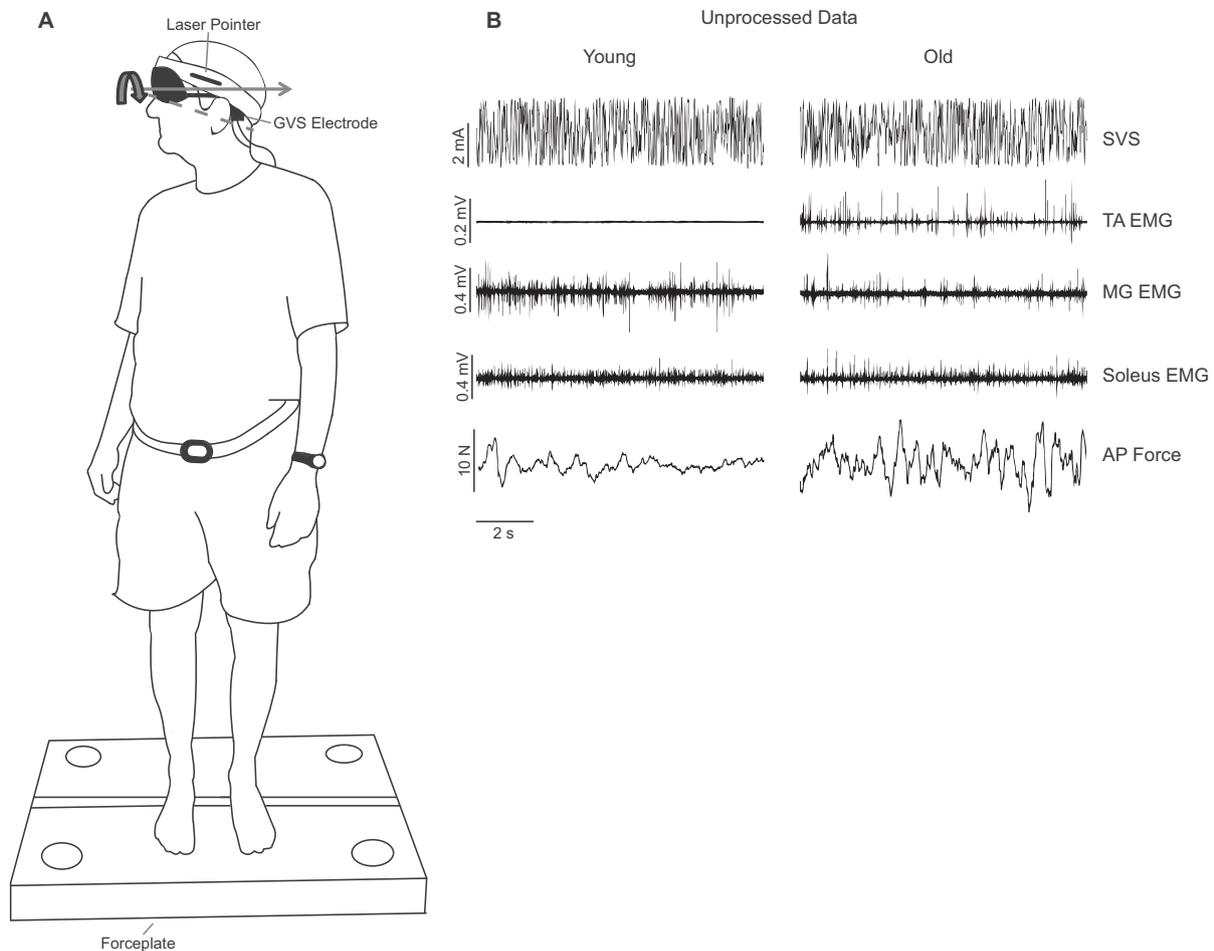


Fig. 1. The experimental set-up (A) showing the head rotated to the right 90°. A laser pointer was secured above the left ear and oriented to Reid's plane (dashed line). The illustration also presents the theoretical GVS vector based on the summation of all vestibular afferents stimulated by the electrical vestibular stimulus (gray arrow). The head was tilted ~18° upward from the horizontal. Thus, the postural response to the electrical vestibular stimulation was aligned primarily with the anteroposterior rotations about the ankles (Cathers et al., 2005; Day and Fitzpatrick, 2005; Mian and Day, 2009), in line with the action of the ankle plantar flexors and dorsiflexors. B depicts 10-s traces of the unprocessed surface electromyography (EMG) for the tibialis anterior (TA), medial gastrocnemius (MG) and soleus, anteroposterior forces (AP force) and stochastic vestibular stimulation (SVS).

and AP forces and not the medio-lateral forces. Additionally, a target was marked on a wall that corresponded with the position of the laser pointer and participants were guided verbally to maintain this head position. Both age groups had no difficulty in maintaining the requisite posture for the one-min trials.

Surface electromyography (EMG) was collected from the left leg because vestibular-evoked muscle responses are larger in the opposite leg to which the head is turned (Britton et al., 1993; Dakin et al., 2007). Prior to electrode (Blue Sensor M, M-00-S; Ambu A/S Ballerup, Denmark) set-up, the skin locations were cleaned with alcohol. Recordings were made from the medial gastrocnemius, soleus and tibialis anterior using a bipolar set-up with an inter-electrode distance of 2 cm (center-to-center) in line with the muscle fibers. For the medial gastrocnemius the electrodes were placed over the muscle belly. The soleus recording electrodes were positioned 2 cm distal to the border of the lateral gastrocnemius over the lateral aspect of the soleus. For the tibialis anterior the electrodes were placed over the proximal portion of the muscle, 2 cm lateral to the anterior tibial border and 7 cm distal to the tibial tuberosity. A ground electrode was positioned over the medial malleolus. Surface EMG signals were pre-amplified ($\times 100$; NL844, Digitimer Ltd., Welwyn Garden City, UK), amplified ($\times 2$; NL820A, Digitimer Ltd., Welwyn Garden City, UK), and band-pass filtered (30–1000 Hz; NL 136 & NL 144, Digitimer Ltd., Welwyn Garden City, UK). The vestibular stimuli, force plate data

and surface EMG were digitized (Power 1401, Cambridge Electronics Design, Cambridge, UK) and sampled online. Based on limitations of the analog-to-digital board the sampling rate was 2041 Hz.

2.4. Data analysis

The AP forces and surface EMG from the triceps surae and tibialis anterior were used to characterize the vestibular-evoked balance responses. Representative unprocessed data traces are provided in Fig. 1B. The sampled AP forces (F_y) and surface EMG signals were time-locked to the SVS onset and the repeated trials were concatenated to create data records of ~177 s for the surface EMG (segment length: ~1.003 s and resolution: ~0.997 Hz) and ~174-s records for the AP forces (segment length: ~2.007 s and resolution: ~0.498 Hz) for each participant. The concatenated data were used to estimate relationships between the SVS signal (input) and the physiological outputs (full-wave rectified surface EMG (see Dakin et al., 2014) and AP forces) in the frequency (coherence and gain) and time (cumulant density) domains. Coherence, cumulant density and gain estimates were derived using an archive of MATLAB (MathWorks, Natick, MA) functions based on multivariate Fourier analysis (NeuroSpec, <http://www.neurospec.org>). The methods have been described previously by Halliday et al. (1995) and Rosenberg et al. (1989). For visual display (Figs. 2 and 3) and further

data analysis, coherence, gain and cumulant density functions were derived using concatenated data across all participants for each age group.

To explore the frequency bandwidth of the vestibular reflexes evoked in the muscles and AP forces between age groups, coherence estimates were derived. Coherence represents a measure of linear relationship between an input (i.e., electrical vestibular stimulation) and an output (i.e., muscle activity or AP force) across a given range of frequencies. For every frequency point, coherence varies from 0 (no linear relation) to 1 (linear system containing no noise). Coherence between the stimulation input and the muscle and AP force was considered significant when the values were greater than the 95% confidence limit (Fig. 2; dashed horizontal line). The 95% confidence limit for coherence spectra was estimated from the total segments per subject to distinguish frequencies that were significantly different than 0 (Halliday et al., 1995). Because coherence functions are essentially normalized for the magnitude of the output signal, SVS is likely a better technique to compare different populations (i.e., young and old adults) than traditional GVS. To describe the coherence bandwidth for each age group, we defined the operating range as all significant coherence frequencies less than the lowest frequency that did not exceed the 95% confidence limit in the concatenated data across participants.

To describe the frequency response of the vestibular evoked reflexes at frequencies with significant coherence, gain–frequency functions were derived. The gain estimates were normalized within each muscle and AP force to the average gain at the lowest frequency data point (1 Hz). Thus, the gain function is a unit-less measure and represents the magnitude of the output (EMG and AP force) relative to the input signal (electrical vestibular stimulation). The gain function is also a tool to identify muscle-dependent filtering behavior that tends to decrease with an increase in frequency (Forbes et al., 2013). To compare old and young men, point wise 95% confidence limits were constructed for each age group (Fig. 2E–H) and the frequencies for which gain confidence limits did not overlap were considered statistically different.

Cumulant density functions were estimated to represent time domain relationships between the vestibular stimuli and measured physiological signals (EMG and AP forces). A cumulant density estimate derived between two signals is a correlation-like measure and is interpreted as an associative rather than a causal relationship. Accordingly, the SVS–EMG and SVS–AP force cumulant density estimates represent related responses that hold no physical values. Cumulant density estimates were derived by transforming the cross-spectra between the SVS signal and the forces or surface EMG signals into the time domain. Then, the amplitudes of the cumulant density functions were normalized by the product of the vector norms of the SVS input and the motor output (EMG or AP force) signals (Dakin et al., 2010). This method of normalization essentially transforms the cumulant density values into an equivalent of a cross-correlation (r values confined between -1 and 1). This normalization procedure allows for a reasonable comparison between age groups that are not influenced by the known differences in lower limb muscle activation during standing balance (Baudry et al., 2012, 2014; Benjuya et al., 2004; Laughton et al., 2003).

To determine significance, 95% confidence intervals were calculated for individual participants and evaluated on a participant-by-participant basis (i.e., when the peak amplitude values of the short and medium latencies exceeded the calculated confidence intervals). The short latency peak amplitude refers to the first peak (or trough) of the cumulant density function, whereas the peak amplitude of the medium latency response is the second peak (or trough) value of opposite polarity (Fig. 3). The cumulant density function represents the evoked response to vestibular stimulation and exhibits similar short and medium latency responses as traditional galvanic vestibular stimulation (GVS) (Dakin et al., 2007). By convention, an anode right (cathode

left) current represents a positive vestibular signal whereby a positive cumulant density estimate depicts the anode right (cathode left) facilitating muscle activity or eliciting forces applied to the body directed anteriorly.

Because the short latency is likely shaped primarily by higher frequencies (>10 Hz) and the medium latency likely reflects lower frequencies (Dakin et al., 2007, 2010) in the EMG vestibular response, peak coherence at low (EMG: <10 Hz, AP force: <4 Hz) and high (EMG: >10 Hz, AP force: >4 Hz) frequencies was compared (after applying Fisher's Z transformation) between groups using an unpaired T-test. The frequency cut-off was lower in the AP forces because the AP force and sway correlate with the vestibular input at a lower and compressed frequency bandwidth than the muscle response (Dakin et al., 2010; Reynolds, 2010). To compare between age groups for the time domain, unpaired T-tests were conducted for the short and medium latency peak amplitudes of the cumulant density function of the SVS–EMG and SVS–AP force. Statistical significance was set at $p \leq 0.05$. Effect sizes (ES) were calculated using the Cohen's d method to explore the strength of apparent statistical effects. Pearson correlation coefficients (r) were performed to evaluate the relationship between the medium latency response for each muscle and the AP force. Descriptive statistics are reported as means \pm standard deviations.

3. Results

3.1. Frequency domain

The coherence function reached significance (95% confidence limit) in all subjects for the medial gastrocnemius and soleus (Fig. 2), and in all but one young subject for the tibialis anterior. For the plantar flexor muscles, the old men displayed a compressed and lower frequency bandwidth range than the young (Fig. 2A and B). Vestibular stimulation to EMG coherence initially declined below the 95% confidence limit at 12 Hz and 13 Hz for the soleus and medial gastrocnemius, respectively, in the old men; whereas in the young, coherence exceeded the 95% confidence limit up to 24 Hz and 20 Hz for the soleus and medial gastrocnemius, respectively. Thus, peak coherence at the low frequencies (<10 Hz) did not differ between age groups for the soleus ($t(14) = 1.24, p = 0.12$) and medial gastrocnemius ($t(14) = 0.82, p = 0.21$), but was 66% and 60% smaller at the higher frequencies (>10 Hz) in the old than young men for the soleus ($t(14) = 2.70, p < 0.01, ES = 1.35$) and medial gastrocnemius ($t(14) = 1.73, p = 0.05, ES = 0.87$), respectively. The old men exhibited a 122% larger peak coherence ($t(14) = -2.34, p < 0.05, ES = 1.17$) than the young at the lower (<10 Hz), but not the higher frequencies ($t(14) = -1.15, p = 0.13$) for the tibialis anterior (Fig. 2C). For the SVS–AP force, peak coherence was 17% larger for the old than young men at the lower frequencies ($t(14) = -1.84, p < 0.05, ES = 0.92$) but no significant difference was detected for the higher frequencies ($t(14) = -0.36, p = 0.36$; Fig. 2D). However, SVS–AP force coherence initially declined below the 95% confidence limits at 4 Hz for the old, but 6 Hz for the young men. In support of the aforementioned results, the relative gain–frequency function was enhanced at low frequencies for all muscles and AP force for the old men (Fig. 2E–H). The gain initially increased and peaked at frequencies <5 Hz for all muscles and AP force. This peak was followed by a rapid decline towards lower values. Except for the tibialis anterior, the gain–frequency function for the young men decreased immediately, but with a shallower slope than the old, thus remaining closer to unity over a larger bandwidth of frequencies (Fig. 2E–H). As a result, older adults exhibited greater relative gain than the young below 6, 5, 8 and 2.5 Hz for the soleus, medial gastrocnemius, tibialis anterior and AP force, respectively. Oppositely, the older adults had lower relative gain than the young at frequency bandwidths of 7–14 and 21–25 Hz for the soleus and 7–14, 18–20 and 22–23 Hz for the medial gastrocnemius (Fig. 2E–H).

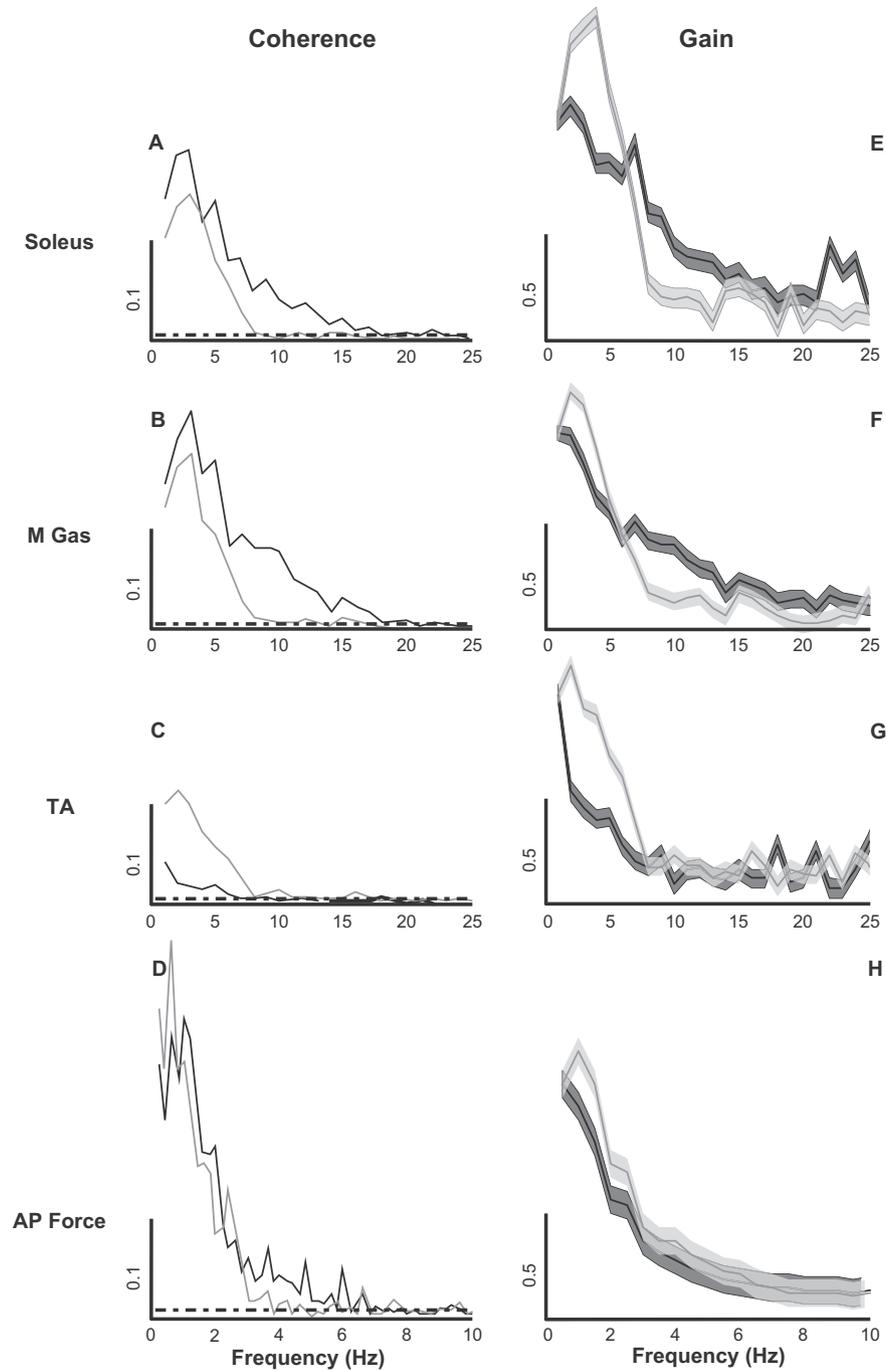


Fig. 2. Vestibular-evoked frequency responses computed from concatenated data among all participants for the old (gray: $n = 8$) and young (black: $n = 8$) men. Coherence (A–D) functions reached significance in both age groups for the electromyographic activity of soleus, medial gastrocnemius (M Gas) and tibialis anterior (TA) and anteroposterior forces (AP Force). Dashed black horizontal lines depict 95% confidence limits. Gain estimates (E–H) were enhanced for the lowest frequencies for the old men with a precipitous decline thereafter; whereas the young exhibited a more gradual slope indicating a larger operational frequency bandwidth. The gray and black shaded areas represent point wise 95% confidence limits for the old and young men, respectively. The regions in which confidence limits did not overlap were considered statistically different.

3.2. Time domain

The cumulant density reached significance in all subjects (Fig. 3), except for the tibialis anterior, in which the correlation did not reach the 95% confidence limits for three young men (data not shown). The old men had a 58%, 64% and 45% smaller short latency peak amplitude for the soleus ($t(14) = 3.81, p < 0.01, ES = 2.04$), medial gastrocnemius ($t(14) = 3.83, p < 0.01, ES = 2.05$) and AP forces ($t(14) = 2.36, p < 0.05, ES = 1.26$), respectively, than the young; whereas no statistical differences were detected for the tibialis anterior between age

groups ($t(14) = -1.34, p = 0.20$; Figs. 3A–D and 4A–D). For the medium latency response, the results were opposite than those of the short latency. The old men exhibited a 31% larger AP force peak amplitude than the young ($t(14) = -3.19, p < 0.01, ES = 1.59$; Figs. 3D and 4H). The tibialis anterior medium latency peak amplitude was 190% larger ($t(14) = -3.48, p < 0.01, ES = 1.86$) for the old than the young men with no detectable differences for the soleus ($t(14) = 1.09, p = 0.30$) and medial gastrocnemius ($t(14) = 0.79, p = 0.45$; Figs. 3A–C and 4E–G). A strong correlation was detected between the peak medium latency responses of the tibialis anterior and the

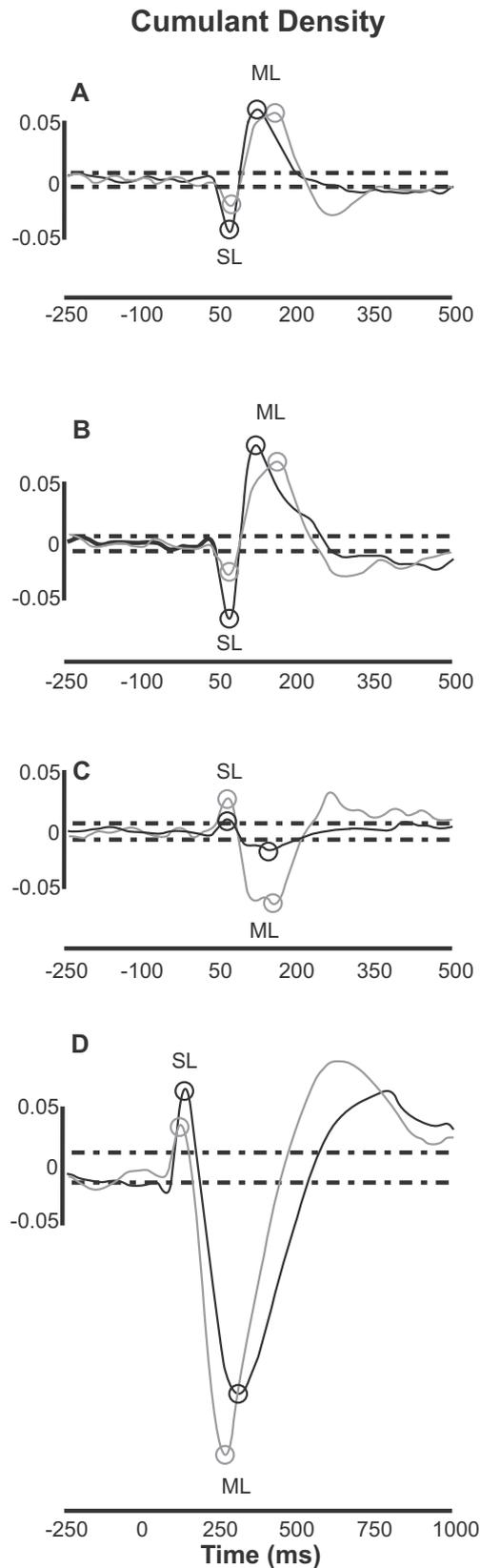


Fig. 3. Vestibular-evoked time domain responses computed from concatenated data among all participants as depicted by the cumulant density function for the soleus (A), medial gastrocnemius (B), tibialis anterior (C) and anteroposterior force (D). The gray and black lines represent the responses observed for the old ($n = 8$) and young men ($n = 8$) respectively. Open circles highlight the short (SL) and medium latency (ML) peak amplitudes. Dashed horizontal lines represent 95% confidence limits.

AP force ($r(14) = 0.80, p < 0.01$), but not with the soleus ($r(14) = 0.09, p = 0.75$) or medial gastrocnemius ($r(14) = 0.32, p = 0.23$) and the AP force, respectively.

4. Discussion

The aim of the present study was to assess the effect of adult aging on the frequency (coherence and gain) and time (cumulant density) domain characteristics of vestibular reflexes in various muscles acting at the ankle and to determine how these reflexes are summated and expressed at the whole-body level (net evoked AP force). Our main findings corroborate our hypotheses: 1) the frequency response of vestibular reflexes is limited to lower frequencies in older adults (Fig. 2) and 2) the peak amplitude of the short latency vestibular response was lower, except for the tibialis anterior, and the medium latency response was maintained in the plantar flexors but larger in the tibialis anterior and whole-body response (AP forces) for the old men than young. Thus, the vestibular reflex is modulated over a narrower frequency bandwidth in old men, which likely represents a low-pass filtering or inefficiency of the aged system to operate at higher physiological frequencies comparable to the young.

Novel to the present study is the narrower frequency bandwidth of vestibular reflexes evoked in the plantar flexor muscles of the old men than the young. The SVS–EMG coherence estimates from the soleus and medial gastrocnemius were confined to lower frequencies for the old men; whereas SVS–EMG coherence spanned frequencies up to and exceeding 20 Hz for the young adults (see also Dakin et al., 2007; Forbes et al., 2013). In young adults, SVS–whole-body relationship is observed over a lower frequency bandwidth (typically < 8 Hz) due to low-pass filtering from the muscle to the AP force (Dakin et al., 2010). In the present study, the SVS–EMG gain function of the old men was amplified at the lower frequencies. Once reaching a peak at < 5 Hz for the muscle and 2 Hz for the whole-body (AP force) responses, the relative SVS–Gain function exhibited a precipitous decline thereafter for the old men. For the young, the relative gain declined more gradually. Thus, our results elucidate a preferential operational bandwidth of vestibular reflexes towards lower frequencies for the old men while these reflexes operate over a broader frequency range for the young. A featured characteristic of adult aging is the impairment in detecting higher frequency sensory stimuli compared with younger adults (Wells et al., 2003; Willott, 1984). For example, older adults exhibit higher detection thresholds at frequencies ≥ 50 Hz for tactile sensation, whereas detection thresholds for lower frequencies are age invariant (Wells et al., 2003). Our findings suggest that, in the balance system, sensorimotor processing of a vestibular error is decreased at higher frequencies for old men compared with young.

Within the motor system, motor unit firing rates decrease with healthy adult aging in most muscles tested (Barry et al., 2007; Dalton et al., 2009, 2010; Rubinstein and Kamen, 2005) and motor unit properties can affect the frequency bandwidth of brain–muscle correlations (Ushiyama et al., 2012). It is plausible that the slower motor unit properties in the old men may shift the expression of the vestibular reflex towards a lower frequency bandwidth when compared with the young. Recently, it was determined that vestibular reflexes in the neck are represented over a larger frequency bandwidth than those for lower limb muscles, and this frequency difference may be related to the underlying motor unit firing rates of these muscles (Forbes et al., 2013). However, based on numerical modeling, motor unit firing rate cannot explain exclusively the large frequency bandwidth differences between the neck and lower limb muscles of young adults (Forbes et al., 2013). Even though the soleus and its constitutive motor units maintain their properties well into the eighth decade of life (Dalton et al., 2008, 2009), we also observed a lower frequency bandwidth in the old men than in the young for this muscle. Similar to the muscle-dependent variability in neuromuscular properties and function, the different bandwidth frequencies between age groups are likely not explained solely by the age-related variance in motor unit

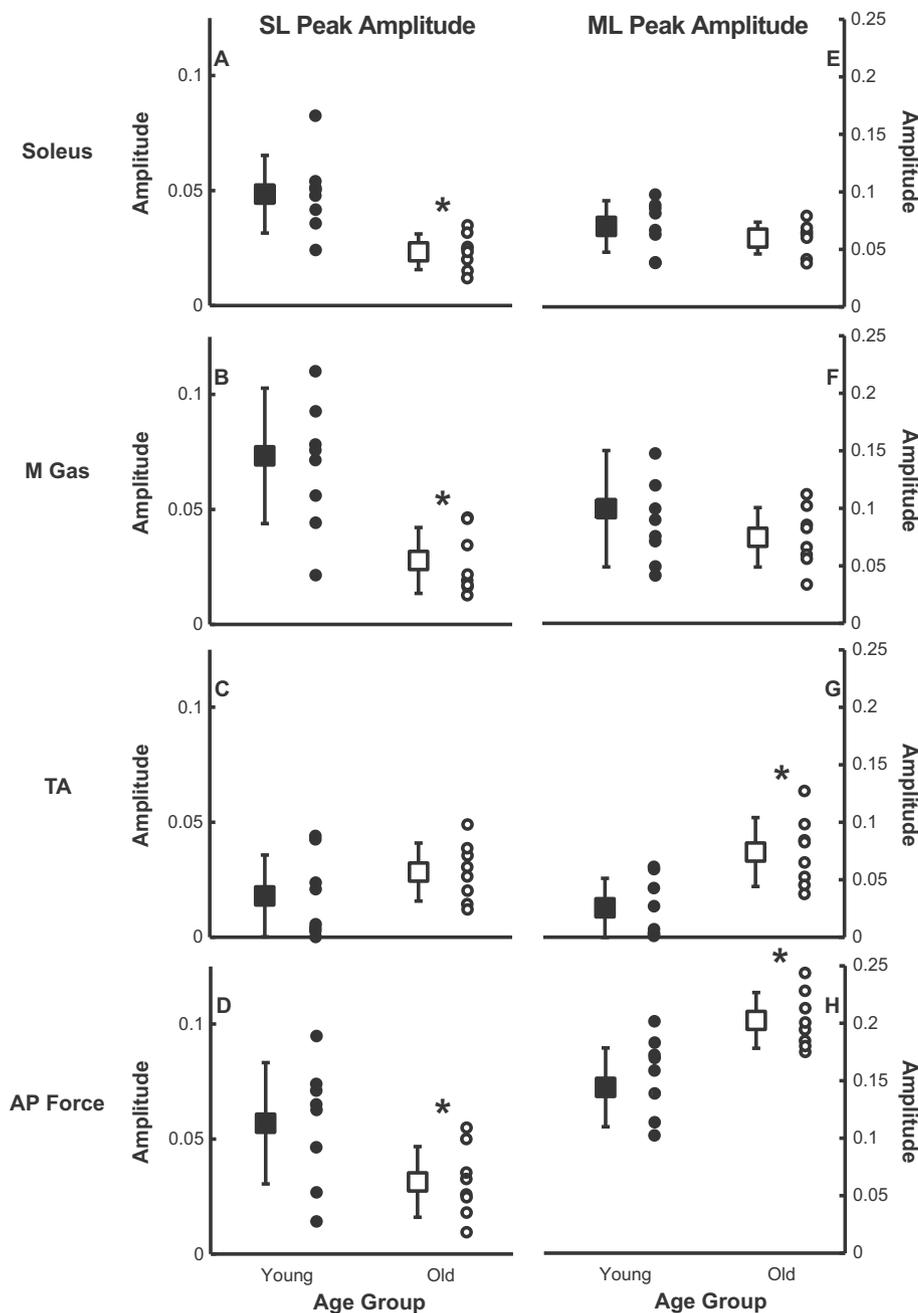


Fig. 4. Vestibular-evoked short (SL; A–D) and medium (ML; E–H) latency peak amplitudes of the cumulant density function. The polarity of the SL and ML responses are opposite but for visualization, the SL and ML responses are presented as positive values. The SL peak amplitude was lower in the soleus, medial gastrocnemius (M Gas) and anteroposterior forces (AP force), but not in the tibialis anterior (TA) for the old (unfilled square) men than for the young (filled square). The ML peak amplitude was larger in the TA and AP force, but not in the soleus or M Gas for the old men than for the young. * represents old men values different than young ($p \leq 0.05$). Values are means \pm standard deviations. Circles represent individual values for the old (unfilled) and young (filled) men.

properties. Forbes et al. (2013) suggested that the narrower bandwidth in the lower limb compared with the neck muscles was due to additional neural filtering. It is likely that the aged neuromuscular system of the old men may also act as a greater low-pass filter of the vestibular reflex than the young, which is reflected in a lower representative frequency range. Although unknown, these vestibulo-motor changes may be linked to age-related vestibular cell loss (Merchant et al., 2000), especially thick myelinated fibers (Rosenhall, 1973), neuronal degeneration in the vestibular nerve (Bergstrom, 1973) and Scarpa's ganglion (Richter, 1980), decrease in the quantity and surface density of vestibular-cerebellar synapses (Bertoni-Freddari et al., 1986), and anatomical and physiological alterations at the spinal level (Aagaard et al., 2010).

Similar to and extending previous results (Welgampola and Colebatch, 2002), the soleus and medial gastrocnemius medium latency peak amplitude was the same for the old and young men (Fig. 4E and F). However, until now, the functional consequences (i.e., whole-body postural response as measured by AP force in our study) related to balance control in response to a known vestibular error in older adults was unknown. The medium latency component of the vestibular-evoked whole-body response represents the postural or body reaction to the vestibular error signal (Marsden et al., 2002; Mian and Day, 2009). If our findings were based solely on the plantar flexor muscle responses, the wrong conclusion would materialize in that the vestibular postural reflex is not modified with adult aging.

However, the medium latency peak amplitude was 33% larger (Fig. 4H) for the AP force (whole-body response) of the old compared with young men indicating that indeed the vestibular-evoked postural response is altered with adult aging.

The vestibular-evoked response in AP force represents the net result of all postural muscles and cannot be explained by the similar results in the old and young men for the plantar flexor muscles. Healthy adult aging is accompanied by a decrease in muscle mass and alterations of architecture and mechanical properties of the triceps surae muscle-tendon unit (Baudry et al., 2012; Onambele et al., 2006), which is accompanied by altered motor control strategies for quiet standing in the older adult. Because older adults exhibit greater muscle activity and cortical drive during standing balance than their younger counterparts (Baudry et al., 2012, 2014; Benjuya et al., 2004), they likely respond differently to a vestibular error signal than the young. One explanation may be the increased activation of antagonistic muscles in the old men (Baudry et al., 2012; Benjuya et al., 2004). Even though we tested only three muscles acting at the ankle, the tibialis anterior displayed a greater medium latency peak amplitude response in the old than young. This larger medium latency response in the tibialis anterior was strongly correlated with a larger medium latency peak amplitude response in the AP force. Previous reports have speculated that increased central sensitivity of the vestibular input may overcompensate for the peripheral degeneration within the relevant structures for vestibular function (Jahn et al., 2003; Welgampola and Colebatch, 2002) or alternatively, the perception of vestibular information may be altered (Menant et al., 2012) in old men compared with the young. For example, increased anxiety (Brown et al., 2006) and attentional demands (Woollacott and Shumway-Cook, 2002) in older adults alter motor strategies during quiet standing compared with younger adults and may be tied to the heightened cortical processing in the old. Furthermore, somatosensory integration with the vestibulospinal reflex could also influence age-related differences (Welgampola and Colebatch, 2001). Thus, centrally mediated mechanisms may represent the underlying factors for the greater tibialis anterior activity and hence, an overcompensation in response to the vestibular error signal.

Furthermore, we observed a smaller short latency peak amplitude from the soleus of old men than the young similar to one previous report (Welgampola and Colebatch, 2002). Here, we extend these findings to the medial gastrocnemius and the whole-body postural response. Healthy adult aging is associated with impairments in the anatomical structures and physiological pathways within the vestibular system (Bergstrom, 1973; Merchant et al., 2000; Rosenhall, 1973), which may lead to a lower peak amplitude response for the short latency reflex in the old men compared with young. Additionally, the short latency is likely comprised of characteristics primarily related to a higher frequency bandwidth (10–25 Hz); whereas the medium latency response reflects lower frequencies (<10 Hz) at the muscle level. The disparate age-related alterations in the short and medium latency peak amplitude responses, or more specifically the smaller short latency peak amplitude response in the old compared with young, may relate to the absence of higher frequencies exhibited in the operating range of the vestibular-evoked reflex of the old men. Regardless of the mechanism, we confirm here that the short and medium latency peak amplitude responses not only display disparate age-related changes within the muscle, but these differences are observed when summated and presented at the whole-body level (AP force).

5. Conclusions

In summary, we demonstrated that the vestibular control of balance exhibits amplification in relative gain at lower frequencies in the old men; whereas vestibular reflexes operate over a wider frequency bandwidth in the young (Fig. 2E–H). The net output of all vestibular-evoked muscle responses led to smaller short and larger medium latency peak amplitudes in AP force for the old, which is likely related to lower

operational frequencies for the vestibulo-motor pathways and amplified activity in the tibialis anterior. Irrespective of the underlying mechanisms, vestibular control of standing balance is characterized over a lower and compressed frequency bandwidth in the old men when compared with younger counterparts. This lower frequency range represented at the muscle and whole-body level may reflect the greater instability older adults experience during standing balance.

Conflicts of interest

The authors have no conflicts of interest to disclose.

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B.H.D. conceived the study concept, collected and analyzed data, wrote, reviewed, and edited the manuscript. M.D.A. recruited participants, collected data, and reviewed and edited the manuscript. J.T.I. and J.S.B. assisted in developing the study, aided in interpretation of the results, and edited and reviewed the manuscript. C.L.R. aided in interpretation of the results, and edited and reviewed the manuscript.

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