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RESEARCH PAPER

Older adults show elevated intermuscular coherence in eyes-open standing but only young adults increase coherence in response to closing the eyes

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Abstract

Understanding neural control of standing balance is important to identify age-related degeneration and design interventions to maintain function. Here, intermuscular coherence between antagonist muscle pairs around the ankle-joint during standing balance tasks was investigated before and after strength training. Ten young (18–31 years; YOUNG) and nine older adults (66–73 years; OLDER) stood on a force plate for 120 s with eyes open followed by 120 s with eyes closed before and after 14 weeks of strength training. Postural sway was quantified from centre-of-pressure displacement based on 3-D force moments. Electromyography (EMG) was recorded from the gastrocnemius medialis (GM), soleus (SOL) and tibialis anterior (TA) muscles of the right leg. Coherence between rectified EMG pairs (GM–TA, SOL–TA) was calculated for each 120 s epoch separately. Postural sway was lower in YOUNG compared to OLDER in eyes-open (6.8 ± 1.3 vs. 10.3 ± 4.7 mm s⁻¹, $P = 0.028$) and eyes-closed (10.9 ± 3.1 vs. 24.4 ± 18.3 mm s⁻¹, $P = 0.032$) tasks. For both muscle pairs, OLDER had more prominent common input over 4–14 Hz with eyes open, but when the proprioceptive demand was enhanced in the eyes-closed task the YOUNG were able to further enhance their common input at 6–36 Hz ($P < 0.05$). Strength training reduced the instability from closing the eyes in OLDER but did not alter coherence. This may highlight a greater functional reserve in YOUNG than in OLDER and possible emerging proprioceptive degeneration in OLDER. However, the findings question the functional role of coherence for balance.

KEYWORDS

ageing, corticomuscular, corticospinal coupling, intervention, motor control, strength training

1 | INTRODUCTION

Approximately one-third of people over 65 years will experience one or more falls annually (Campbell, Borrie, & Spears, 1989). This leads to estimated economic costs of >\$23 billion in the USA and >\$1.6 billion in the UK (Davis et al., 2010), not to mention the impact on fear of future falls, independence and increased risk of mortality. It is of the utmost importance to understand potential neuromuscular deficiencies in balance control and to devise interventions to improve such qualities.

Bipedal stance can be biomechanically described as an inverted pendulum rotating about the ankle joint (Baudry, 2016); therefore investigating neuromuscular mechanisms controlling the ankle joint is pertinent. A sufficient level of ankle stiffness is required to prevent falling, which needs to be provided by the muscle-tendon unit and other surrounding tissue (Baudry, 2016). Since not all the required stiffness can be provided passively (Loram & Lakie, 2002), the neuromuscular system must actively modulate ankle stiffness to the adequate level. Here, the successful integration of visual, vestibular and somatosensory systems (Peterka, 2002) is required for optimal

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balance control, but age negatively affects the functioning of these systems (Shaffer & Harrison, 2007).

Active neuronal modulation has been shown to occur at both the supraspinal (Baudry, Collignon, & Duchateau, 2015; Tokuno, Cresswell, Thorstensson, & Carpenter, 2010) and the spinal level (Katz, Meunier, & Pierrot-Deseilligny, 1988) during different standing balance tasks. It has been suggested that neural control of standing balance operates under feedforward control with cortical sources exerting an influence on spinal mechanisms (Papegaaij, Taube, Baudry, Otten, & Hortobágyi, 2014). Especially in the case of reduced sensory input (e.g. closing the eyes during stance increases the emphasis of proprioception during standing) and increased task difficulty (e.g. an unstable surface), a greater emphasis on supraspinal control of balance seems to occur (Ozdemir, Contreras-Vidal, & Paloski, 2018).

Using electroencephalography, Ozdemir et al. (2018) observed greater cortical activity at 0.1–4 Hz in frontal and central cortices during an eyes-closed standing task, suggesting increased attention and cognition during challenging proprioceptive tasks. Papegaaij et al. (2014) proposed that the observed age-related changes in the neuronal control of standing balance could be partly due to the heightened relative difficulty of maintaining standing balance in older adults, as young people demonstrate similar changes during more complex balance tasks.

A potential approach is to quantify the level of common synaptic input to the muscles around the ankle joint to identify ageing-related neuronal degeneration. Intermuscular coherence reflects common synaptic input to spinal α -motoneurons by computing the correlation between signals of two muscles in the frequency domain (Halliday et al., 1995), and requires only simple non-invasive recording of (surface) EMG from a muscle pair. Coherence measured from two muscle pairs may reflect cortical, subcortical and/or spinal influences (Grosse, Cassidy, & Brown, 2002). Coherence in the 0–6 Hz band is thought to be related to force production/fluctuations (Bourguignon et al., 2017), while in the 8–14 Hz band coherence could reflect proprioceptive feedback from Ia afferents (Lippold 1970), and coherence in the 15–30 Hz band seems to have a strong supraspinal component (Aguiar, Baker, Gant, Bohorquez, & Thomas, 2018; Farmer, Swash, Ingram, & Stephens, 1993; Norton, Wood, Marsden, & Day, 2003). The interest in the 15–30 Hz band in human movement studies investigating the corticospinal tract seems justified since stroke and spinal cord injury reduce or ablate coherence during isometric contraction (Aguiar et al., 2018; Farmer et al., 1993; Norton et al. 2006). Nevertheless, the origin of coherence within each specific band is not explicitly known.

Previous studies investigating intermuscular coherence during bipedal standing balance tasks have shown strong coherence <6 Hz for a range of muscle pairings (Garcia-Masso, Pellicer-Chenoll, Gonzalez, & Toca-Herrera, 2016) and over 1–10 Hz in anterior and posterior muscle pairings (Danna-Dos-Santos et al., 2015) in young adults. When directly comparing young and older adults during standing, the same frequencies (i.e. <10 Hz) appear to be significant in both groups; however, coherence was stronger for older adults in unrestricted bipedal stance in posterior muscles and triceps surae muscle pairs

New Findings

- **What is the central question of this study?**

Can a 14-week strength-training programme modify intermuscular coherence levels during bipedal standing tasks with eyes open and eyes closed and reduce age-related differences?

- **What is the main finding and its importance?**

Older adults had more prominent common input over 4–14 Hz with eyes open, but during the eyes-closed task the young adults were able to further enhance their common input at 6–36 Hz. This indicates that young adults are better at modulating common input in different motor tasks.

(Dagani et al. 2017; Watanabe, Saito, Ishida, Tanabe, & Nojima, 2018a; Watanabe, Saito, Ishida, Tanabe, & Nojima, 2018b). Furthermore, increasing the difficulty of maintaining balance by performing unipedal stance (Watanabe et al., 2018a) or leaning forward (Watanabe et al., 2018b) led to increased strength of intermuscular coherence in both the 15–30 Hz band and at ~40 Hz in both age groups, but the evidence suggested that this response was blunted in the older adults (Watanabe et al., 2018b). However, closing the eyes, which would cause an increased reliance on proprioception, served to reduce coherence levels in these young adults (Danna-Dos-Santos et al., 2015). This seems to contradict the findings of Watanabe et al. (2018a,b) and should be clarified through further study.

These, and other previous studies, have increased knowledge regarding strategies of the central nervous system to maintain balance during stance, but there remains a lack of information on whether the observed differences between age groups are modifiable. It is, therefore, important to identify and counteract age-related sensorimotor impairments by developing effective (exercise) interventions for older adults and various patient groups. As an intervention strategy, strength training has been shown to improve corticospinal drive (which may potentially be relevant to reverse the blunting of the 15–30 Hz band response to challenging postural control) as opposed to endurance training (Vila-Cha, Falla, Correia, & Farina, 2012). Additionally, strength training has great importance in maintaining older adults' health and daily functioning (Turpela, Häkkinen, Haff, & Walker, 2017).

Consequently, the purpose of the present study was to investigate the effects of a 14-week strength training intervention on intermuscular coherence and standing balance performance. The primary aims of the study were: (1) to determine the strength of intermuscular coherence in agonist–antagonist muscle pairs about the ankle joint, and (2) to determine whether a short-term strength training intervention would modify intermuscular coherence during standing in young and older adults. Secondly, the study used regression analyses between postural sway and intermuscular coherence to indicate potential functionality of the quantified intermuscular coherence. We

hypothesized that: (1) older adults would display greater intermuscular coherence during standing with eyes open, and (2) strength training would reduce postural sway and increase intermuscular coherence at 15–30 Hz during standing with eyes closed in older adults.

2 | METHODS

2.1 | Ethical approval

The subjects were thoroughly informed (both written and verbally) about the study's objectives, methods, use of results, and possible risks/harms from participation, and were given the opportunity to ask questions of the researchers regarding the information provided. All subjects provided written informed consent prior to the study. The study was approved by the ethical committee of the University of Jyväskylä (2601.2016) and was performed according to the *Declaration of Helsinki* (2013), except for registration in a database.

2.2 | Subjects

Sixteen young (YOUNG, age range: 18–31 years, 4 men and 12 women) and 17 older (OLDER, age range: 66–73 years, 8 men and 9 women) adults volunteered for the study after responding to a local advertisement. None of the subjects had any history of neurological conditions including diabetes mellitus, none took any neurotropic medication, and none had any lower limb injuries or disabilities. Additionally, all older subjects underwent a medical examination to ensure there were no contraindications to performing maximal effort testing and strength training. *A priori* based on $\beta = 0.8$, $\alpha = 0.05$, effect size = 0.2 (G*power software, Heinrich-Heine University, Dusseldorf, Germany), it was determined that 10 subjects should be included in each group.

Importantly, the young and the older groups were similar for habitual physical activity levels to allow true evaluation of the effect of ageing. Similar physical activity levels and health status were ensured by the exclusion criteria: (1) regular aerobic exercise (>180 min·week⁻¹), (2) any previous strength training experience, (3) body mass index >37 , (4) serious cardiovascular disease or lower limb injuries/disease that may lead to complications during exercise or affect the ability to perform testing and training, (5) use of walking aids, (6) use of medication that affects the neuromuscular or endocrine systems, (7) previous testosterone-altering treatment, and (8) smoking.

One young and three older subjects did not complete the strength training intervention for various reasons and dropped out of the study (illness not related to the study, loss of interest, one older man suffered injury during the training). Additionally, two young subjects and one older subject whose EMG quality was bad (undecipherable signal-to-noise ratio and equipment malfunction) were removed. Finally, following removal of these subjects, significant intermuscular coherence at the expected frequency range was then observed in 10 out of 13 young and in 9 out of 13 older subjects. Data from these were then used in subsequent analyses.

2.3 | Test procedures

2.3.1 | Electromyography

EMG electrodes were placed following SENIAM guidelines (Hermens et al. 1999) and marked for the post-training testing session using indelible ink tattoos for m. soleus (SOL), gastrocnemius medialis (GM) and tibialis anterior (TA) of the right leg. Thereafter, bipolar electrodes were placed so that the tattoo fell at the mid-point between the two EMG electrodes.

Skin around the electrode position was shaved and abraded lightly with sand paper. Bipolar Ag/AgCl electrodes (5 mm diameter, 20 mm inter-electrode distance; Ambu BlueSensor N, Ballerup, Denmark) were positioned in-line with the orientation of the underlying fascicles of the target muscle, and guided by the tattoos to ensure reproducibility from session to session. Raw signals were sent from a hip-mounted pack to a receiving box (Telemetry 2400R, Noraxon, Scottsdale, AZ, USA) where they were sampled at 1000 Hz amplified at a gain of 500 (bandwidth 10–500 Hz, common mode rejection ratio >100 dB, input impedance >100 M Ω , baseline noise <1 μ V rms). EMG signals were then relayed to an analog-to-digital converter (Micro1401, Cambridge Electronic Design, Cambridge, UK) and stored by Signal 4.10 software (Cambridge Electronic Design).

2.3.2 | Balance tests

For the standing balance task, subjects stood unshod on a force plate (AMTI, OR6-6 model, Watertown, MA, USA) with feet hip-width apart and toes facing directly forward. Hands were held together in front of and resting on the body at hip level. First, the subjects stood quietly for 2 min with their gaze focused on a cross on the wall at eye-level 3 m in front, yielding a continuous 120 s recording. After a brief pause (<1 min), subjects closed their eyes and tried to maintain the same stable posture as before for a further 2 min. The subjects were not allowed to move their feet during the break between recordings, only to relax their legs, hips and upper body. It has been shown that reliable recordings of standing balance require a minimum of 90 s recording (Ruhe, Fejer, & Walker, 2010).

2.3.3 | Strength tests

After the balance tests, a maximal unilateral isometric ankle plantarflexion test was performed on a custom-built dynamometer. Subjects sat with their arms folded across the chest and secured so that their right leg was fully extended (hip angle = 110° , knee angle = 180°) and ankle positioned at 90° . After a standardized warm-up, subjects were instructed to push the footplate with the ball of their foot as hard as possible for approximately 3 s while under verbal encouragement. Subjects performed at least three trials, and if the force in the third trial was more than 5% greater than that of trial 1 or 2 then a fourth trial was performed. The highest instantaneous force value from the best trial was taken as the maximum voluntary contraction strength.

Finally, a maximal concentric strength test was performed on a horizontal leg press machine (David210, David Sports Ltd, Helsinki,

Finland). This strength test utilizes hip, knee and ankle extensors and was the primary exercise trained during the training intervention. Subjects performed a warm-up consisting of incremental sub-maximal loads and a decreasing number of repetitions (10–7–5–3–2–1). Thereafter, subjects attempted to extend the legs from a flexed position (hip angle = $\sim 70^\circ$, knee angle = $\sim 60^\circ$) to a fully extended position (hip angle = 110° , knee angle = 180°). If successful, the load was increased (approx. 2.5 or 5 kg) and a new attempt was made following 1.5 min rest. This procedure continued until the subject could no longer fully extend their legs against the given load. The last successful repetition was considered as the one-repetition maximum (1-RM) load.

2.4 | Strength training intervention

The subjects completed a supervised 14-week whole-body strength training intervention at a frequency of twice per week (i.e. 28 training sessions in total). The specific training programme details have been previously published (Walker et al., 2019). Briefly, all major muscle groups were trained using a linearly periodized programme with resistance machines used exclusively during the first 7 weeks (e.g. leg press, seated calf raise) and thereafter free-weight exercises were introduced (e.g. lunge, dumbbell shoulder press). Subjects were instructed how to perform each exercise, and their technique was constantly monitored by qualified instructors. Subjects were allowed to continue their habitual physical activities external to the study intervention, such as low intensity walking, cycling and swimming at a frequency of 1–3 times per week. Seven days after completing the final training session (to allow sufficient recovery), the subjects were re-tested in the standing balance and strength tests.

2.5 | Signal analyses

2.5.1 | Postural stability

Anterior–posterior (X) and medio-lateral (Y) forces directed to the force plate were sampled at 1000 Hz and later low-pass filtered offline at 7 Hz. Postural sway was quantified by first computing XY-magnitude of centre-of-pressure (CoP) distance (mm) from sample to sample, and then multiplying it with the sampling frequency (1000 Hz) in order to obtain the mean velocity ($\text{mm} \cdot \text{s}^{-1}$) of the CoP for both tasks separately. This measure was used to estimate the overall postural stability.

2.5.2 | Coherence analysis

Analyses were performed using Matlab (The Mathworks, Natick, MA, USA) using customized scripts in a similar manner as previously reported (Walker et al., 2019). Intermuscular coherence was calculated for the two antagonist muscle pairs (SOL–TA and GM–TA). The muscle pair GM–SOL was also investigated, but the high coherence values (~ 0.1 – 0.3 , over 2–40 Hz) clearly indicated that cross-talk had influenced the signals and, therefore, we resolved to focus on antagonist muscle pairs.

EMG signals were full-wave rectified prior to analyses. Previous studies have used rectified signals to compute intermuscular coherence during standing (e.g. Danna-Dos-Santos et al., 2015; Watanabe et al., 2018a). Rectification follows guidelines from simulation studies (Boonstra and Breakspear 2012) and likely allows capturing the temporal firing patterns of the motor units (Halliday et al., 1995).

The data were separated into non-overlapping windows of 512 samples (0.512 s) in length, which were subjected to fast Fourier transform, giving a frequency resolution of 1.95 Hz.

Denoting the Fourier transform of the two signals in the l th window at frequency λ as $F_{1,l}(\lambda)$ and $F_{2,l}(\lambda)$, the auto-spectrum of the first signal was given by:

$$f_{11}(\lambda) = \frac{1}{L} \sum_{l=1}^L F_{1,l}(\lambda) F_{1,l}(\lambda)^*$$

The cross-spectrum was calculated as:

$$f_{12}(\lambda) = \frac{1}{L} \sum_{l=1}^L F_{1,l}(\lambda) F_{2,l}(\lambda)^*$$

Here $*$ denotes the complex conjugate, and L is the total number of sections. The mean L -values for both pre- and post-training was 227 (range = 226–229).

Coherence was calculated as the cross-spectrum normalized by the auto-spectrum:

$$C(\lambda) = \frac{|f_{12}(\lambda)|^2}{f_{11}(\lambda) f_{22}(\lambda)}$$

Where $|\cdot|$ denotes the absolute value. Coherence above Z was considered significantly above chance, according to the formula developed by Brillinger (1981) and given by Rosenberg, Amjad, Breeze, Brillinger D, and Halliday (1989):

$$Z = 1 - \alpha^{1/(L-1)}$$

Where the significance level α was set to 0.05.

Intermuscular coherence spectra up to 100 Hz for each antagonist pair (i.e. SOL–TA and GM–TA) were averaged across subjects in each age-group (i.e. YOUNG and OLDER). The group significance level was then determined using the method of Evans and Baker (2003). Thereafter, coherence was sectioned into pre-defined bands: 2–6 Hz (theta), 8–14 Hz (alpha), 16–30 Hz (beta), and 40–60 Hz (gamma) and the average coherence within each window used to compare between groups and time points.

2.6 | Statistical analyses

Results are reported as means and standard deviations (SD). All statistical analyses were performed using SPSS Statistics software version 24 (IBM Corp., Armonk, NY, USA). To compare coherence–frequency curves both within and between groups, Z -scores via a hyperbolic arctan transform were generated according to the methods of Jaiser, Baker, and Baker (2016). Significant differences

for each frequency bin based on the Z-score analysis were estimated using Monte-Carlo simulations. Thereafter, coherence values from each bin within frequency bands 2–6, 8–14, 16–30 and 40–60 Hz were averaged. Neither average coherence values across the various frequency bands nor postural sway measures (XY sway $\text{mm} \cdot \text{s}^{-1}$) were normally distributed and so the data were \log_{10} transformed prior to statistical analyses. Repeated measures ANOVA was performed (2 group (YOUNG and OLDER) \times 2 condition (eyes open and eyes closed)) on the log transformed variables, and *post hoc* tests were performed if a significant main effect for Condition, Group or Condition \times Group interaction was observed. *Post hoc* tests were performed using an independent Student's *t* test (between-group comparisons) and a paired *t* test (within-group comparisons). Linear multiple regression analysis was performed to estimate the role of average intermuscular coherence in 2–6, 8–14, 16–30 and 40–60 Hz frequency bands in predicting postural sway using the forward stepwise method in SPSS.

3 | RESULTS

3.1 | Maximum strength

There were no between-group differences in 1-RM before (YOUNG: 120 ± 53 kg vs. OLDER: 134 ± 19 kg, $P = 0.717$) or after (YOUNG: 150 ± 48 kg vs. OLDER: 154 ± 27 kg, $P = 0.661$) the training period. In both groups, training similarly increased their 1-RM load (YOUNG: $\Delta 21 \pm 12$ kg, $P < 0.001$; OLDER: $\Delta 18 \pm 10$ kg, $P = 0.002$).

Similarly to 1-RM findings, isometric plantarflexion strength did not differ before (YOUNG: 155 ± 42 N m vs. OLDER: 154 ± 39 N m, $P = 0.952$) or after (YOUNG: 169 ± 45 N m vs. OLDER: 157 ± 34 N m, $P = 0.530$) training. However, in this test, only YOUNG showed improved strength to training (YOUNG: $\Delta 13 \pm 11$ N m, $P = 0.010$; OLDER: $\Delta 3 \pm 19$ N m, $P = 0.705$).

3.2 | Postural stability

Before the training period, postural sway (XY -magnitude) was lower in YOUNG compared to OLDER both with eyes open (YOUNG: 6.8 ± 1.3 vs. OLDER: 10.3 ± 4.7 $\text{mm} \cdot \text{s}^{-1}$, $P = 0.028$) and eyes closed (YOUNG: 10.9 ± 3.1 vs. OLDER: 24.4 ± 18.3 $\text{mm} \cdot \text{s}^{-1}$, $P = 0.032$). Closing the eyes led to greater instability in both YOUNG and OLDER ($P < 0.01$). Fourteen weeks of strength training did not alter the postural sway (XY -magnitude) in either group, and there remained the significant difference between eyes-open and eyes-closed tasks ($P < 0.01$) in both groups. However, the significant Time \times Group interaction observed ($F = 5.2$, $P = 0.036$) before training was no longer observed after training ($F = 2.9$, $P = 0.108$), indicating that the increase in postural sway from the eyes-open task to the eyes-closed task was greater in OLDER than YOUNG before ($\Delta 14 \pm 14$ $\text{mm} \cdot \text{s}^{-1}$ vs. 5 ± 2 $\text{mm} \cdot \text{s}^{-1}$, respectively) but not after training ($\Delta 10 \pm 10$ $\text{mm} \cdot \text{s}^{-1}$ vs. 4 ± 1 $\text{mm} \cdot \text{s}^{-1}$, respectively).

3.3 | Intermuscular coherence

3.3.1 | Individual coherence spectra for GM-TA and SOL-TA pairs

Figure 1 shows single-subject coherence spectra for two young and two older subjects before the training period. The intermuscular coherence peaked at approximately 10 Hz in most individuals regardless of age. Coherence was strongest in the eyes-closed task compared to the eyes-open task in general. However, while all YOUNG showed stronger intermuscular coherence when closing the eyes, there was a varied response in OLDER with some showing stronger coherence and others weaker coherence over 6–40 Hz frequencies (all individual data not shown).

3.3.2 | Group-averaged coherence spectra for GM-TA and SOL-TA pairs

Before training, there was a clear strengthening of GM-TA intermuscular coherence level to closing the eyes in YOUNG, which was not observed in OLDER. This resulted in significantly ($P < 0.05$, Z-score analyses) greater intermuscular coherence in OLDER with eyes open between 4 and 14 Hz (Figure 2a), but significantly greater coherence in YOUNG with eyes closed between 6 and 36 Hz (Figure 2b).

Again, a clear increase in SOL-TA intermuscular coherence was observed in YOUNG over a broad spectrum when closing the eyes. OLDER showed an increase in coherence from approximately 18 to 42 Hz. This resulted in significantly ($P < 0.05$, Z-score analyses) greater intermuscular coherence in OLDER with eyes open at 2, 4 and 14 Hz (Figure 3a), but significantly greater coherence in YOUNG with eyes closed between 6 and 22 Hz and also 32–34 Hz (Figure 3b).

3.3.3 | Group-averaged GM-TA and SOL-TA pairs within pre-defined bands

When the coherence values from each bin were averaged over 2–6, 8–14, 16–30 and 40–60 Hz, YOUNG displayed significant increases from eyes-open to eyes-closed tasks in the GM-TA muscle pair, with the exception of 40–60 Hz (Figure 4a). Such increases were not observed in OLDER. Fourteen weeks of strength training did not alter the intermuscular coherence responses from eyes-open to eyes-closed task in either group in the GM-TA muscle pair.

Averaged coherence in 2–6, 8–14 and 16–30 Hz frequency bands of the SOL-TA muscle pair showed significant increases from the eyes-open to eyes-closed task in YOUNG only (Figure 4b). The increase in 16–30 Hz in OLDER did not reach statistical significance ($P = 0.058$).

Strength training did not alter the significant coherence increase from eyes-open to eyes-closed task in either muscle pair. The only training-induced change in the magnitude of the coherence was observed in SOL-TA for the 16–30 Hz band during the eyes-closed task, which was weaker in YOUNG after training (before training: 0.051 ± 0.055 vs. after training: 0.031 ± 0.057 , $P = 0.012$, Figure 5).

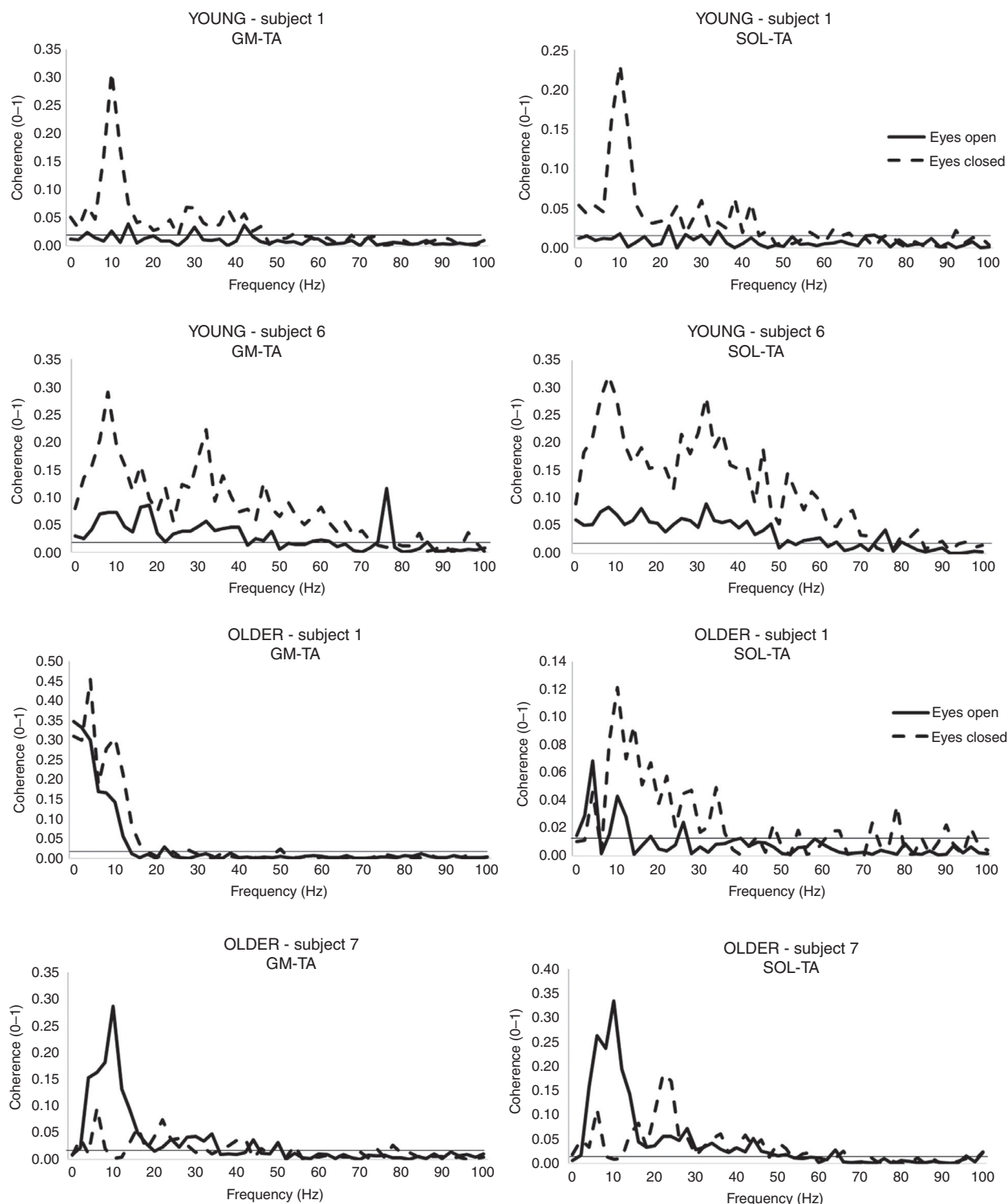


FIGURE 1 Coherence spectra (0–100 Hz) for agonist–antagonist muscle pairs during a standing balance test with eyes open (continuous line) and eyes closed (dashed line) in representative subjects before the training period. The horizontal lines represent the level of significance for the coherence

3.4 | Relationships between postural sway and intermuscular coherence

Regression analyses were performed to assess whether intermuscular coherence levels across predefined frequency bands could predict

postural sway. Significant findings were only observed during the eyes-closed task. Before training, postural sway was explained (adjusted $r^2 = 0.747$) by SOL-TA coherence at 16–30 Hz (coefficient = 219, $P < 0.001$, contribution = 0.536), GM-TA coherence at 16–30 Hz (coefficient = –387, $P < 0.001$, contribution = 0.401) and GM-TA

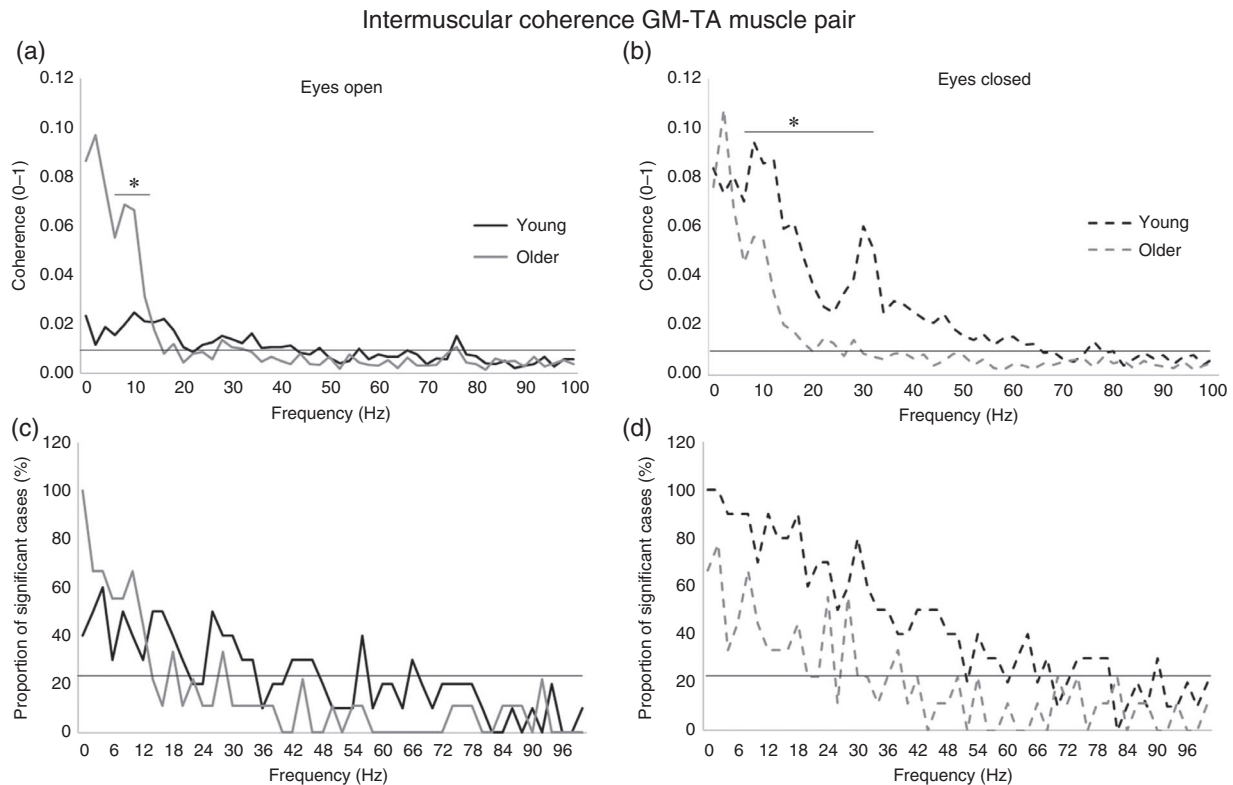


FIGURE 2 GM-TA muscle pair. Grand-average coherence spectra (0–100 Hz) during standing balance with test eyes open (a, continuous lines) and eyes closed (b, dashed lines) and the corresponding proportion of subjects within each group that showed significant coherence within each frequency bin (c,d) before the training period. The horizontal lines represent the level of significance. * $P < 0.05$ between groups based on Z-scores

coherence at 2–6 Hz (coefficient = 56, $P = 0.034$, contribution = 0.63). After training, postural sway was explained (adjusted $r^2 = 0.363$) by SOL-TA coherence at 16–30 Hz (coefficient = -0.455 , $P = 0.005$, contribution = 0.69) and GM-TA coherence at 16–30 Hz (coefficient = 0.370, $P = 0.043$, contribution = 0.31).

Regression analyses were also run for the change in postural sway (from eyes-open to eyes-closed task) against the change in intermuscular coherence across the different frequency bands. Before training, the change in postural sway was explained (adjusted $r^2 = 0.666$) by the change in SOL-TA coherence at 16–30 Hz (coefficient = 199, $P < 0.001$, contribution = 0.64) and the change in GM-TA coherence at 16–30 Hz (coefficient = -321 , $P < 0.001$, contribution = 0.36).

4 | DISCUSSION

YOUNG showed better postural stability during standing than OLDER with eyes open and eyes closed both before and after strength training. Closing the eyes, i.e. reducing visual input to enhance proprioceptive emphasis during standing balance, led to a greater increase in postural sway in OLDER, particularly before training. Interestingly, OLDER already showed elevated intermuscular coherence during the eyes-open task, particularly over 4–14 Hz, while a more robust strengthening of intermuscular coherence to closing the eyes was observed in YOUNG over 6–36 Hz. In this regard, we accept our

first hypothesis. Results of the regression models suggest that intermuscular coherence only predicts postural sway during standing with eyes closed rather than with eyes open. Finally, the strength training intervention was successful in that both YOUNG and OLDER demonstrated the expected increases in maximum leg press strength; however, it did not statistically improve standing balance performance in our healthy adults. Strength training also had little to no effect on intermuscular coherence during standing balance in either group. Consequently, our second hypothesis should be rejected.

4.1 | Coherence at 2–14 Hz

Aguiar et al. (2018) observed significant intermuscular coherence in lower-limb muscle pairs over 2–13 Hz in spinal cord injury patients, suggesting that coherence in these frequencies can be generated by spinal circuits. This interpretation would agree with the notion that ~ 10 Hz coherence could be generated at the spinal level by Ia afferent activity (Lippold 1970). Another possible source of the intermuscular coherence at 2–14 Hz could be the vestibular system. Dakin, Son, Inglis, and Blouin (2007) reported preferential transmission of 2–10 Hz (peaking at 7 Hz) and 11–20 Hz (peaking at 14 Hz) band coherence stochastic vestibular stimulation while standing. The authors tentatively identified these frequency bands with the vestibulospinal and reticulospinal pathways, respectively. Regardless of the precise origin of the coherence within this frequency range in the

Intermuscular coherence SOL-TA muscle pair

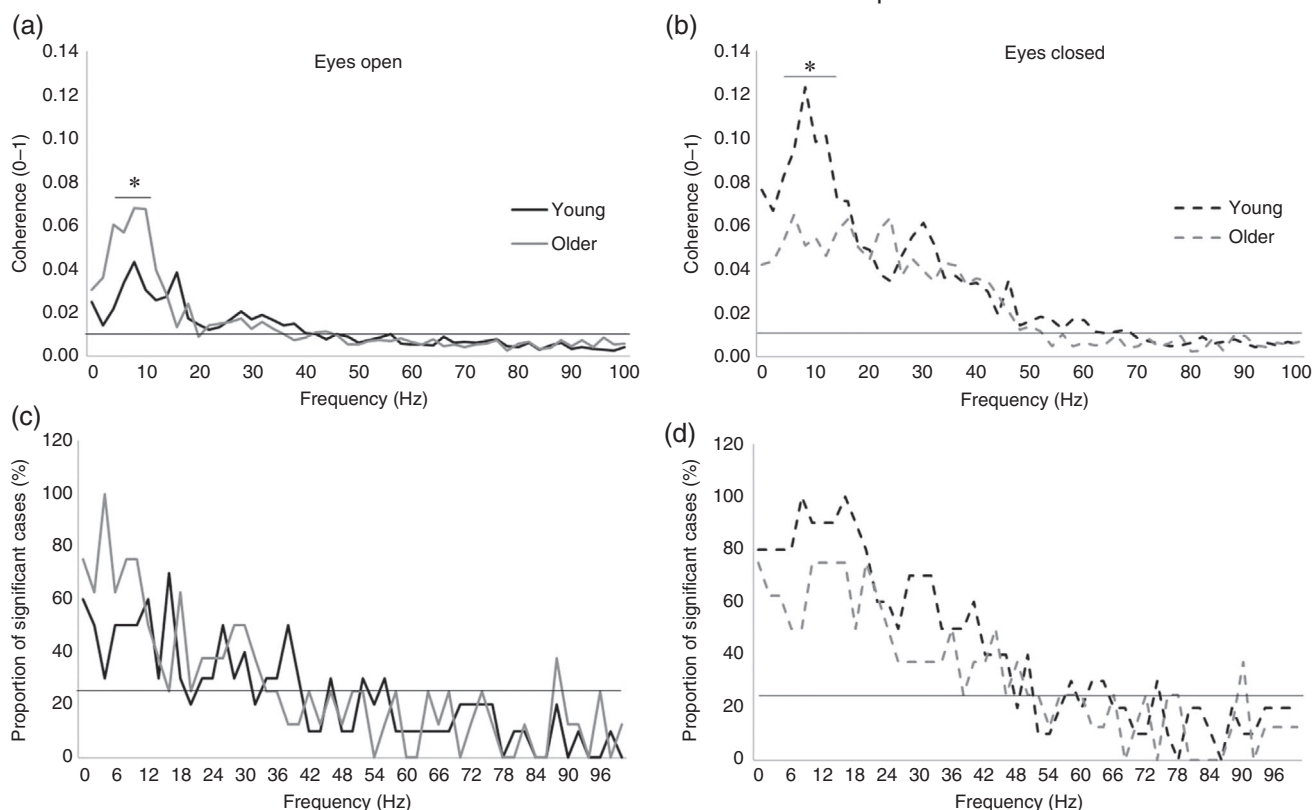


FIGURE 3 SOL-TA muscle pair. Grand-average coherence spectra (0–100 Hz) during standing balance test with eyes open (a, continuous lines) and eyes closed (b, dashed lines) and the corresponding proportion of subjects within each group that showed significant coherence within each frequency bin (c,d) before the training period. The horizontal lines represent the level of significance. * $P < 0.05$ between groups based on Z-scores

present study, it appears likely that the source is subcortical. However, we cannot fully rule out possible contribution of the neocortex with our data.

Balance control requires successful integration of visual, vestibular and somatosensory systems (Peterka, 2002). Since OLDER showed greater coherence at 2–14 Hz during standing with eyes open and lower modulation of coherence to closing the eyes, their postural control strategy differed from the YOUNG. These findings during unrestricted standing and the lack of modulation to a more challenging task are in agreement with previous studies investigating intermuscular coherence (Dagani et al. 2017; Watanabe et al., 2018a). Perhaps OLDER needed to up-regulate the vestibular/somatosensory information to counteract deficiencies in, for example, proprioception (Piitulainen, Seipäjärvi, Avela, Parviainen, & Walker, 2018) in order to control posture in the eyes-open task to the same level as YOUNG. Otherwise, the greater low frequency (i.e. <6 Hz) coherence may have been a consequence of greater XY sway in OLDER (Bourguignon et al., 2017; Garcia-Masso et al., 2016).

The only other study, to our knowledge, that investigated the influence of vision on standing balance and intermuscular coherence was performed by Danna-Dos-Santos et al. (2015). Interestingly, young subjects demonstrated significant intermuscular coherence only <10 Hz. The reason for the conflicting findings is unclear, since the postural sway in our study and Danna-Dos-Santos et al. (2015)

was very similar ($\sim 7 \text{ mm} \cdot \text{s}^{-1}$ with eyes open and $11 \text{ mm} \cdot \text{s}^{-1}$ with eyes closed), suggesting equivalent balance performance. Perhaps the source of the discrepancy lies in the selected muscle pairs, since the present study focused on muscles about the ankle (GM, SOL, TA) whereas the previous study matched proximal and distal muscles. One possibility, and a weakness of the present study, is that the locus of control has shifted between eyes open and eyes closed conditions. As the muscles of the hip- and knee-joint are also involved in standing balance, it is possible that the dominant coherent pairings during eyes open could be proximal and distal muscle pairs, which then shift to distal muscle pairs during eyes closed. This conflict in the findings, and speculative explanations provided, should be tested specifically in future studies.

In the present study, both YOUNG and OLDER demonstrated significant intermuscular coherence at $\sim 10 \text{ Hz}$ during the eyes-open task, but YOUNG strengthened coherence in this frequency range when closing the eyes. Reducing vision would naturally lead to an increased reliance on vestibular and somatosensory (especially proprioceptive) systems and, given the evidence above, lead to an increase in coherence at $\sim 10 \text{ Hz}$. We propose that OLDER already relied heavily on vestibular/somatosensory inputs even with eyes open, and hence the already elevated coherence at 2–14 Hz compared to YOUNG. It appears that there was no additional reserve in OLDER to utilize when closing the eyes.

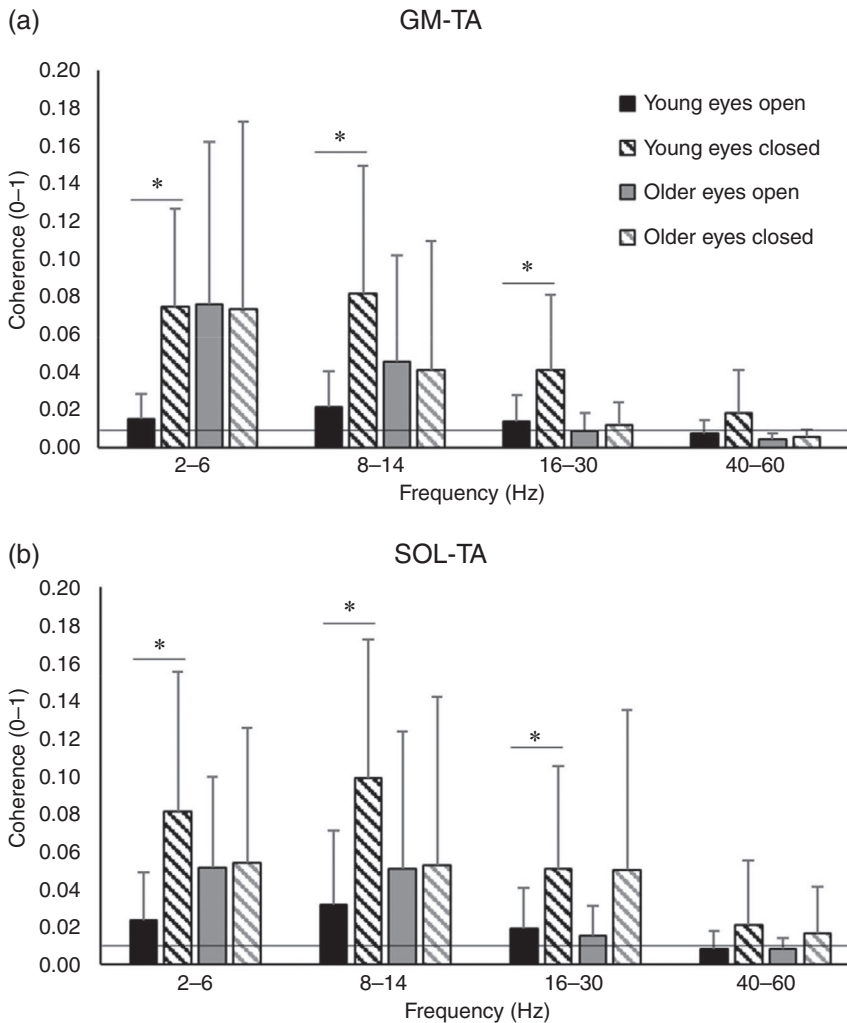


FIGURE 4 Grand-average intermuscular coherence at different frequency bands of interest for agonist-antagonist muscle pairs during standing balance test with eyes open (filled bars) and eyes closed (dashed bars) before the training period. * $P < 0.05$

4.2 | Coherence at 20–40 Hz

Intermuscular coherence within the 15–30 Hz frequency band has been shown to reflect common cortical input to spinal α -motoneurons (Baker, Olivier, & Lemon, 1997; Baker, Pinches, & Lemon, 2003; Farmer et al., 1993) and it seems to have a strong supraspinal component since stroke and spinal cord injury reduces or ablates coherence (Aguar et al., 2018; Farmer et al., 1993; Norton et al. 2006) during isometric contraction. The group-averaged coherence spectra showed that neither YOUNG nor OLDER demonstrated clear and significant coherence in the eyes-open standing task. Strikingly, once YOUNG closed their eyes, a prominent coherence peak at ~30 Hz appeared for both GM-TA and SOL-TA muscle pairs (Figure 2b and 3b). This would be predictable since more challenging balance tasks would lead to greater need for corticospinal influence (Watanabe et al., 2018a). However, the same phenomenon did not occur systematically in OLDER.

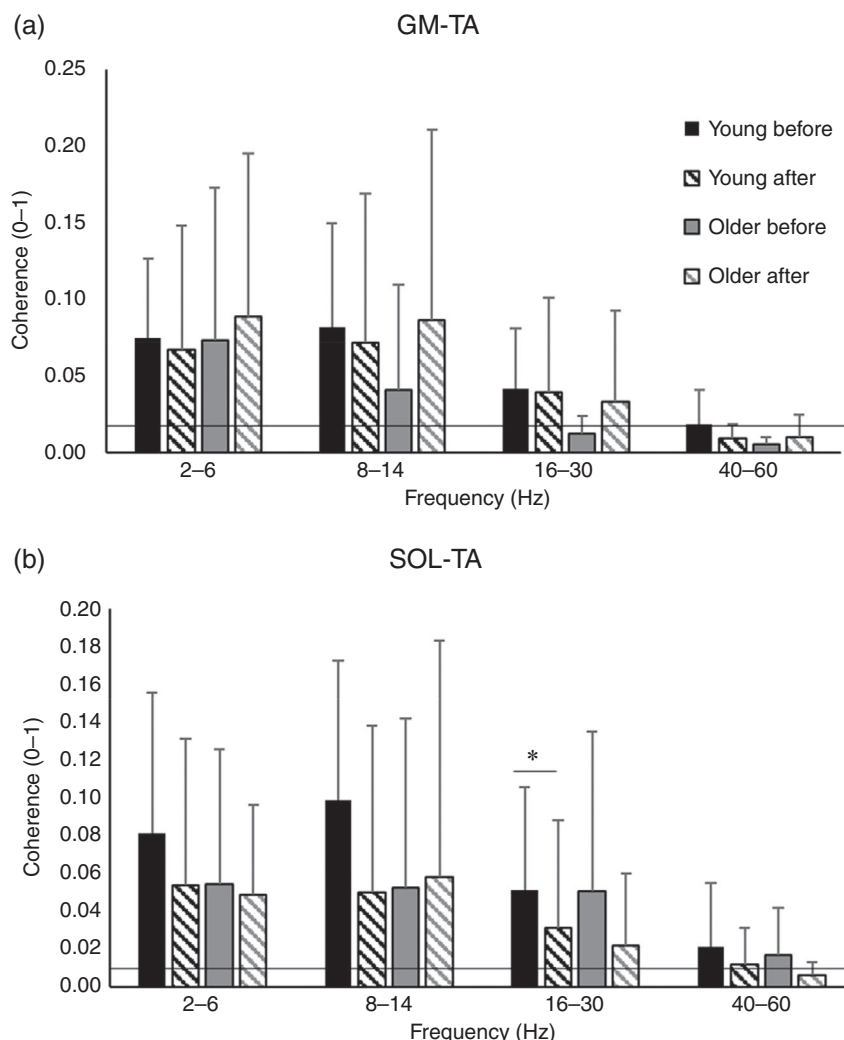
These findings match those of Watanabe and colleagues (2018b) who observed more pronounced modulation of ~30 Hz in young compared to older adults when challenging balance by leaning forward. It is unclear why such a robust increase in coherence at 20–40 Hz does not occur in older adults. However, the interindividual variability

was high in OLDER in the present study (Figure 1). Nevertheless, it appears that OLDER were not able to functionally coordinate (via corticospinal mechanisms) the antagonist muscles about the ankle joint. One possibility is that YOUNG could more readily adapt their ~20 Hz rhythm based on low frequency (<3 Hz) postural sway and the consequent somatosensory (primarily proprioceptive) feedback to the cortex, as seen in isometric contractions (Bourguignon et al., 2017), thereby demonstrating improved sensorimotor integration and more efficient postural control.

4.3 | Training intervention considerations

Strength training is very important to counteract age-related effects on health and daily function (Turpela et al., 2017), but our intervention did not improve balance control. Strength training and balance training have been shown to produce differing neural adaptations (Gruber et al., 2007) and strength training alone does not necessarily improve balance performance (Santos et al., 2017). Although free-weight exercises to challenge postural stability were implemented during the last 7 weeks of the present study's intervention, this may not have provided a sufficient sensorimotor stimulus in these subjects. Only modest (~9%) increases in plantarflexion strength were

FIGURE 5 Grand-average intermuscular coherence at different frequency bands of interest for GM-TA (a) and SOL-TA (b) agonist-antagonist muscle pairs during standing balance test before (filled bars) and after (dashed bars) the training period in the eyes-closed task. * $P < 0.05$



observed in YOUNG with no change in OLDER. As balance control is largely determined by ankle stiffness (Baudry, 2016), strength training interventions that improve plantarflexor strength may be warranted.

Perhaps using unstable surfaces during strength training over a longer duration may provide a stimulus for improving balance (Behm, Muehlbauer, Kibele, & Granacher, 2015). Alternatively, the duration of the intervention may not have been sufficient, since habitually (long-term) physically active older adults out-performed sedentary older adults during a standing balance task (Prioli et al. 2005).

4.4 | Intermuscular coherence as a test of sensorimotor function

Regression analyses show that postural sway (XY-magnitude) with eyes closed is related to the level of intermuscular coherence. These results suggest that intermuscular coherence reflects motor control strategies during standing balance tasks. Nevertheless, there remains uncertainty about the mechanisms contributing to the intermuscular coherence, as well as their exact role in balance control. This uncertainty is accentuated by the combined positive and negative

coefficients within the regression results. Therefore, caution should be used in their interpretation.

The notion of using surface EMG during standing balance tasks as a biomarker of sensorimotor ageing or deficiency is appealing. The test is easy to implement and could be widely distributed (Jaiser et al., 2016), and has the potential to be a useful biomarker for early detection of neuronal degradation or subclinical disease (Fisher, Zaaimi, Williams, Baker, & Baker, 2012; Larsen, Zibrandtsen, & Wienecke, 2017). However, our regression equations suggest that it would be unlikely that it would be possible to develop thresholds for diagnosis, and previous evidence suggests that the level of coherence does not readily (linearly) associate with postural sway (Watanabe et al., 2018a). Furthermore, there are methodological considerations that should be taken into account prior to recommending intermuscular coherence as a biomarker, e.g. reliability.

Suboptimal reliability scores have been observed in tasks in which force output is not precisely matched (Jaiser et al., 2016), which may be one reason for the lack of training-induced change in intermuscular coherence in the present study. As the standing balance task (and CoP displacement) may differ from one session to the next, so may the coherence differ. Nevertheless, we measured standing balance over

a longer than typical time period (120 s) in order to minimize task variability. Another methodological disadvantage is the various noise components in the frequencies of interest for the coherence analyses, and especially harmful are broad-band noise sources. Averaging across multiple frequency bins can somewhat alleviate this problem, since we increased the signal-to-noise ratio (by $\sqrt{3} \approx 1.7$ in 2–6 Hz, by $\sqrt{4} = 2$ in 8–14 Hz, and by $\sqrt{8} \approx 2.8$ in 16–30 Hz) of our analyses. Finally, we cannot be completely certain that some of the findings were not influenced by the small sample size. To satisfy statistical power estimates, there should have been at least 10 subjects in each group. While we recruited more than this number, the final n in OLDER was 9.

In conclusion, YOUNG had less postural sway than OLDER in both eyes-open and eyes-closed tasks. OLDER demonstrated stronger intermuscular coherence during standing with eyes open, while YOUNG showed greater capacity to modulate intermuscular coherence during the more demanding eyes-closed standing task that emphasizes more somatosensory, primarily proprioceptive afference. The results of the present study may, therefore, demonstrate a functional reserve in YOUNG that can be utilized under sensory reduction. OLDER, on the other hand, may well not have such a functional reserve, which was reflected in (1) the already elevated coherence, and (2) the lack of intermuscular coherence modulation. Strength training increased maximum force production of the leg extensors in both groups, and the significant difference between age groups in the eyes-closed standing task was not present after training. However, 14 weeks of strength training did not modify intermuscular coherence during standing, which questions its functional relevance.

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COMPETING INTERESTS

None declared.

AUTHOR CONTRIBUTIONS

S.W., H.P., J.A. and S.N.B. conceptualized the study and formulated its design. S.W. and T.M. collected the data. S.W. and S.N.B. analysed the data. S.W. acquired funding for the study. S.W. wrote the first draft of the manuscript. S.W., H.P., T.M., J.A. and S.N.B. reviewed and edited the manuscript. All authors have read and approved the final version of this manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part

of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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REFERENCES

- Aguilar, S. A., Baker, S. N., Gant, K., Bohorquez, J., & Thomas, C. K. (2018). Spasms after spinal cord injury show low-frequency intermuscular coherence. *Journal of Neurophysiology*, 120(4), 1765–1771.
- Baker, S. N., Olivier, E., & Lemon, R. N. (1997). Coherent oscillations in monkey motor cortex and hand muscle EMG show task-dependent modulation. *Journal of Physiology*, 501(1), 225–241.
- Baker, S. N., Pinches, E. M., & Lemon, R. N. (2003). Synchronization in monkey motor cortex during a precision grip task. II. effect of oscillatory activity on corticospinal output. *Journal of Neurophysiology*, 89(4), 1941–1953.
- Baudry, S. (2016). Aging changes the contribution of spinal and corticospinal pathways to control balance. *Exercise and Sport Sciences Reviews*, 44(3), 104–109.
- Baudry, S., Collignon, S., & Duchateau, J. (2015). Influence of age and posture on spinal and corticospinal excitability. *Experimental Gerontology*, 69, 62–69.
- Behm, D. G., Muehlbauer, T., Kibele, A., & Granacher, U. (2015). Effects of strength training using unstable surfaces on strength, power and balance performance across the lifespan: a systematic review and meta-analysis. *Sports Medicine*, 45(12), 1645–1669.
- Boonstra T. W., & Breakspear M. (2012). Neural mechanisms of intermuscular coherence: implications for the rectification of surface electromyography. *Journal of Neurophysiology*, 107(3), 796–807.
- Bourguignon, M., Piitulainen, H., Smeds, E., Zhou, G., Jousmäki, V., & Hari, R. (2017). MEG insight into the spectral dynamics underlying steady isometric muscle contraction. *Journal of Neuroscience*, 37, 10421–10437.
- Brillinger, D. R. (1981). *Time Series—Data Analysis and Theory* (2nd ed., pp. 570). San Francisco: Holden Day.
- Campbell, J. A., Borrie, M. J., & Spears, G. F. (1989). Risk factors for falls in a community-based prospective study of people 70 years and older. *Journal of Gerontology*, 44(4), M112–M117.
- Dagani, A. M., Leonard, C. T., & Danna-Dos-Santos, A. (2017). The use of intermuscular coherence analysis as a novel approach to detect age-related changes on postural muscle synergy. *Neuroscience Letters*, 656, 108–113.
- Dakin, C. J., Son, G. M., Inglis, J. T., & Blouin, J. S. (2007). Frequency response of human vestibular reflexes characterized by stochastic stimuli. *Journal of Physiology*, 583(3), 1117–1127.
- Danna-Dos-Santos, A., Degani, A. M., Boonstra, T. W., Mochizuki, L., Harney, A. M., Schmeckpeper, M. M., ... Leonard, C. T. (2015). The influence of visual information on multi-muscle control during quiet stance: A spectral analysis approach. *Experimental Brain Research*, 233, 657–669.
- Davis, J. C., Robertson, M. C., Ashe, M. C., Liu-Ambrose, T., Khan, K. M., & Marra, C. A. (2010). International comparison of cost of falls in older adults living in the community: A systematic review. *Osteoporosis International*, 21, 1295–1306.
- Evans, C. M., & Baker, S. N. (2003). Task-dependent intermanual coupling of 8-Hz discontinuities during slow finger movements. *European Journal of Neuroscience*, 18, 453–456.
- Farmer, S. F., Swash, M., Ingram, D. A., & Stephens, J. A. (1993). Changes in motor unit synchronization following central nervous lesions in man. *Journal of Physiology*, 463, 83–105.

- Fisher, K. M., Zaimi, B., Williams, T. L., Baker, S. N., & Baker, M. R. (2012). Beta-band intermuscular coherence: A novel biomarker of upper motor neuron dysfunction in motor neuron disease. *Brain*, 135, 2849–2864.
- Garcia-Masso, X., Pellicer-Chenoll, M., Gonzalez, L. M., & Toca-Herrera, J. L. (2016). The difficulty of the postural control task affects multi-muscle control during quiet standing. *Experimental Brain Research*, 234, 1977–1986.
- Grosse, P., Cassidy, M. J., & Brown, P. (2002). EEG-EMG, MEG-EMG and EMG-EMG frequency analysis: Physiological principles and clinical applications. *Clinical Neurophysiology*, 113, 523–531.
- Gruber, M., Gruber, S. B., Taube, W., Schubert, M., Beck, S. C., & Gollhofer, A. (2007). Differential effects of ballistic versus sensorimotor training on rate of force development and neural activation in humans. *Journal of Strength and Conditioning Research*, 21(1), 274–282.
- Halliday, D. M., Rosenberg, J. R., Amjad, A. M., Breeze, P., Conway, B. A., & Farmer, S. F. (1995). A framework for the analysis of mixed time series/point process data – theory and application to the study of physiological tremor, single motor unit discharges and electromyograms. *Progress in Biophysics and Molecular Biology*, 64(2–3), 237–278.
- Hermens, H., Freriks, B., Merletti, R., et al. (Eds.) (1999). *SENIAM European Recommendations for Surface Electromyography*. Enschede, The Netherlands: Roessingh Research and Development.
- Jaiser, S. R., Baker, M. R., & Baker, S. N. (2016). Intermuscular coherence in normal adults: Variability and changes with age. *PLoS One*, 11, e0149029.
- Katz, R., Meunier, S., & Pierrot-Deseilligny, E. (1988). Changes in pre-synaptic inhibition of Ia fibres in man while standing. *Brain*, 111(2), 417–437.
- Larsen, L. H., Zibrandtsen, I. C., Wienecke, T. et al. (2017). Corticomuscular coherence in the acute and subacute phase after stroke. *Clinical Neurophysiology*, 128, 2217–2226.
- Lippold, O. C. (1970). Oscillations in the stretch reflex arc and the origin of the rhythmical 8–12 C-S component of physiological tremor. *Journal of Physiology*, 206, 359–382.
- Loram, I. D., & Lakie, M. (2002). Direct measurement of human ankle stiffness during quiet standing: The intrinsic mechanical stiffness is insufficient for stability. *Journal of Physiology*, 545(3), 1041–1053.
- Norton, J. A., & Gorassini, M. A. (2006). Changes in cortically related intermuscular coherence accompanying improvements in locomotor skills in incomplete spinal cord injury. *Journal of Neurophysiology*, 95(4), 2580–2589.
- Norton, J. A., Wood, D. E., Marsden, J. F., & Day, B. L. (2003). Spinally generated electromyographic oscillations and spasms in a low-thoracic complete paraplegic. *Movement Disorders*, 18(1), 101–106.
- Ozdemir, R. A., Contreras-Vidal, J. L., & Paloski, W. H. (2018). Cortical control of upright stance in elderly. *Mechanisms of Ageing and Development*, 169, 19–31.
- Papegaaij, S., Taube, W., Baudry, S., Otten, E., & Hortobágyi, T. (2014). Aging causes a reorganization of cortical and spinal control of posture. *Frontiers in Aging Neuroscience*, 6, 28.
- Peterka, R. J. (2002). Sensorimotor integration in human postural control. *Journal of Neurophysiology*, 88, 1097–1118.
- Piitulainen, H., Seipäjärvä, S., Avela, J., Parviainen, T., & Walker, S. (2018). Cortical proprioceptive processing is altered by aging. *Frontiers in Aging Neuroscience*, 10, 147.
- Prioli, A. C., Freitas Júnior, P. B., & Barela, J. A. (2005). Physical activity and postural control in the elderly: coupling between visual information and body sway. *Gerontology*, 51(3), 145–148.
- Rosenberg, J. R., Amjad, A. M., Breeze, P., Brillinger D. R., & Halliday, D. M. (1989). The Fourier approach to the identification of functional coupling between neuronal spike trains. *Progress in Biophysics and Molecular Biology*, 53, 1–31.
- Ruhe, A., Fejer, R., & Walker, B. (2010). The test-retest reliability of centre of pressure measures in bipedal static task conditions – A systematic review of the literature. *Gait & Posture*, 32, 436–445.
- Shaffer, S. W., & Harrison, A. L. (2007). Aging of the somatosensory system: A translational perspective. *Physical Therapy*, 87, 193–207.
- Santos, S. M., da Silva, R. A., Terra, M. B., Almeida, I. A., deMelo, L. B., & Ferraz, H. B. (2017). Balance versus resistance training on postural control in patients with Parkinson's disease: A randomized controlled trial. *European Journal of Physical and Rehabilitation Medicine*, 53(2), 173–183.
- Tokuno, C. D., Cresswell, A. G., Thorstensson, A., & Carpenter, M. G. (2010). Age-related changes in postural responses revealed by support-surface translations with a long acceleration-deceleration interval. *Clinical Neurophysiology*, 121(1), 109–117.
- Turpela, M., Häkkinen, K., Haff, G. G., & Walker, S. (2017). Effects of different strength training frequencies on maximum strength, body composition and functional capacity in healthy older individuals. *Experimental Gerontology*, 98, 13–21.
- Vila-Cha, C., Falla, D., Correia, M. V., & Farina, D. (2012). Changes in H reflex and V wave following short-term endurance and strength training. *Journal of Applied Physiology*, 112, 54–63.
- Walker, S., Avela, J., Wikgren, J., Meeusen, R., Piitulainen, H., Baker, S. N., & Parviainen, T. M. (2019). Aging and strength training influence knee extensor intermuscular coherence during low- and high-force isometric contractions. *Frontiers in Physiology*, 9, 1933.
- Watanabe, T., Saito, K., Ishida, K., Tanabe, S., & Nojima, I. (2018a). Coordination of plantar flexor muscles during bipedal and unipedal stances in young and elderly adults. *Experimental Brain Research*, 236, 1229–1239.
- Watanabe, T., Saito, K., Ishida, K., Tanabe, S., & Nojima, I. (2018b). Age-related declines in the ability to modulate common input to bilateral and unilateral plantar flexors during forward postural lean. *Frontiers in Human Neuroscience*, 12, 254.

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