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Corticospinal control of normal and visually guided gait in healthy older and younger adults

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ABSTRACT

We investigated age-related differences in corticospinal control of muscle activity during normal and visually guided (VG) walking. Young (n = 15, 22.1 ± 1.7 years) and older (n = 15, 68.3 ± 2.7 years) participants performed normal walking and VG walking requiring precise foot placement based on visual cues. Coherence analysis was used to quantify coupling between electroencephalography and electromyography from the anterior tibial muscle (corticomuscular) and between the 2 ends of the anterior tibial muscle (intramuscular) at 15–50 Hz during the swing phase of walking as markers of corticospinal activity. Our results indicated that corticomuscular and intramuscular coherence was lower in older compared to young participants during both tasks. In addition, coherence was generally greater during VG than during normal walking across age groups, although during late swing, older participants drove several of the observed task-related coherence increases. Performance on the VG task was lower in older compared to young participants and was correlated with task-related corticomuscular coherence modulations within the older group. These results suggest age-related differences in the corticospinal control of walking, with possible implications for precision control of foot placement based on visual information.

1. Introduction

Gait is a fundamental motor function for humans and is a critical component of mobility, allowing us to move around in our environment. Successful navigation in our surroundings requires that the nervous system not only generates complex rhythmically alternating flexion and extension limb movements but also that this basic gait pattern is modified according to sensory feedback, including visual information about conditions in unfamiliar and unpredictable environments.

However, gait function declines with advancing age. The prevalence of gait impairment increases markedly from ~10% at ages 60–69 years to over 60% in elderly over 80 years (Mahlknecht et al., 2013). This has a negative impact on quality of life (Mahlknecht et al., 2013) and personal freedom (Verghese et al., 2006). Gait problems are important precipitating causes of falling in the elderly (Rubenstein, 2006) and are associated with impaired mobility and increased mortality (Newman et al., 2006; Verghese et al., 2006). Importantly, age differences in gait function appear particularly pronounced when changes in the walking pattern are implemented in response to visual information (Patla, 1993).

The causes of age-related gait impairments appear to be both central and peripheral; earlier research has focused on peripheral mechanisms, for example, sarcopenia (Bassey et al., 1988; Fiatarone et al., 1990; Landi et al., 2012), but deficiencies in the ability of the central nervous system to process and integrate information may be more important (Seidler et al., 2010). Much of the previous work on the role of impaired central nervous system function for gait problems in the elderly has focused on specific pathological conditions (Rosso et al., 2013), yet an understanding of the neural mechanisms mediating gait declines in elderly without overt neurological diseases is lacking and is an important basis for developing rehabilitation strategies.

Human bipedal gait is coordinated by integrated activity in brain and spinal neuronal networks (Nielsen, 2003). It is possible to attain insight into the organization of these networks by using coherence analysis of motor unit firing behavior during walking (Barthelemy et al., 2010; Halliday et al., 2003; Hansen et al., 2001). Coherence is a correlational measure indicating the strength of association

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between 2 signals as a function of frequency (Halliday et al., 1995) and thus allows for describing the frequency content of common presynaptic inputs synchronizing firing among different motor unit populations (Farmer et al., 1993).

In healthy young adults, coherence analysis has been used to demonstrate that motor unit populations within the same muscle receive common synaptic input at ~15–50 Hz (intramuscular coherence) during walking, and that input at these frequencies is modulated across the gait cycle (Halliday et al., 2003; Hansen et al., 2001). Seeing as stroke patients and patients with spinal cord lesions exhibit strongly reduced or absent intramuscular coherence at ~15–50 Hz during walking, it has been argued that functional corticospinal drive is a prerequisite for the occurrence of coherence at these frequencies (Barthelemy et al., 2010; Hansen et al., 2005; Nielsen et al., 2008). More direct evidence of corticospinal involvement has also been provided by the demonstration of coherence at ~24–40 Hz between electroencephalography (EEG) from the sensorimotor cortex and electromyography (EMG) from the anterior tibial (TA) muscle (corticomuscular coherence) during walking (Petersen et al., 2012). The functional importance of this activity for normal gait function is exemplified by associations between the amount of intramuscular coherence in TA during walking and the degree of foot drop in patients with spinal cord injury (Barthelemy and Nielsen, 2010). Few studies have investigated neural networks underlying the control of visually guided (VG) gait modifications in humans (Jensen et al., 2018; Schubert et al., 1999), although a recent study found increased intramuscular TA coherence during walking requiring precise foot placement based on visual input compared to normal walking (Jensen et al., 2018). These results suggest that the corticospinal involvement in gait control increases when foot placement during walking is guided by visual information.

Aging may entail functional changes in the corticospinal pathway to the ankle muscles, evidenced in findings of lower corticomuscular and intramuscular coherence in older compared to young adults during a simple static motor task (Spedden et al., 2018), as well as lower corticomuscular coherence during gait-like ankle movements (Yoshida et al., 2017). However, the effect of aging on corticomuscular and intramuscular coherence during actual walking, as well as during VG gait modifications, has yet to be determined. To this end, we aimed to investigate corticomuscular and intramuscular coherence in TA at 15–50 Hz in young compared to older adults during 2 tasks: normal, steady-state walking, and a VG gait task requiring precise foot placement according to visual cues. Our hypothesis was that coherence would be lower in older compared to young participants during both tasks, based on previous findings of less corticomuscular coherence in older adults during simpler tasks involving the ankle muscles (Spedden et al., 2018; Yoshida et al., 2017). On the basis that corticospinal activity contributes to the implementation of VG gait modifications (Jensen et al., 2018; Schubert et al., 1999), we further expected that young participants would increase coherence from normal to VG walking, and that these increases would be associated with better task performance. We also hypothesized that older participants would fail to exhibit task-related increases in coherence in parallel with reduced performance on the VG task, in accordance with results from a recent study suggesting that the ability to modulate coherence may be impaired in older adults (Watanabe et al., 2018).

2. Methods

2.1. Participants

Thirty healthy participants, 15 young (age range 20–26 years; 8 women) and 15 older (age range 65–73 years; 8 women) adults, were recruited from the community by convenience sampling (Table 1). No participants reported neurological disorders or conditions affecting gait function, and none received medication influencing neuromuscular function. Participants were deemed cognitively intact based on Mini-Mental State Examination scores ≥26 of 30 (Folstein et al., 1975). Written, informed consent was obtained before participation according to the Declaration of Helsinki, and the protocol was approved by the ethics committee for the Capital Region of Denmark (H-16021214). In addition to the gait tasks that are the focus of this study, participants also performed other motor tasks (Spedden et al., 2018), but gait data have not been previously published.

2.2. Overview

This study utilized a cross-sectional design to investigate age-related differences in corticomuscular and intramuscular coherence in TA during normal and VG walking. Young and older participants were tested over 2 days. On the first test day, participants completed questionnaires, an acuity assessment, and balance and cognitive tests. On the second test day, participants performed normal and VG walking, while electrophysiological and motion capture data were recorded.

2.3. Questionnaires

Leg dominancy was evaluated by the Waterloo Footedness Questionnaire (Elias and Bryden, 1998), which categorizes "footedness" as right, left, or mixed footed based on reported foot preference in active and stabilizing tasks. The International Physical Activity Questionnaire-short form (IPAQ-SF) was used to estimate physical activity level quantified as metabolic equivalent (MET) minutes per week based on reported frequency and duration of walking, moderate-intensity, and vigorous-intensity activities for the previous 7 days (Cheng, 2016; Craig et al., 2003). The Falls Efficacy Scale-International version assessed confidence in performing various activities of daily living without falling (Yardley et al., 2005) and provides a score ranging from 16 to 64, where a higher score indicates greater concerns about the possibility of falling. On the second test day, before performance of gait tasks, alertness was evaluated with the Stanford Sleepiness Scale on a scale of 1 (feeling alert) to 7 (approaching sleep onset) (Hoddes et al., 1973).

Table 1
Characteristics of the participants

Variables	Young ($n = 15$)	Older ($n = 15$)
Age (y)	22.1 ± 1.7	68.3 ± 2.7***
Gender (M/F)	7/8	7/8
Height (m)	1.76 ± 0.08	1.73 ± 0.11
Body mass (kg)	72.95 ± 15.89	81.45 ± 14.12
MMSE (score out of 30)	29.0 ± 1.1	28.9 ± 1.0
Footedness (R/L/B)	11/1/3	10/1/4
Snellen acuity ratio	0.99 ± 0.1	0.93 ± 0.1
Physical activity (MET min/wk)	3591 ± 1780	1992 ± 1255**
FES-I score (range from 16 to 61)	17.5 ± 1.6	18.7 ± 2.5
Sleepiness (scale from 1 to 7)	2.0 ± 0.5	1.7 ± 0.8
Reaction time (ms)	261 ± 22	322 ± 48***
RVP score (range from 0 to 1)	0.91 ± 0.06	0.89 ± 0.04
COP path length EO (m)	0.46 ± 0.12	0.74 ± 0.37*
COP path length EC (m)	0.72 ± 0.18	1.47 ± 0.88**

Descriptive statistics are presented as mean ± standard deviation except for footedness and gender. Significant age group differences are indicated by ***$p < 0.001$, ** $p < 0.010$, *$p < 0.050$.

Key: B, both; COP, center of pressure; EO, eyes open; EC, eyes closed; FES-I, Falls Efficacy Scale-International; L, left; MET, metabolic equivalent; MMSE, Mini-Mental State Examination; R, right; RVP, Rapid Visual Information Processing.

2.4. Acuity

Binocular visual acuity (VA) was tested using a Snellen letter chart with optical correction, that is, glasses or contact lenses, when relevant. The chart line successfully read aloud with a maximum of 2 mistakes was noted and an acuity ratio was calculated as $VA = D'/D$, where D' is the distance to the chart (6 m) and D is the line number, indicating the distance at which each letter in the line subtends 5 minutes of arc (Kalloniatis and Luu, 2007). Ratios were calculated for $D \geq 6$ (i.e., the maximal obtainable score was $6/6 = 1$).

2.5. Balance tests

Postural stability was quantified on the basis of its importance for age-related differences in gait function (Woollacott and Tang, 1997). Center of pressure path length was determined for 30s bipedal stance with feet together in socks on a force plate (AMTI, model OR6-6-1000, USA) in 2 conditions: with eyes open and eyes closed. Force plate data were sampled online at 1000 Hz, then down sampled offline to 100 Hz, and filtered using a Butterworth filter with a cutoff of 10 Hz (Ruhe et al., 2010). Path length was determined by summing the distance between successive center of pressure locations.

2.6. Cognitive tests

A Cambridge Neuropsychological Test Automated Battery (CANTAB, Cambridge Cognition, UK) was utilized to assess function in 2 cognitive domains potentially pertinent to VG walking performance: processing speed (based on simple reaction time) and sustained visual attention. Tests were performed on a monitor with a touchscreen, and the dominant hand was used to press a button and/or touch the screen in response to visual stimuli.

Simple reaction time (RTI) was evaluated in a single-choice paradigm where participants responded to the appearance of a yellow spot in the center of the screen. At the start of each trial, participants pressed a button down; when the spot appeared, they released the button and touched the spot on the screen as quickly as possible. As follows, this task allows for roughly separating processing speed (how quickly the button is released) from movement time (how quickly participants touched the screen). The processing speed component was of primary interest because of its potential relevance for the VG task, so RTI performance was quantified as the latency from stimulus presentation to button release (in ms). Because reaction time tends toward a positive skew, the median reaction time across trials was used for each participant.

The rapid visual information processing test was administered to measure sustained attention ability. In this test, pseudorandom one-digit numbers appeared successively on the screen (100 numbers/min) for 4 minutes, while participants identified the occurrence of 3 sequences consisting of 3 digits each by pressing a button. The final outcome for rapid visual information processing was a score ranging from 0 to 1 (higher is better), calculated from the probability of a hit and the probability of a false alarm during the last 3 minutes of the test, reflecting the ability to detect the target sequences (referred to as A' in CANTAB software). More detailed information about CANTAB tests and outcomes is available at http://www.cambridgecognition.com/cantab/cognitive-tests.

2.7. Gait tasks

2.7.1. Motion capture

A ProReflex motion capture system with 6 cameras (Qualisys, Sweden) was used to record 3-D positions of reflective markers placed on anatomical landmarks during the VG gait task. Markers (12 mm diameter) were positioned bilaterally on the acromion process (shoulder), anterior superior iliac spine (pelvis), greater trochanter (hip), lateral joint space (knee), lateral malleolus (ankle), calcaneus (heel), and 5th metatarsal head (toe), and marker positions were sampled at 100 Hz.

2.7.2. Experimental setup

Participants were familiarized with treadmill (TechnoGym model D-140, Italy) walking for ~3 minutes before performing normal and VG walking measurements. Treadmill speed for both tasks was normalized to leg length, measured from the left greater trochanter to the left lateral malleolus, and set to match cadence between participants during VG walking (see Choi et al., 2016). During all recordings, participants were asked to relax face and neck muscles to reduce muscle artifacts in EEG signals and to loosely cross their arms in front of them to avoid interfering with acquisition of motion capture data. One older participant was permitted to use poles positioned on each side of the treadmill for balance during both gait tasks.

Following treadmill familiarization, participants walked for 5 minutes with their gaze directed at a cross on the wall in front of them. After a short rest, participants performed 5 minutes of a VG gait task requiring adjustment of step length to hit visual targets displayed on the wall in front of them as described previously (Jensen et al., 2018) (see Fig. 1). In short, the real-time position of the swing leg foot and stepping targets were projected (Toshiba TDP-T 355) onto the wall in front of the treadmill on a 125 cm high × 167 cm wide screen. Targets were 16 × 16 cm gray squares appearing alternately at the top right and left side of the screen before moving downward at a speed matching the treadmill speed. Targets turned red to indicate the current target for the swing leg. Foot position for the swing leg was shown as a blue circle. Participants were asked to adjust their step length to step on the targets (i.e., so the blue circle hit the center of the red square). Emphasis was placed on instructing participants to continue walking normally and only to modify the length of their steps. Target step length was normalized to 2/3 of leg length. A step was considered successful if the center of the foot was ≤8 cm from the center of the target, and one point was issued for each hit. Points were updated continuously and shown at the top right-hand corner of the screen.

The primary outcome for performance during VG walking was a percent score: *hits/total steps · 100%*. Mean error was also quantified in the anterior-posterior direction as the absolute difference between the center of the foot versus center of the target and normalized to leg length.

2.8. Electrophysiological recordings

During gait tasks, 64-channel EEG as well as EMG from the proximal and distal ends of the left anterior TA muscle (TA_{prox} and TA_{dist}, respectively; interelectrode distance ~1.5 cm; average distance between electrode pairs, 12 cm) were sampled at 2048 Hz using active surface electrodes (BioSemi, the Netherlands) and ActiView software (version 6.05). EEG electrodes were positioned in compliance with the international 10/20 system using a headcap (BioSemi, The Netherlands). In the BioSemi system, the ground electrode is formed by a Common Mode Sense active electrode and Driven Right Leg passive electrode. Electrode offsets were contained to ± 25 μV during all recordings. Participants wore a custom-designed backpack carrying the amplifier and battery for the BioSemi system to allow full mobility while walking. A footswitch (ZeroWire, Italy) was placed under the left heel to indicate the time of the left heel strike in the electrophysiological data.

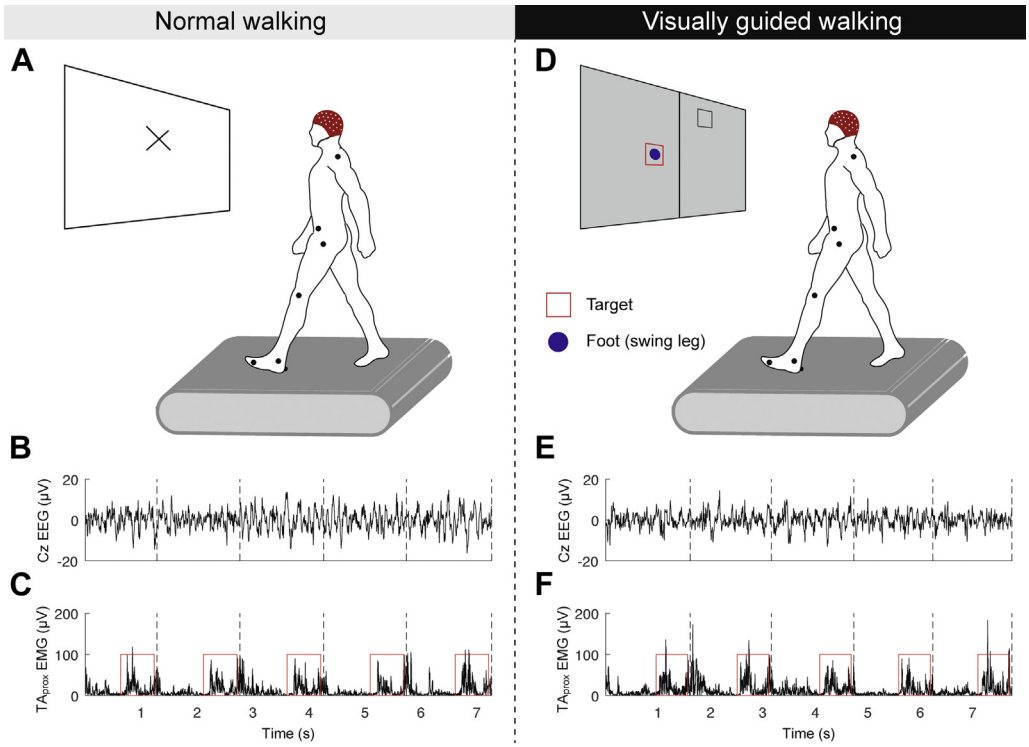

Fig. 1. Experimental setup. Young and older participants performed 5 minutes of normal and VG walking on a treadmill while electrophysiological and motion capture data were recorded. During normal walking (A), participants walked while looking at a cross on the wall in front of them. For the VG walking task (D), stepping targets (red square) and foot position for the swing leg (blue circle) were projected on to the wall in front of the treadmill. Participants were asked to modify their step length to make the blue circle hit the center of the red square. During both tasks, EEG was recorded from the cortex (Cz electrode shown in B,E), and EMG was recorded from the proximal and distal ends of the left anterior tibial muscle (proximal end, TA_{prox}, rectified signal shown in C,F). Depicted signals have been band-pass filtered between 4–80 Hz. Dashed vertical lines in B,C,E, and F indicate the times of left heel strike. Red squares in C and F indicate the time window used for coherence analysis, corresponding to the TA bursts during the swing phase (−650 to −50 ms before heel strike). Abbreviations: EEG, electroencephalography; EMG, electromyography; VG, visually guided.

2.8.1. Preprocessing

Preprocessing was conducted using EEGLAB (Delorme and Makeig, 2004) software in MATLAB (R2016 b). EEG and EMG signals were initially downsampled to 256 Hz, rereferenced to average reference excluding any noisy channels and EMG, and band-pass filtered between 4 and 80 Hz.

Continuous data were epoched from −650 to −50 ms relative to the footswitch trigger (heel strike) to isolate the period of the swing phase where TA EMG activity is present (Halliday et al., 2003; Petersen et al., 2012). Visual inspection of EMG signals in relation to the footswitch trigger confirmed that TA activity indeed occurred primarily in this window during swing (see examples in Fig. 1). Although TA activity continues into the stance phase, the heel strike period was avoided because of the risk of motion artifacts contaminating EEG signals.

Data were subsequently carefully pruned of noisy epochs demonstrating high-amplitude deflections before independent components analysis was performed on EEG signals using the runica algorithm in EEGLAB (Delorme and Makeig, 2004). Signal components exhibiting unambiguous topography, spectra, and/or time course of eye blinks and EMG artifact were removed (Chaumon et al., 2015). EMG signals were rectified to maximize temporal information about motor unit action potentials in the signals (Halliday and Farmer, 2010). Before coherence analysis, all signals were also linearly detrended.

2.8.2. Coherence analysis

Coherence analysis was used to describe the frequency-domain coupling between EEG and TA EMG (EEG-TA_{prox}, EEG-TA_{dist}) as well as between proximal and distal TA EMG (TA_{prox}-TA_{dist}). EEG-TA coherence quantifies the strength and frequencies of the coupling between cortical and muscular activity, whereas TA_{prox}-TA_{dist} coherence describes the strength and frequencies of common rhythmic drive distributed across the motoneuron pool. The frequency range of interest was 15–50 Hz, encompassing beta and gamma bands (Halliday et al., 2003; Jensen et al., 2018; Petersen et al., 2012).

Coherence analysis was based on spectral estimates for EEG and EMG signals constructed using the discrete Fourier transform of nonoverlapping data segments at given offsets relative to heel strike for each gait cycle. Spectral estimates for each offset were averaged across steps and used to calculate coherence as the squared modulus of the cross-spectrum normalized by the product of the 2 auto-spectra for each Fourier frequency f:

$$C_{xy}(f) = \frac{|S_{xy}(f)|^2}{S_{xx}(f) \cdot S_{yy}(f)}$$

where S_{xx} and S_{yy} are the auto-spectra of each signal, and S_{xy} is the cross-spectrum. Coherence ranges from 0 to 1, indicating the fraction of activity in one signal that can be predicted by another signal at a given frequency, and reflects the constancy of phase relationships and amplitude ratios between signals.

First, coherence was calculated for each EEG electrode and TA EMG for the 600 ms period of interest. Peak coherence was then averaged across participants for each age group to create grand average scalp plots as an overview of the spatial distribution (see Fig. 2). Because the precise frequency at which peak coherence

occurred in the range of interest (15–50 Hz) varied between participants, coherence peaks were aligned across participants by basing group means on coherence at the frequency where it was maximal at the vertex (Cz electrode) for each participant. Although this introduces a bias toward the Cz electrode, it may be considered reasonable based on previous findings that coherence at these frequencies exhibits a somatotopic arrangement (Brown et al., 1998; Salenius et al., 1997) and was necessary to account for the observed individual differences. These plots indicated that coherence amplitudes were maximal at Cz, so this electrode was used for all further analyses.

Time-frequency coherence analysis for Cz-TA_{prox}, Cz-TA_{dist}, and TA_{prox}-TA_{dist} was then performed over 600 ms epochs using a sliding window of 250 ms, increments of 35 ms, and a frequency resolution of 2 Hz. These analyses indicated that the temporal localization of 15–50 Hz coherence during the swing phase varied between participants; coherence was present at either early (−650 to −350 ms) or late (−350 to −50 ms before heel strike) swing or, in some participants, in both periods (see Fig. 3 for examples). The final coherence analysis was thus then performed for the two 300 ms periods representing early and late swing with a frequency resolution of 1 Hz. TA_{prox}-TA_{dist} results were reviewed to ensure that cross-talk, evidenced in high coherence across all frequencies and close to zero lag time-domain synchronization, was not present (Farmer et al., 2007).

To investigate coherence on the group level, individual estimates were combined into pooled estimates for each analysis and age group. Pooled estimates provide a single coherence estimate for each frequency representative of the coupling within each group. To permit statistical testing of group differences in these estimates, coherency estimates were Fisher transformed before pooling to stabilize variance (Halliday and Rosenberg, 2000).

All coherence analyses were performed using NeuroSpec 2.0 software (www.neurospec.org) (Halliday et al., 1995). During analysis of electrophysiological signals, technical problems were identified in data from 4 participants (2 older and 2 young), whose data were subsequently excluded from all coherence analyses. In addition, we excluded an older participant from VG coherence and gait analyses on the basis of a VG score (12%) that was markedly lower than scores for other participants in this age group, as this was taken to indicate that the participant was not able to perform the task.

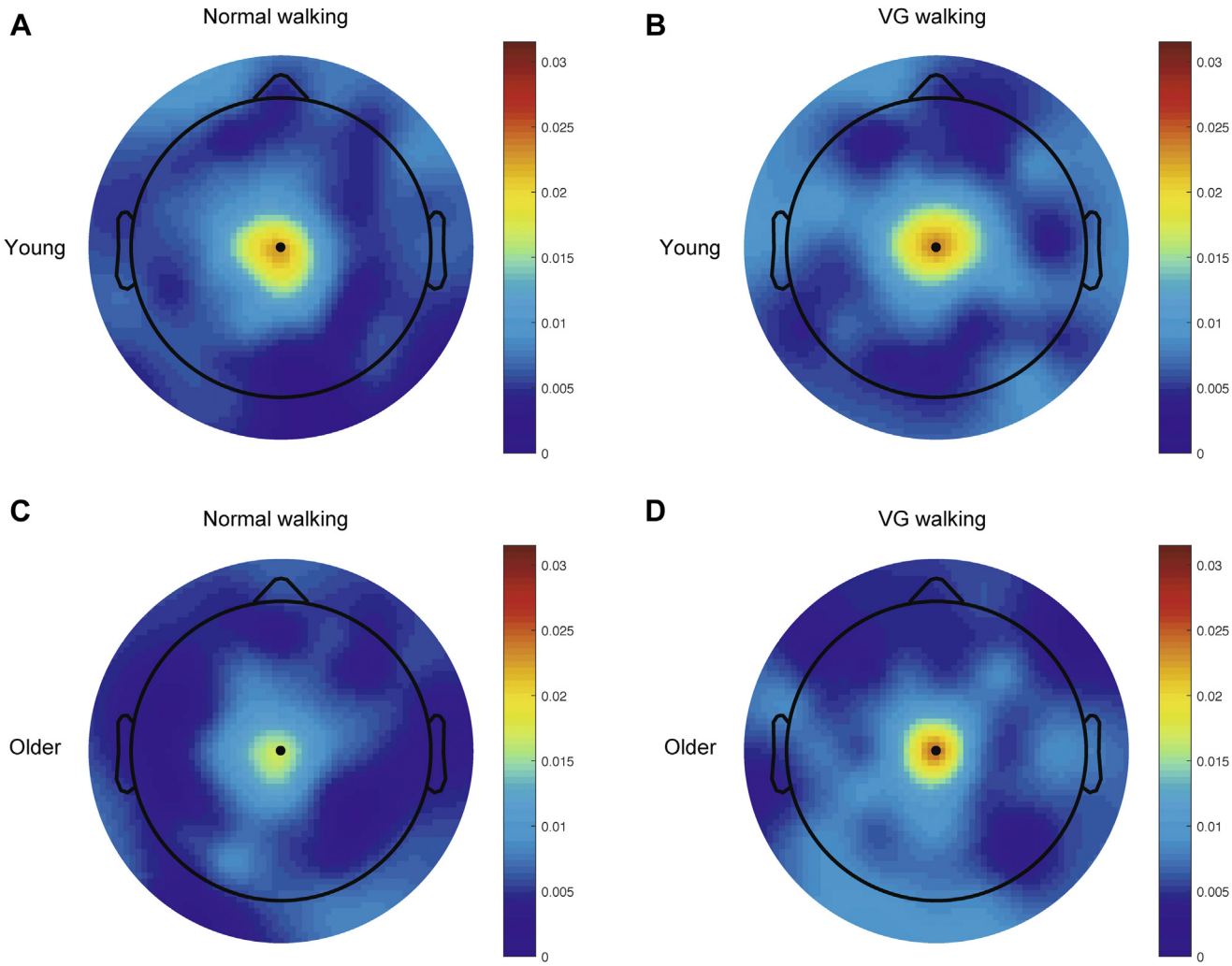

Fig. 2. Grand average scalp maps. Coherence between each of the 64 EEG electrodes and the proximal and distal ends of the anterior tibial muscle (TA_{dist} shown here) was calculated for the period of the swing phase where TA EMG activity was present (−650 to −50 ms before heel strike) and averaged for young (A,B) and older (C,D) participants during normal (A,C) and visually guided ([VG], B,D) walking. Because the precise frequency at which peak coherence occurred in the range of interest (15–50 Hz) varied between participants, coherence peaks were aligned across participants by basing group means on coherence at the frequency where it was maximal at the vertex (Cz electrode) for each participant. Abbreviations: TA, anterior tibial muscle; VG, visually guided.

2.9. Statistics

The upper 95% confidence limit for individual coherence estimates is given by:

$$1 - (\alpha)^{\frac{1}{L-1}}$$

where α is the significance level (0.05) and L is the number of segments (steps) used for the analysis (Halliday et al., 1995). Similarly, pooled estimates were considered to be significant if they exceeded the upper 95% confidence limit calculated with L as the total number of segments in the pooled coherence estimate (Amjad et al., 1997). To statistically compare group (pooled) estimates at each frequency, the χ^2 difference of coherence test was performed. This test provides a metric of amount of pooled coherence difference at each frequency between the 2 groups (Amjad et al., 1997; Farmer et al., 2007). A χ^2 test statistic greater than the confidence limit

$$\chi^2(\alpha; k-1)$$

where k is the number of groups compared, indicates that the null hypothesis is not plausible for frequency f.

In addition, the amount of corticomuscular and intramuscular coherence was quantified as the sum of coherence estimates (i.e., area) in the 2 frequency bands of interest: beta (15–35 Hz) and gamma (35–50 Hz) for each participant. Coherence area values were logarithmically transformed to symmetrize distributions for statistical testing, and resulting normality was confirmed by visual inspection of histograms.

Effects of age group and task on beta and gamma coherence area were evaluated using a two-way mixed model ANOVA. In these models, we entered age group as a between-subjects factor, task as a within-subjects factor, and included an interaction for age group and task. Model assumptions were checked graphically using Q-Q and residual plots. ANOVA analyses were performed in R (v. 3.5.1) using the "afex" package (Singmann et al., 2018) to construct and test global models and the "lsmeans" package to conduct post hoc tests (Lenth, 2016). All other group wise comparisons (i.e., descriptive variables, performance on motor and cognitive tasks) were evaluated with unpaired t-tests.

To investigate the functional significance of coherence, Pearson correlations were used to assess associations between coherence and performance during VG walking (score). Because of interindividual variations in the amount of coherence (Ushiyama et al., 2011), we chose to use the change in coherence from normal to VG walking (Δ coherence area; VG area—normal area) for these analyses, expecting that the ability to modulate coherence according to task demands would be a more sensitive measure than absolute coherence values. Correlational analysis was only performed within groups, as we predicted that correlations across groups would be driven by both coherence and performance covarying with age. In addition, previous studies have suggested that associations between coherence and functional parameters may differ in older and young participants (Johnson and Shinohara, 2012; Watanabe et al., 2018). Descriptive statistics are presented as mean ± standard deviation unless otherwise indicated, and an alpha level of <0.050 was used to reject the null hypotheses.

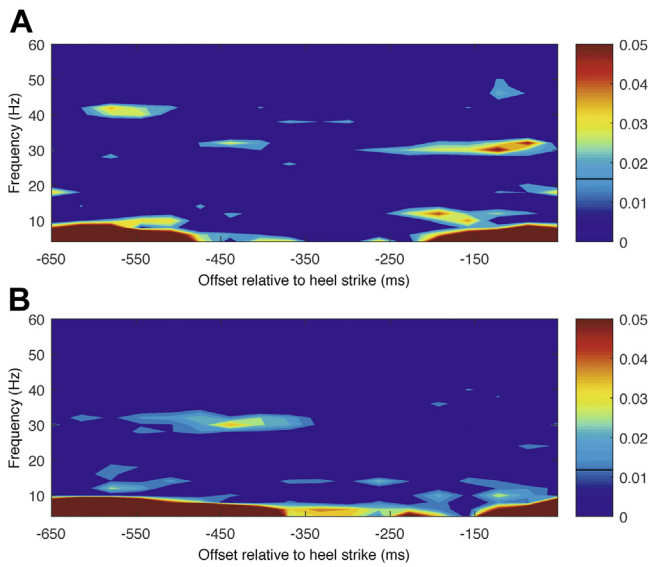

Fig. 3. Single participant time-frequency plots. Coherence between the Cz electrode and the anterior tibial muscle (TA_{prox}) for the period of the swing phase where TA EMG was present (−650 to −50 ms before heel strike), as illustrated here for one young (A) and one older (B) participant. These participants exhibited coherence in the beta-gamma range in either both early and late (A) or primarily in the early part of the swing phase (B). To construct plots, a sliding window of 250 ms and increments of 35 ms were used. Offset values on the horizontal axes indicate the beginning of each analysis window. Black lines on color bars indicate upper 95% confidence limits for coherence estimates. Abbreviation: TA, anterior tibial muscle.

3. Results

3.1. Participant characteristics

Table 1 summarizes participant characteristics by age group. The older group exhibited longer reaction time (RTI, $p < 0.001$), lower self-reported physical activity level (MET min/wk, $p = 0.008$), and longer sway path length (eyes open, $p = 0.010$; eyes closed, $p = 0.003$), but other descriptive characteristics were comparable for the 2 age groups.

3.2. Gait tasks

During normal and VG walking, treadmill speed was similar for young (2.13 ± 0.12 km/h) and older (2.15 ± 0.16 km/h) groups ($p = 0.698$). Target step lengths during the VG task for young (0.55 ± 0.03 m) and older (0.55 ± 0.04 m) groups were also comparable ($p = 0.924$).

3.2.1. Age-related differences in corticomuscular and intramuscular coherence estimates during walking

Examples of time-frequency coherence plots for Cz-TA_{prox} during normal walking for a young and an older participant are shown in Fig. 3. For the first (young) participant (Fig. 3A), 2 prominent areas of coherence were apparent in the frequency range of interest: during early swing (~550 ms before heel strike) at ~40 Hz, and during late swing (~100 ms before heel strike) at ~30 Hz. For the second (older) participant (Fig. 3B), coherence was primarily present during early swing (−550 to −350 ms before heel strike) around 30–35 Hz. Coherence was also observed at low frequencies for both participants, which likely reflects the periodic modulation of the EMG envelope (Halliday et al., 2003).

Pooled coherence estimates for each group during normal walking are given in Fig. 4. For Cz-TA_{prox} and Cz-TA_{dist}, the young group demonstrated coherence peaks within the 15–50 Hz band during both early (Fig. 4A and C) and late (Fig. 4G and I) swing, whereas the older group generally exhibited lower coherence magnitudes in this frequency band for both periods. The χ^2 test statistic did not, however, reach statistical significance at any of the frequencies of interest, although tendencies were present at

~45 Hz (Cz-TA_{prox}, late swing, Fig. 4H; and Cz-TA_{dist}, early swing, Fig. 4D) and ~30 Hz (Cz-TA_{dist}, late swing, Fig. 4J). TA_{prox}-TA_{dist} coherence was present during both early and late swing for young and older participants and was, similar to Cz-TA coherence, lower in older participants (Fig. 4E and K). These group differences were significant for the entire frequency range of interest (15–50 Hz) and appeared more prominent for late compared to early swing (Fig. 4F and L).

For VG walking, group differences were generally analogous to those observed during normal walking (Fig. 5). The pooled data for Cz-TA_{prox} (Fig. 5A and G) and Cz-TA_{dist} (Fig. 5C and I) suggested that coherence magnitudes for older participants were generally lower within the beta-gamma range. The χ^2 statistic did not exceed the significance level for these comparisons (Fig. 5B, D, H and J), but a tendency was observed for Cz-TA_{dist} during early swing at ~30 Hz (Fig. 5D). For TA_{prox}-TA_{dist}, young participants had significantly higher coherence throughout the 15–50 Hz band (Fig. 5E, F, K and L), and differences again appeared more pronounced for late compared to early swing (Fig. 5F and L).

3.2.2. Age- and task-related differences in corticomuscular and intramuscular coherence areas during walking

We also assessed whether beta and gamma coherence areas differed by age group and task, and whether these factors interacted in their possible effects on coherence. Mean coherence area values by age group and task are presented in Table 2.

For Cz-TA_{prox} during early swing, beta band coherence area did not show significant main or interaction effects (range for p-values, $p = 0.060–0.940$), but a significant effect of age was present in the gamma band ($F_{1,23} = 5.207$, $\eta^2 = 0.100$, $p = 0.032$), indicating lower coherence in older than in young participants (other p-values, 0.122–0.999). For late swing, a main effect of task was present in the beta band ($F_{1,23} = 4.570$, $\eta^2 = 0.083$, $p = 0.043$), indicating greater coherence during VG compared to normal walking across age groups. In the gamma band, both a main effect of task ($F_{1,23} = 5.169$, $\eta^2 = 0.052$, $p = 0.033$) and an age-task interaction ($F_{1,23} = 5.307$, $\eta^2 = 0.058$, $p = 0.031$) were detected (range for other p-values, 0.163–0.791). Post hoc tests showed that older participants increased coherence from normal to VG conditions (Cohen's $d = 1.061$, $p = 0.004$), whereas young participants did not ($p = 0.983$).

For Cz-TA_{dist}, a main effect of age in the beta band ($F_{1,23} = 4.849$, $\eta^2 = 0.067$, $p = 0.038$) was observed during early swing, indicating lower coherence in older than in young participants, but coherence did not significantly differ by age group for the gamma band ($p = 0.058$). Main effects of task were also present for this period in both frequency bands (beta, $F_{1,23} = 16.708$, $\eta^2 = 0.260$, $p < 0.001$; gamma, $F_{1,23} = 7.250$, $\eta^2 = 0.124$, $p = 0.013$), with both effects showing greater coherence during VG than normal walking (other p-values, 0.482–0.798). During the late swing period, neither main nor interaction effects were significant for the beta band (range for p-values 0.099–0.779); for the gamma band, however, an age-task interaction was detected ($F_{1,23} = 6.937$, $\eta^2 = 0.103$, $p = 0.015$). Post hoc testing indicated that older participants tended to increase coherence from normal to VG walking ($p = 0.051$), whereas younger participants did not ($p = 0.111$; other p-values, 0.529–0.738).

For TA_{prox}-TA_{dist} during early swing, a main effect of age in both the beta band ($F_{1,23} = 4.880$, $\eta^2 = 0.164$, $p = 0.037$) and in the

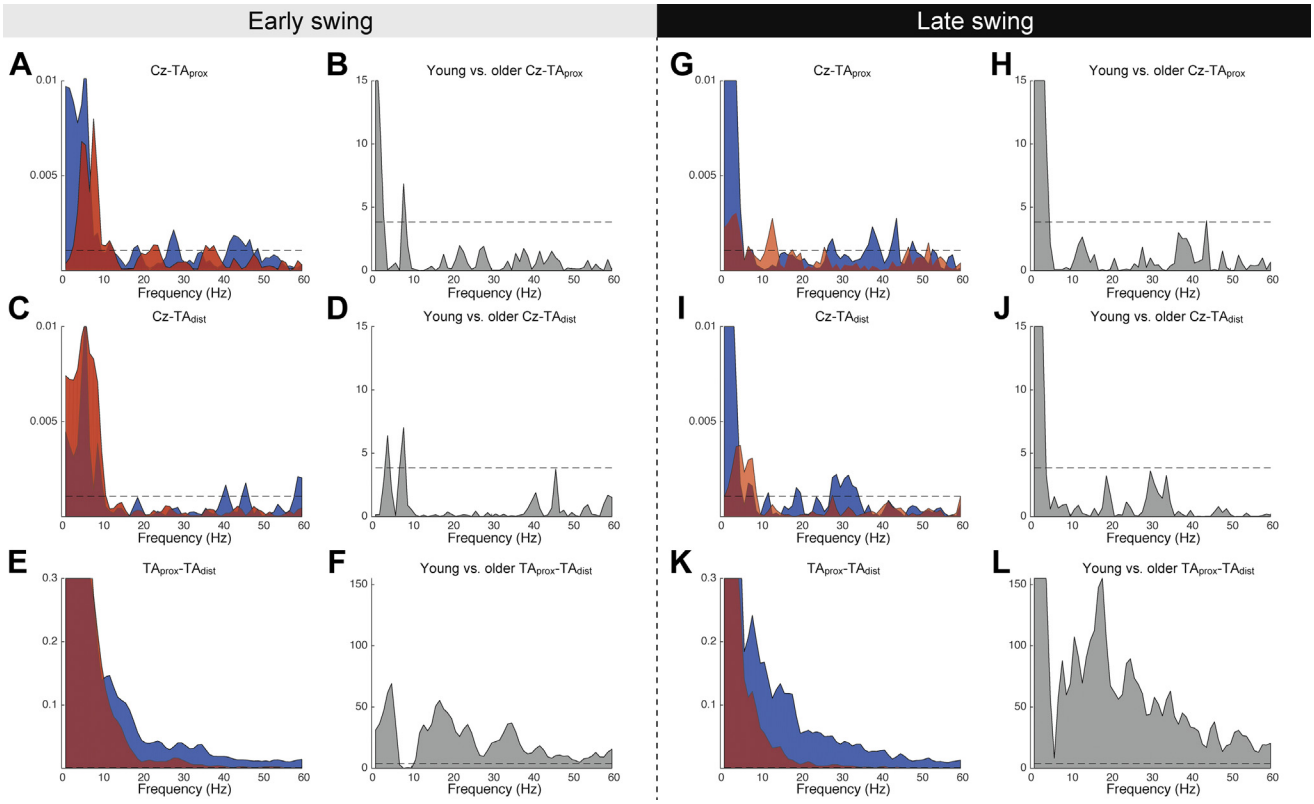

Fig. 4. Pooled coherence during normal walking. Pooled coherence estimates for young (blue) and older (red) participants as a function of frequency during early (A,C,E) and late (G,I,K) swing. The statistical significance of group differences is indicated by χ^2 test statistics as a function of frequency (B,D,F; H,J,L). Dashed lines indicate confidence limits for coherence estimates and χ^2 statistics. Abbreviations: TA_{prox}, proximal end of anterior tibial muscle, TA_{dist}, distal end of anterior tibial muscle. Note that coherence and χ^2 axes are scaled differently for Cz-TA_{prox}/Cz-TA_{dist} and TA_{prox}-TA_{dist} measures.

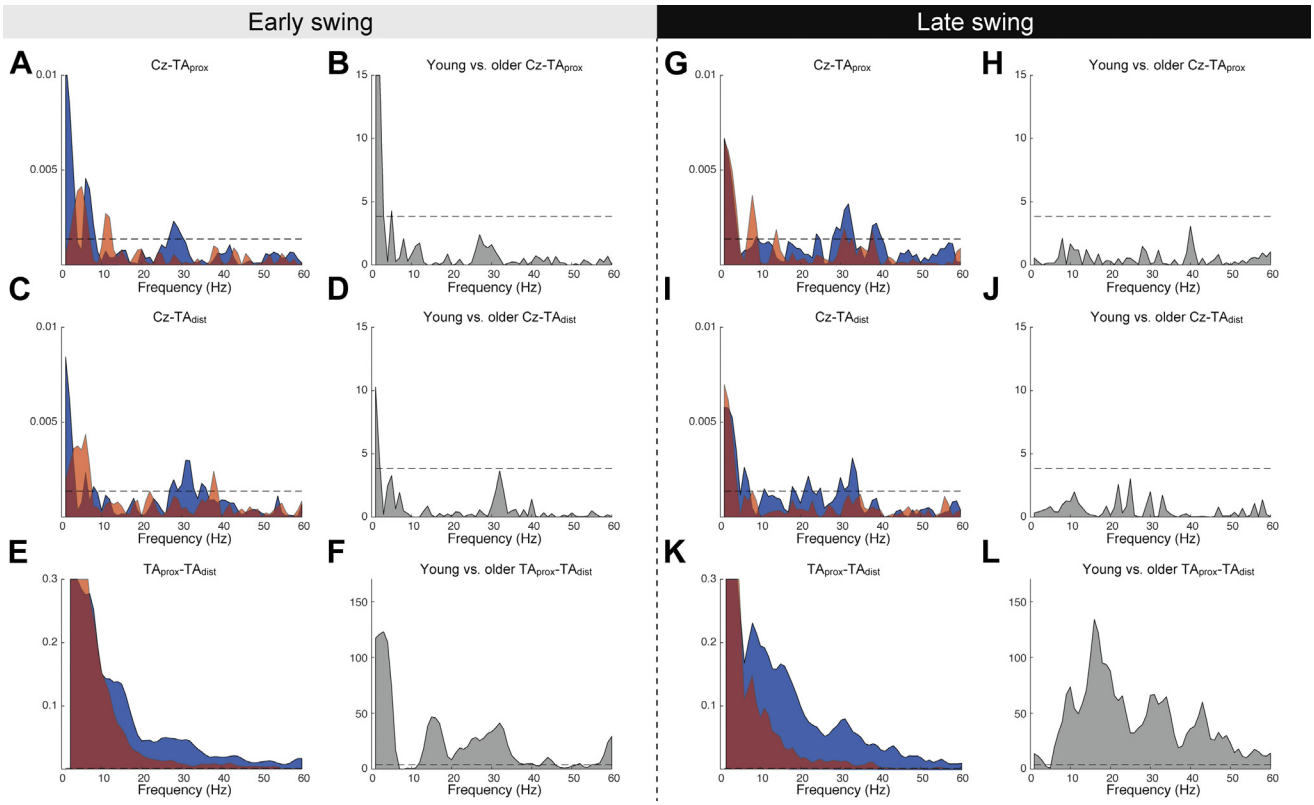

Fig. 5. Pooled coherence during VG walking. Pooled coherence estimates for young (blue) and older (red) participants as a function of frequency during early (A,C,E) and late (G,I,K) swing. The statistical significance of group differences is indicated by χ^2 test statistics as a function of frequency (B,D,F; H,J,L). Dashed lines indicate confidence limits for coherence estimates and χ^2 statistics. Note that coherence and χ^2 axes are scaled differently for Cz-TA_{prox}/Cz-TA_{dist} and TA_{prox}-TA_{dist} measures. Abbreviations: TA_{prox}; proximal end of anterior tibial muscle, TA_{dist}; distal end of anterior tibial muscle.

gamma band ($F_{1,23} = 5.954$, $\eta^2 = 0.188$, $p = 0.023$) was detected, indicating lower coherence in older than in young participants, but task and interaction effects were not significant (range for other *p*-values 0.057–0.905). During late swing, main effects of both age and task were present for beta (age, $F_{1,23} = 25.986$, $\eta^2 = 0.467$, $p < 0.001$; task, $F_{1,23} = 22.894$, $\eta^2 = 0.052$, $p < 0.001$) and gamma (age, $F_{1,23} = 19.327$, $\eta^2 = 0.381$, $p < 0.001$; task, $F_{1,23} = 8.402$, $\eta^2 = 0.042$, $p = 0.008$) bands, suggesting lower coherence in older compared to young participants, as well as greater coherence during VG compared to normal walking. In addition, an age-task interaction was present for the beta band ($F_{1,23} = 5.731$, $\eta^2 = 0.014$, $p = 0.025$). Post hoc tests showed that older participants increased coherence from normal to VG walking (Cohen's $d = 0.790$, $p < 0.001$), but that young participants did not ($p = 0.098$; *p*-value for gamma band interaction, 0.276).

3.2.3. *Performance during VG walking*

Fig. 6 presents group wise performance during VG walking. Scores (Fig. 6A) were higher for young (320 ± 35 points out of 394 ± 20 steps) than older (275 ± 35 points out of 393 ± 4 steps) participants, corresponding to respective hit rates of 81.5 ± 9.1% and 70.0 ± 9.0% that were significantly different ($p = 0.002$). In line with group differences for scores, normalized error in the anterior-posterior direction (Fig. 6B) was greater in older (7.1 ± 1.7% leg length) than young (4.3 ± 1.9% leg length) participants and differed significantly between groups ($p < 0.001$).

Table 2
Corticomuscular and intramuscular coherence areas

Coherence variables	Early swing				Late swing			
	Beta		Gamma		Beta		Gamma	
	Young	Older	Young	Older	Young	Older	Young	Older
Cz-TA_{prox}								
Normal	−2.08 ± 0.30	−2.30 ± 0.40	−2.36 ± 0.43	−2.83 ± 0.48	−2.19 ± 0.32	−2.29 ± 0.36	−2.43 ± 0.42	−2.81 ± 0.49
VG	−2.07 ± 0.20	−2.28 ± 0.38	−2.56 ± 0.55	−2.59 ± 0.41	−1.96 ± 0.40	−2.10 ± 0.28	−2.44 ± 0.37	−2.37 ± 0.50
Cz-TA_{dist}								
Normal	−2.31 ± 0.15	−2.44 ± 0.24	−2.59 ± 0.49	−2.90 ± 0.35	−2.17 ± 0.33	−2.23 ± 0.23	−2.39 ± 0.29	−2.67 ± 0.37
VG	−2.00 ± 0.31	−2.14 ± 0.27	−2.34 ± 0.40	−2.48 ± 0.48	−2.05 ± 0.40	−2.10 ± 0.20	−2.63 ± 0.48	−2.46 ± 0.52
TA_{prox}-TA_{dist}								
Normal	−0.06 ± 1.14	−0.90 ± 0.75	−1.07 ± 1.16	−2.35 ± 1.13	0.28 ± 0.79	−1.33 ± 0.77	−1.02 ± 1.09	−2.50 ± 0.69
VG	0.07 ± 1.04	−0.80 ± 0.82	−1.17 ± 1.14	−1.96 ± 1.06	0.53 ± 0.84	−0.61 ± 0.82	−0.72 ± 1.07	−1.85 ± 0.86

Logarithmic area of beta (15–35 Hz) and gamma (35–50 Hz) coherence during normal and VG walking for age groups divided into early and late swing periods (mean ± standard deviation).
Key: TA_{prox}, proximal end of anterior tibial muscle; TA_{dist}, distal end of anterior tibial muscle; VG, visually guided.

To further explore the basis of the observed group differences in VG walking performance, we investigated sway path length (eyes closed), RTI, and estimated physical activity level (MET min/wk) as possible explanatory factors, as these variables also exhibited significant age group differences. When an ANCOVA model was constructed to compare VG score between groups while controlling for these factors, the difference between groups remained significant ($F_{4,24} = 3.880$, $\eta^2 = 0.301$, $p = 0.014$), indicating that the group difference in VG score could not merely be attributed to differences in processing speed, postural control, or physical activity.

3.2.4. Correlations between corticomuscular and intramuscular coherence and VG walking performance

To investigate whether the ability to modulate coherence according to task demands was related to VG walking performance, correlations between the difference in coherence area during VG versus normal walking (Δ coherence, area VG−area normal), and VG score were explored within each age group. Correlations for corticomuscular coherence were performed using the average coherence difference for Cz-TA_{prox} and Cz-TA_{dist}, as the 2 measures represent similar underlying processes.

For young participants, neither Cz-TA beta nor gamma Δ areas during early or late swing were correlated with VG score (range for *p*-values 0.432–0.862, range for r −0.144–0.239). For TA_{prox}-TA_{dist}, however, Δ beta area during late swing was negatively correlated with VG score ($p = 0.029$, $r = -0.603$; range for other *p*-values, 0.252–0.713, range for r, −0.113–0.312).

In the older group, Cz-TA Δ beta area during early swing was positively correlated with VG score ($p = 0.001$, $r = 0.812$), whereas Δ gamma area was not ($p = 0.781$, $r = -0.090$). For late swing, negative correlations were detected in the older group between VG score and Δ beta area ($p = 0.028$, $r = -0.631$) and Δ gamma area ($p = 0.017$, $r = -0.669$). No significant correlations were present in this group for TA_{prox}-TA_{dist} (range for *p*-values, 0.585–0.884, range for r, −0.176–0.087).

On the basis that these associations could be affected by sway, physical activity level, and processing speed, we undertook a partial correlation analysis including eyes closed path length, estimated physical activity level (MET min/wk), and RTI as covariates for statistically significant correlations. With this approach, the positive correlation in the older group between Cz-TA Δ beta area during early swing and VG score remained significant ($p = 0.012$, $r = 0.785$), as did the negative correlation between Cz-TA Δ beta area during late swing and VG score ($p = 0.019$, $r = -0.752$). However, the negative correlation in the young group between TA_{prox}-TA_{dist} and Δ beta area (late swing) was no longer significant ($p = 0.137$, $r = -0.504$). This was also the case for the negative correlation between Cz-TA Δ gamma area (late swing) and VG score in the older group with the inclusion of covariates ($p = 0.081$, $r = -0.610$).

4. Discussion

In this study, we have demonstrated that corticomuscular and intramuscular coherence in TA within the 15–50 Hz frequency band exhibits age-related differences during the swing phase of normal and VG walking. Our primary findings were as follows: (1) corticomuscular and intramuscular coherence was lower in older compared to younger participants during both walking tasks; (2) corticomuscular and intramuscular coherence was generally greater during VG compared to normal walking; (3) during late swing, older participants were driving several of the observed task-related corticomuscular and intramuscular coherence increases from normal to VG walking; and (4) task-related increases in corticomuscular coherence in older participants were associated with VG performance.

4.1. Age-related differences in corticomuscular and intramuscular coherence during walking

The present results confirmed that significant corticomuscular and intramuscular coherence in TA occurs during the swing phase of normal treadmill walking in young adults, in agreement with results from previous studies (Halliday et al., 2003; Jensen et al., 2018; Petersen et al., 2012). The corticomuscular and intramuscular coherence we observed falls into similar frequency bands, although amplitudes for both measures were slightly lower than those presented previously for the TA muscle (Halliday et al., 2003; Jensen et al., 2018; Petersen et al., 2012). Considerable evidence from both animal and human studies using a range of approaches supports that beta and gamma band corticomuscular and intramuscular coherence reflects activity in the corticospinal tract, both during static contractions (Baker et al., 1999; Brown et al., 1998; Farmer et al., 1993; Hansen and Nielsen, 2004; Mima et al., 2000) and during gait (Barthelemy et al., 2010; Hansen et al., 2005; Nielsen et al., 2008; Petersen et al., 2012). Thus, we interpret our results as indicating a significant contribution from oscillatory corticospinal activity to TA activity during the swing phase of normal walking in healthy young adults, as has been argued previously (Petersen et al., 2012).

It has also been suggested that corticomuscular coherence may not only reflect descending corticospinal activity but also ascending activity in sensory pathways, forming an oscillatory sensorimotor loop (Riddle and Baker, 2005; Witham et al., 2011), although there is no real consensus on this to date (van Wijk et al., 2012). However, when considering walking specifically, available evidence suggests a descending directionality for TA control during the swing phase, based on the sign of the imaginary part of beta-gamma corticomuscular coherency (Petersen et al., 2012) and other directed connectivity measures (Artoni et al., 2017). This supports that the most reliable interpretation of the observed corticomuscular and

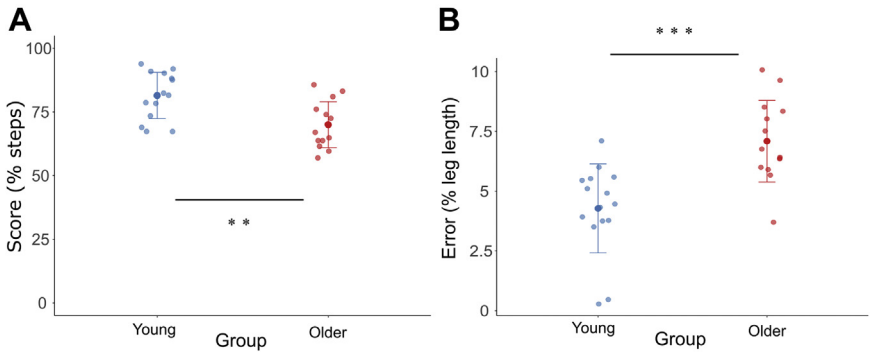

Fig. 6. | Performance during VG walking. Age group differences in score (A) and error normalized to leg length (B). Error bars indicate standard deviations. Significant differences between young and older groups are indicated by $^{**}p < 0.010$, $^{***}p < 0.001$. Abbreviation: VG, visually guided.

intramuscular coherence is indeed descending activity in the corticospinal pathway.

The lower corticomuscular and intramuscular coherence we observed in older compared to young participants is consistent with recent findings demonstrating lower magnitudes of corticomuscular coherence in ankle muscles for older compared to young participants during a gait-like task involving cyclical plantar and dorsiflexion (Yoshida et al., 2017). Whether this was also the case specifically for beta and gamma frequencies is, however, unclear, as Yoshida et al. compared the magnitude of significant coherence over a broad frequency band (6–100 Hz) in young and older participants. Nonetheless, the present findings suggest that the contribution from oscillatory corticospinal activity to TA activity during the swing phase of both normal and VG walking is reduced in older compared to young adults.

Lower gait-related corticomuscular and intramuscular coherence in older participants may be due to morphological and/or functional changes that occur in the nervous system with aging. Older adults exhibit fewer and larger motor units (Deschenes, 2011), which may affect the amplitude of oscillations in the EMG, but not likely the constancy of the ratio between the amplitudes of oscillatory activity in the 2 signals as quantified in coherence. It has also been suggested that the functionality of cortico-motoneurons declines markedly with advancing age (Eisen et al., 1996), which could potentially lead to impaired transmission of oscillations to the spinal cord and thus less corticomuscular and intramuscular coherence. Lower myelinated fiber density and myelination markers in the corticospinal tract in older adults (Sala et al., 2012; Terao et al., 1994) likely entail slower conduction velocity (Peters, 2002), although this should not affect the degree of consistent phase locking between cortical and spinal oscillations quantified in coherence. However, if age-related demyelination generally resulted in greater variation in conduction velocities between axons, the precise temporal relationships necessary for generating oscillatory activity could potentially be disrupted. Other possible influences on the ability to produce and synchronize oscillatory activity include less dendritic arborization (Anderson and Rutledge, 1996) and lower synaptic density (Huttenlocher, 1979) in older adults. On the systems level, age-related reorganization of sensorimotor networks (Seidler et al., 2010; Ward, 2006) may also contribute to the observed age differences. For example, patterns of dedifferentiated neural activity or compensatory activation could alter network synchronization patterns and thus oscillatory corticospinal activity. However, it should be noted that it has yet to be demonstrated that corticomuscular or intramuscular coherence is in fact sensitive to any of these age-related differences.

The age group differences we observed were most consistent for intramuscular compared to corticomuscular coherence, which is not too surprising, considering the higher signal-to-noise ratio for EMG compared to EEG signals. Evidence from both humans and monkeys indicates that corticomuscular and intramuscular coherence are indeed similar indications of oscillatory corticospinal activity (Baker et al., 1997; Grosse et al., 2002; Kilner et al., 1999; Perez et al., 2006). However, it should be noted that for intramuscular coherence, we cannot exclude the possibility that age-related differences in other sources of common drive may have contributed to the observed age group differences.

4.2. Corticomuscular and intramuscular coherence during normal versus VG walking

For both corticomuscular and intramuscular coherence, we detected main effects of task in beta and/or gamma bands, indicating an increase in coherence from normal to VG walking across age groups. However, during late swing, we found that older participants were driving the observed increases in gamma corticomuscular and beta intramuscular coherence.

Our findings of task-related increases in beta and gamma corticomuscular and intramuscular coherence from normal to VG walking across age groups are consistent with results from recent work by Jensen et al. (2018) showing that young participants increased both beta and gamma band intramuscular coherence in TA from normal to VG walking using a VG paradigm identical to ours. Together, these findings indicate that the corticospinal involvement in the control of gait increases when visual guidance of foot placement is required. A role for the motor cortex and corticospinal pathway in VG modifications of the gait pattern is further supported by findings suggesting increased corticospinal excitability during VG precision walking compared to normal walking (Schubert et al., 1999), as well as by experiments performed in the cat demonstrating increased firing of corticospinal neurons when careful paw placement is required to cross ladder rungs and navigate obstacles (Armstrong, 1988; Drew et al., 1996; Drew and Marigold, 2015).

Contrary to our hypothesis, we also found that during late swing, older participants were driving several of the observed task-related increases in corticomuscular and intramuscular coherence. That older participants were indeed able to increase coherence from normal to VG walking indicates interestingly that the aging corticospinal system does have the capacity to modulate oscillatory activity. The coherence increases we observed in older participants are in contrast to recent findings from Watanabe et al. (2018) suggesting that while young adults exhibited task-related coherence modulations, older adults did not. The most obvious explanation for this inconsistency is that Watanabe et al. (2018) utilized a task that was quite different from the VG walking task, involving leaning the body forward toward the edge of the base of support. Nevertheless, our results entail that the lower coherence magnitudes observed in older participants are probably not solely due to morphological changes in the nervous system but are likely also affected by age-related changes in functional mechanisms regulating oscillatory activity and/or differences in neural control strategy.

Speculatively, these selective coherence increases from normal to VG walking in the older group could be related to the relative difficulty of the VG task for the 2 age groups. In support of this, one study has demonstrated a trend toward increased beta band corticomuscular coherence in older adults with increasing task difficulty (Johnson and Shinohara, 2012). It has also been shown that beta band corticomuscular coherence is comodulated with task-related attention (Kristeva-Feige et al., 2002). Thus, if the older group experienced VG walking as more difficult, they may have devoted more attention to the task, which may have in turn driven corticomuscular and intramuscular coherence increases. Our finding that these age-related differences in coherence modulations occurred during late swing supports this interpretation, as late swing (just before when the foot must be placed precisely) is conceivably the period imposing the greatest demands for precise control of TA activity. Future work should account for the effect of this factor to further elucidate the basis for task- and age-related coherence modulations.

4.3. Associations between corticomuscular and intramuscular coherence modulations and VG performance

During the VG task, older participants performed worse than young participants, exhibiting greater error and achieving a lower score. We assessed the significance of task-related coherence modulations for these performance differences by exploring associations between VG score and the change in corticomuscular and intramuscular coherence from normal to VG walking. Within the young group, no significant associations were present after

controlling for processing speed, physical activity level, and postural sway. However, within the older group, VG score was associated with task-related beta band corticomuscular coherence increases during both early and late swing. Interestingly, this association was positive during early swing, indicating that older participants who increased coherence to a greater extent during this period also performed better on the VG task, but negative during late swing, suggesting that coherence increases during this period were accompanied by lower VG score. These associations remained significant after controlling for covariates.

The functional significance of beta and gamma corticomuscular and intramuscular coherence for the control of gait is still unclear, as only few studies have investigated functional correlations. In patients with spinal cord lesions, intramuscular TA coherence at beta and gamma frequencies has been positively correlated with the degree of foot drop during steady-state walking (Barthelemy et al., 2010), suggesting that the corticospinal activity reflected in this coherence does play a functional role in lifting the foot to clear the ground during the swing phase. In addition, lower step-to-step variability in the swing phase of normal walking has been positively associated with intramuscular coherence in the gamma band for TA in healthy children (Petersen et al., 2010), indicating a more specific role for gamma coherence in precision control of the ankle joint. However, a recent study using an identical VG paradigm (Jensen et al., 2018) failed to find associations between beta or gamma intramuscular TA coherence and VG score in young participants. Similarly, we did not find functional associations within the young group in this study.

The associations we observed in the older group were surprising, in that the correlation we detected was positive for early swing but negative for late swing. Because of the nature of the analysis, it is not possible to discern the causality underlying these associations; it may be the case that oscillatory corticospinal activity influenced precision in foot placement, or alternatively that performance compelled modulations in corticospinal activity. Nonetheless, the positive association we found during early swing is in agreement with the notion that beta and gamma coherence may play a role in precision force control (Kristeva et al., 2007; Petersen et al., 2010; Witte et al., 2007). The negative association detected in older participants during late swing is, however, more ambiguous but might be taken to indicate that the precise timing of coherence modulations is important for task performance.

In any case, these correlations should be interpreted cautiously because of the limited number of participants included in these analyses, as well as in light of the limited existing evidence regarding the functional significance of coherence during walking. A conservative interpretation is thus that the correlations detected in the older group indicate that task-related coherence modulations, as well as the timing of these modulations, may be functionally significant for precision in foot placement when walking is visually guided. The reason why significant associations were only observed in the older group is not apparent, although it might simply be due to greater variation (i.e., heterogeneity) in this group, making it easier to detect correlations.

4.4. Methodological considerations

There are a few important methodological considerations related to this study. First, it has been suggested that EEG recordings during dynamic movements are prone to movement artifacts, which may confound the interpretation of signals recorded during walking (Castermans et al., 2014; Snyder et al., 2015). However, a recent study using a novel experimental setup has put forward that motion artifacts in EEG during treadmill walking are only negligible, at least at speeds up to 4.5 km/h (Nathan and Contreras-Vidal, 2016). We also carefully pruned our data of epochs with high-amplitude deflections and excluded the heel strike period from the analyses to minimize possible influences of motion artifacts on results. Finally, a common average reference for EEG signals was used, which has been suggested to reduce artifact components that are similar across all channels (Snyder et al., 2015). Regardless, the most optimal way to separate movement component artifacts from neural signals in EEG data has yet to be determined.

It should also be noted that there are several restraints confining the coherence analyses; using this approach, only linearly coupled oscillatory activity is quantified, whereas any activity that is non-oscillatory in nature or nonlinearly associated is not represented. As well, it is also important to acknowledge that functional outcomes such as score on the VG walking task are the result of coordinated activity in multiple muscles, whereas our analysis only assessed correlations with specific oscillatory drive to the TA muscle.

In addition, EMG cross-talk may also have influenced intramuscular coherence results, that is, EMG activity could have been recorded from overlapping motor unit territories. This is unlikely, however, as electrode pairs were separated by a distance $\geq$8.5 cm (mean 12 cm), which should be sufficient considering that the length of TA fibers is $\sim$7.5 cm (Friederich, 1990; Wickiewicz et al., 1983). Individual results for intramuscular coherence were also visually inspected for high, broadband coherence suggesting the presence of cross-talk (Hansen et al., 2001), but no data displaying this property were observed.

Finally, our results should be interpreted in light of the relatively small sample size of $n = 30$. Based on the earlier findings of Watanabe et al. (2018), we estimated that our power to detect an anticipated effect size of $\eta^2 = 0.028$ for an age-task interaction was in the range of 0.6–0.8. Because this is somewhat less than ideal, further studies with a larger sample are needed to confirm the present findings.

5. Conclusion

In conclusion, our results show that 15–50 Hz corticomuscular and intramuscular coherence in the TA muscle exhibits age-related differences during the swing phase of normal and VG walking, suggesting that aging may affect the way in which the corticospinal tract participates in the control of normal walking and VG gait modifications. The present results contribute to our current understanding of the effect of healthy aging on the sensorimotor control of gait and may provide a basis for the development of novel evidence-based interventions targeting improved gait function in the elderly.

Disclosure

The authors declare that there is no competing interest regarding the publication of this article.

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