Age and interlimb coordination complexity modulate oscillatory spectral dynamics and large-scale functional connectivity
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Age and interlimb coordination complexity modulate oscillatory spectral dynamics and large-scale functional connectivity

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Abbreviations

EEG	electroencephalography
ERD	event-related desynchronization
ERS	event-related synchronization
ERSP	event-related spectral perturbation
fMRI	functional magnetic resonance imaging
GLMM	generalized linear mixed model
LMM	linear mixed model
SD	standard deviation
tACS	transcranial alternating current stimulation

Abstract

Interlimb coordination deteriorates as a result of aging. Due to its ubiquity in daily life, a greater understanding of the underlying neurophysiological changes is required. Here, we combined electroencephalography time-frequency spectral power and functional connectivity analyses to provide a comprehensive overview of the neural dynamics underlying the age-related deterioration of interlimb coordination involving all four limbs. Theta, alpha and beta oscillations in the frontal, central and parietal regions were analyzed in twenty younger (18–30 years) and nineteen older adults (65–78 years) during a complex interlimb reaction time task. Reaction time was significantly higher in older adults across all conditions, and the discrepancy between both age groups was largest in the most complex movement condition. Older adults demonstrated enhanced beta event-related desynchronization (i.e., the attenuation of beta power), which further increased along with task complexity and was positively linked to behavioral performance. Theta functional connectivity between frontal, central and parietal regions generally increased with movement complexity, irrespective of age group. In general, frontoparietal alpha band functional connectivity tended to be reduced in older versus younger adults, although these contrasts did not survive multiple comparison corrections. Overall, spectral results suggest that enhanced beta desynchronization in older adults reflects a successful compensatory mechanism to cope with increased difficulty during complex interlimb coordination. Functional connectivity results suggest that theta and alpha band connectivity are prone to respectively task- and age-related modulations. Future work could target these spectral and functional connectivity dynamics through noninvasive brain stimulation to potentially improve interlimb coordination in older adults.

Keywords: electroencephalography (EEG), interlimb coordination, spectral analyses, functional connectivity, aging, time-frequency

Introduction

Interlimb coordination refers to simultaneously executing coordinated movements with multiple limbs. As interlimb coordination is ubiquitous in our everyday lives (e.g., tying your shoes, taking the stairs, driving a car), its age-related deterioration jeopardizes the functional autonomy of older adults. At the same time, the underlying neural processes remain poorly understood (Maes et al., 2017). Moreover, the scientific field has predominantly focused on bimanual movements. Although bimanual research has provided telltale insights into the constraints governing interlimb coordination (Sisti et al., 2011), it is limited by its inclusion of two fixed end-effectors, namely the upper limbs. In various everyday life situations, the end-effectors required for motor behavior are variable and have to be selected according to task demands. Furthermore, this selection of end-effectors also determines motor processing complexity, next to the dynamics typically investigated by bimanual research (Boisgontier et al., 2014; Boisgontier et al., 2016). Boisgontier et al. (2014) revealed that processing complexity of various movements involving two limbs (e.g., the left hand and left leg, the right arm and left leg) varies widely depending on the recruited limbs, and this has been associated with structural neural markers in the past (Boisgontier et al., 2016; Rasooli et al., 2021). Nevertheless, the functional neural markers underlying these end-effector dependent differences in motor processing complexity remain unclear.

Several modalities can identify the neural markers of interlimb coordination. Electroencephalography (EEG) is highly suited, as its high temporal resolution enables detection of rapidly changing neural interactions underlying interlimb movement preparation and execution (Fujiyama et al., 2016; Kline et al., 2016; Liuzzi et al., 2011; Verstraelen et al., 2021). A consistently reported marker of interlimb movements and motor behavior in general, is the attenuation of sensorimotor alpha (8–12 Hz) and beta (12–30 Hz) band power (Brovelli et al., 2004; Engel and Fries, 2010; Pfurtscheller and Lopes da Silva, 1999). This phenomenon, also known as event-related desynchronization (ERD), reflects sensorimotor network activation, and is suggested to be mediated by enhanced thalamocortical excitation (Kilavik et al., 2013; Neuper and Pfurtscheller, 2001). Theta band (3.5–8 Hz) event-related synchronization (ERS) (i.e., a power increase) is a marker of motor behavior, as well. Mostly observed in the frontal regions, it is hypothesized to reflect movement preparation, execution and sensorimotor integration (Cruikshank et al., 2012; Karrasch et al., 2004; Pellegrino et al., 2018; Van der Lubbe et al., 2021; Yordanova et al., 2020). Besides power modulations, functional connectivity also plays an important role in the context of interlimb movements. Compared to single limb movements, interlimb movements entail a more widespread neural network involving frontal, central and parietal regions (Banerjee et al., 2012; Debaere et al., 2001; Heuninckx et al., 2005; Swinnen, 2002). Although inter-regional functional connectivity is mostly characterized by theta and alpha band coupling during

bimanual coordination tasks (Berger et al., 2018; von Stein and Sarnthein, 2000), Rueda-Delgado et al. (2017) demonstrated that interhemispheric beta coupling increased along with bimanual task difficulty.

Aging affects power and functional connectivity dynamics underlying motor behavior. In general, alpha and beta ERD increase as a result of aging, while theta ERS decreases (Protzak and Gramann, 2021; Rueda-Delgado et al., 2019; Schmiedt-Fehr et al., 2016; Shih et al., 2021; Yordanova et al., 2020). Although the precise nature of these age-related changes mostly remains ambiguous, there is growing consensus that increased beta ERD reflects a compensatory mechanism to cope with elevated baseline beta levels (Heinrichs-Graham and Wilson, 2016; Heinrichs-Graham et al., 2018). Concerning functional connectivity, research has mostly investigated resting-state connectivity, with conflicting results (Esposito et al., 2008; Moezzi et al., 2019; Seidler et al., 2015; Smit et al., 2012; Vysata et al., 2014). In contrast, there is a dearth of task-related functional connectivity studies. Using fMRI during a bimanual task, Heitger et al. (2013) observed a functional connectivity increase along with higher age and increased task complexity. In contrast, Kiyama et al. (2014) reported that higher motor area connectivity is reduced during bimanual task execution in older adults. Regarding EEG, Loehrer et al. (2016) reported interhemispheric central connectivity increases with increasing age during a bimanual tapping task. Rosjat et al. (2018) performed a finger-tapping task in young and older adults. They found age-related increases in functional connectivity as well, likely to represent compensatory mechanisms to preserve performance in older participants.

Here, we set out to investigate the effect of aging on the neural mechanisms underlying complex interlimb coordination involving all four limbs as potential end-effectors. By incorporating time-frequency spectral power and functional connectivity analyses, three frequency bands and three brain regions, we aim to provide the most comprehensive overview of the age-related oscillatory changes underlying complex interlimb coordination to date. A greater understanding of these neural processes could form the basis of future interventions. We hypothesize that older adults will demonstrate enhanced alpha and beta ERD and attenuated theta ERS compared to younger adults and that beta ERD will be positively associated with behavioral performance. Due to a lack of previous research, formulating substantiated hypotheses was impossible for the research questions entailing functional connectivity and interlimb movement complexity.

Experimental procedures

Participants

In total, 20 younger and 20 older adults were recruited. One older adult was excluded due to excessive EEG noise. As such, data of 20 younger [aged 22.3 ± 1.0 years (mean ± standard deviation [SD]), 10 females] and 19 older adults (aged 70.7 ± 3.0 years, 8 females) were analyzed. All participants were right-handed according to the Edinburgh Handedness Inventory (lateralization quotient in younger adults = 92.9 ± 9.2, older adults = 97.6 ± 6.0) (Oldfield, 1971), and scored ≥24 on the Montreal Cognitive Assessment (younger adults = 28.9 ± 1.2, older adults = 26.5 ± 1.7), indicating the absence of mild cognitive impairment (Nasreddine et al., 2005; Thomann et al., 2020). Participants had (corrected to) normal vision, and were excluded if they (1) played a musical instrument, (2) smoked, (3) had a pathological condition affecting the central nervous system and/or (4) used psycho-active medication. All participants provided written informed consent. The study (B1152020000017) was approved by the local Ethical Committee of the University of Hasselt (Belgium) and was in accordance with the Declaration of Helsinki and its amendments (World Medical Association, 1964, 2008).

Motor task and experimental protocol

The multi-limb reaction time task was used to assess interlimb coordination (Boisgontier et al., 2014). Participants were seated in front of a monitor with both hands and forefeet resting on tablets with capacitive proximity switches (Pepperl Fuchs CBN5-F46-E2, sampling frequency: 1000 Hz) (see Fig. 1A). The monitor displayed 4 grey squares, representing the 4 limbs (see Fig. 1B). At task onset, two grey squares turned white (i.e., visual cue onset). Participants were instructed to then lift the corresponding limbs together as fast as possible. Lift-off of both limbs was registered. The difference between visual cue onset and lift-off onset of the slowest limb was defined as reaction time. The difference between the lift-off of the slowest and fastest limb was recorded to evaluate offline that both limbs were moved simultaneously. The task consisted of 6 unique movements [upper (1) or lower limbs (2), left (3) or right limbs (4), left upper–right lower limbs (5) or right upper–left lower limbs (6)]. These 6 movements were pooled into 3 conditions with different complexity levels. Based on Boisgontier et al. (2014), the same limb (upper or lower limb movements), same side (left or right limb movements) and mixed limb (left upper - right lower limb, or right upper – left lower limb movements) conditions were defined as the easy, intermediate and difficult conditions, respectively.

To ensure task comprehension, participants first performed a short familiarization block. Here, each movement was performed 10 consecutive times (i.e., a simple choice reaction time task where the first 10 trials consisted of the upper limb condition, the next 10 trials of the lower limb condition, and so on). Then, EEG was recorded during 4 experimental blocks, each consisting of 78 trials, for a total of 312 trials. In every block, each unique movement was repeated 13 times (i.e., 26 repetitions per

condition). As such, all participants repeated each movement 52 times, and each condition 104 times. Condition order within each block was pseudo-randomized through MATLAB (v2021a, The MathWorks, Massachusetts, USA) to ensure that conditions with a different complexity preceded each other to an equal extent. A trial started after a 1000 ms delay (= intertrial interval) after all the limbs were correctly placed on the tablets. Two triggers were sent to the EEG system: one at visual cue onset and one at lift-off onset of the slowest limb. Experimental trials from the 4 experimental blocks containing reaction times < 200 ms were identified as anticipatory behavior and were not analyzed (Whelan, 2008).
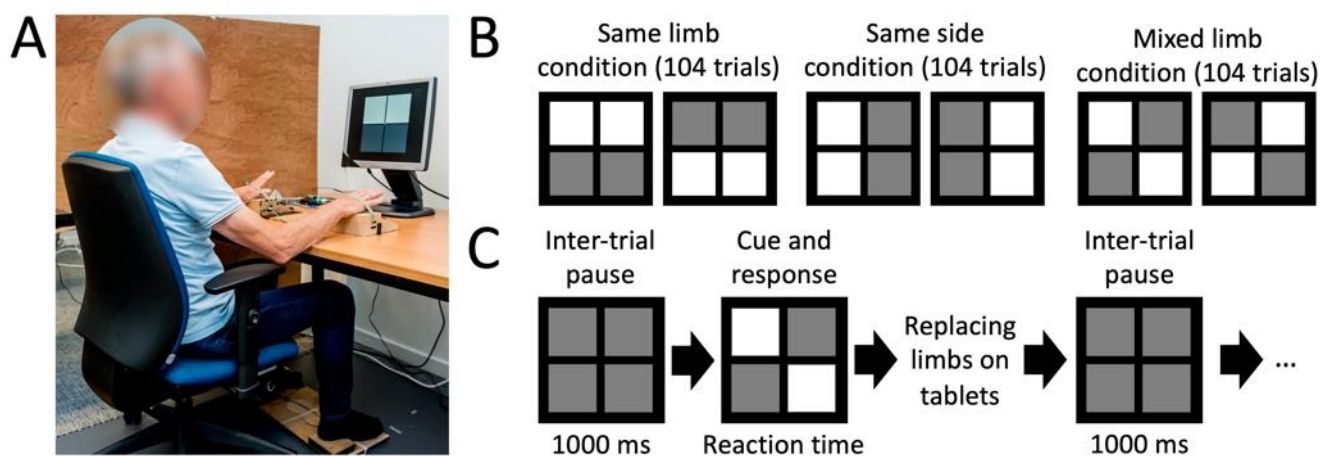
Figure 1. *Multi-limb reaction time task. (A) Experimental set-up. (B) Visual cues displayed to participants for each condition, left and right squares represent left and right limbs, respectively. Upper and lower squares represent hands and forefeet, respectively. White squares represent the cue for lift-off. (C) Example of the course of one trial.*

*EEG data collection and preprocessing*

EEG data were recorded using a 64-channel electrode system [BioSemi ActiveTwo (Biosemi, Amsterdam, The Netherlands)]. The electrode cap was placed in accordance to the international 10–20 system. Data were acquired at 2048 Hz, and were preprocessed offline using the EEGLAB plug-in (v2021.1) (Delorme and Makeig, 2004). Data were down-sampled to 512 Hz and 1–40 Hz band-pass filtered. Noisy channels were rejected via the Clean Rawdata plug-in (v2.0), followed by Common Average Referencing (Delorme, 2021). Removed channels were interpolated, Independent Components Analysis was performed and oculomotor, muscle, heart and channel noise artefacts were removed. High-amplitude data components were removed through Artefact Subspace Rejection, and

a surface Laplacian was applied to render the data appropriate for connectivity analyses (Cohen, 2014; Gulbinaite et al., 2014; Perrin et al., 1989; Srinivasan et al., 2007; Winter et al., 2007). Finally, EEG data were time-locked to the visual cue, and epochs were created from -1000 ms to 2000 ms, with 0 ms being cue-onset.

Selection of frequency bands and electrodes of interest

Based on previous literature (see 1. Introduction), the frontal, central and parietal regions were selected as regions of interest (see Fig. 2A). Data from F3 and F4 (frontal region), C3, C4 and Cz (central region) and P3 and P4 (parietal region) were averaged per region for spectral analyses. For functional connectivity analyses, F3–C4, F3–P3, F3–P4, F4–C3, F4–P3, F4–P4, C3–C4, C3–P4 and C4–P3 were investigated (see Fig. 2B). Only electrode pairs with a moderate inter-electrode distance (> 10 cm) were selected, as electrodes in close vicinity to one another can spuriously affect connectivity analyses due to volume conduction (Cohen, 2015; Srinivasan et al., 2007; Winter et al., 2007).
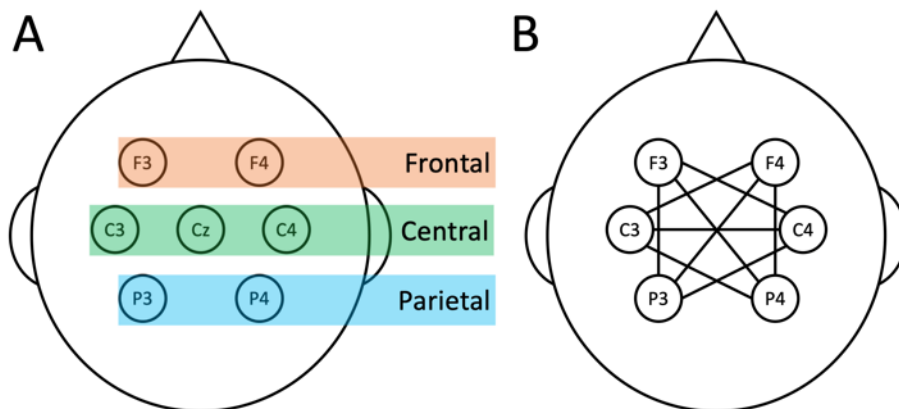
Figure 2. *Overview of selected electrodes. (A) Regions (frontal, central and parietal) selected for power analyses. (B) Electrode pairs selected for functional connectivity analyses.*

EEG time-frequency decomposition

The cue- and response-locked epochs were decomposed into a time-frequency representation using custom MATLAB scripts, based on Cohen (2014). The preprocessed EEG time series data were convolved with a series of complex Morlet wavelets, defined as Gaussian-windowed complex sine waves: $e^{i2\pi tf} * e^{\frac{-t^2}{2*\sigma^2}}$, where i is the complex operator, t is time, f is frequency ranging from 3 to 35 in 30 logarithmic steps, and σ defines wavelet width. Here, σ is $\frac{10}{2\pi f}$ (Cohen, 2014; van Driel et al., 2012).

From this complex signal, frequency-specific power values were extracted at each time point using the squared magnitude of the result of the convolution Z_t: $Power = real[z_t]^2 + imag[z_t]^2$ (Cohen, 2014). Power was decibel normalized: $Power\ (dB) = 10 * log10(\frac{power}{baseline})$, with baseline being defined as the cue-locked participant- and frequency-specific condition-average power values from -500 to -200 ms.

Additionally, inter-site phase clustering was calculated. This measure of functional connectivity assumes that two neural sources are coupled when their oscillations are temporally synchronized: $ISPC_f = \left| n^{-1} * \sum_{t=1}^{n} e^{i(\phi_{xt}-\phi_{yt})} \right|$, where f is frequency, n is number of trials, t is timepoint, i is the complex operator, and $\phi_{xt\ \&\ yt}$ are the phase angles from electrode x and y at each timepoint at frequency f (Cohen, 2014). Inter-site phase clustering was percentage normalized: $Inter-site\ phase\ clustering\ (\%) = 100 * \frac{ISPC-baseline}{baseline}$, with baseline being defined as the cue-locked participant- and frequency-specific condition-average values from -500 to -200 ms.

Statistical analyses

For all results, mean and SD are shown. All analyses were done in RStudio, through the lme4 package (Bates et al., 2015; R Core Team, 2021; RStudio Team, 2020). When generalized linear mixed models (GLMM) or linear mixed models (LMM) were constructed, all multi-way interactions between the fixed factors were included in the initial model. PARTICIPANT was included in each (G)LMM as a random intercept. All (G)LMMs were simplified through stepwise removal of non-significant factors, starting with the factor with the highest p-value not contained in any higher-level interactions. Normality of the final (G)LMMs was assessed through visual inspection of the Q–Q plots. Through the Emmeans package, Bonferroni-corrected pairwise contrasts were used to interpret significant factors (Lenth, 2021). The significance level for all tests was α = 0.05.

Behavioral data

Reaction time was analyzed with a GLMM, to ensure maximally interpretable results whilst adhering to all statistical test requirements (Lo and Andrews, 2015). The fixed factors were GROUP (younger or older adults), CONDITION (same limb, same side or mixed limb) and their interaction. Next to PARTICIPANT, BLOCK was also included as a random intercept. For the theoretical distribution, an Inverse Gaussian and Gamma distribution were considered to account for the heavy right-tailed reaction time data distribution. Likewise, an identity and inverse link were considered as link functions.

The Inverse Gaussian – Inverse link combination resulted in the best fitting model according to the AIC/BIC criteria.

Next to reaction time, in a supplementary analysis (Cf., Supplementary materials 2), we also investigated accuracy on the behavioral task via a binomial GLMM. The same fixed and random effects were used.

EEG data

Grand-average cue-locked time-frequency matrices were created per region (power) or electrode pair (functional connectivity). As these matrices averaged all the data across groups and conditions, they were blind to the factors of interest. A time-frequency statistical mask was obtained from the grand-average matrices, by comparing each power/functional connectivity value within the time-interval of interest (0 to 1800 ms) against the distribution of power/functional connectivity values in the baseline period (-500 to -200 ms), using t-tests. A multiple comparison correction was applied: α was divided by the number of performed t-tests, with this number equaling the number of frequencies tested * the number of time-points in the window of interest. As such, the resulting significance threshold was $1.90*10^{-6}$. P-values lower than this value were used to create the statistical mask in MATLAB and were constrained to the theta, alpha, and beta frequency bands (see Fig. 3 and supplementary materials). Power/functional connectivity values within the mask were extracted and averaged per frequency band, participant and condition. This approach was chosen as it is best suited for the multi-factorial design of the current work (Cohen, 2014; van Driel et al., 2012). Next, LMMs were performed per region/electrode pair and frequency band, with the average POWER/FUNCTIONAL CONNECTIVITY serving as dependent variable. GROUP, CONDITION and their interaction were included as fixed factors. As aforementioned, post-hoc tests were used to interpret results.
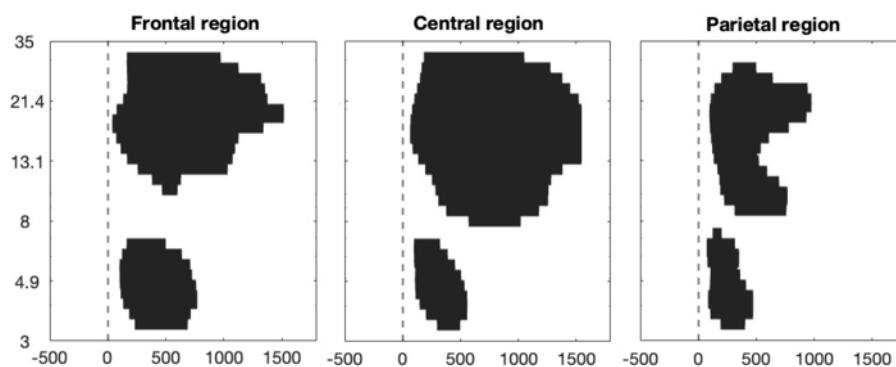
Figure 3. *Statistical masks (black) used for spectral analyses, defined as significant changes in grand-average time-frequency matrix with respect to baseline. The y-axis displays frequency (Hz), the x-axis displays cue-locked time (ms).*

*Relationship between behavior and neural data*

In an exploratory analysis, we linked neural activity to task performance. Consistent with the previous analyses, LMMs per frequency band and region/electrode pair were constructed. REACTION TIME was used as dependent variable. GROUP, CONDITION, and POWER/FUNCTIONAL CONNECTIVITY were used as fixed factors. All interactions were included. If an interaction containing POWER/FUNCTIONAL CONNECTIVITY was present in the final model, the emtrends function (Emmeans package) was used for post-hoc comparisons.

<u>Results</u>

<u>*Behavioral performance*</u>

The average value for the movement onset difference across both limbs per age group and condition remained well below 100 ms (maximum: 85.3 ms), indicating that participants moved both limbs simultaneously. In total, 7.44% of the trials were removed due to being incorrect responses (7.4%) or anticipatory behavior (0.04%).

Reaction time was related to CONDITION * GROUP (χ^2_2 = 6.40, p = 0.041) (see Fig. 4). Reaction times were higher in older (same limb: 806.2 ± 253.5 ms, same side: 834.1 ± 251.8 ms, mixed limb: 1366.1 ± 527.3 ms) versus younger adults (same limb: 583.1 ± 120.2 ms, same side: 604.8 ± 127.5 ms, mixed limb: 834.7 ± 293.2 ms) (same limb: z = 6.07, same side: z = 5.77, mixed limb: z = 6.18, all p-values < 0.001). The CONDITION * GROUP interaction seemed to be driven by the mixed limb condition, where an average difference of 531.4 ms across both groups was present, compared to the 223.1 and 229.3 ms differences in the same limb and same side conditions, respectively. In both groups, reaction time was higher in the mixed limb versus same limb (younger adults: z = 50.49, older adults: z = 60.61, all p-values < 0.001) and same side (younger adults: z = 44.35, older adults: z = 54.59, all p-values < 0.001) movements, and reaction time was significantly higher in the same side versus same limb condition (younger adults: z = 5.78, older adults: z = 5.78, all p-values < 0.001).
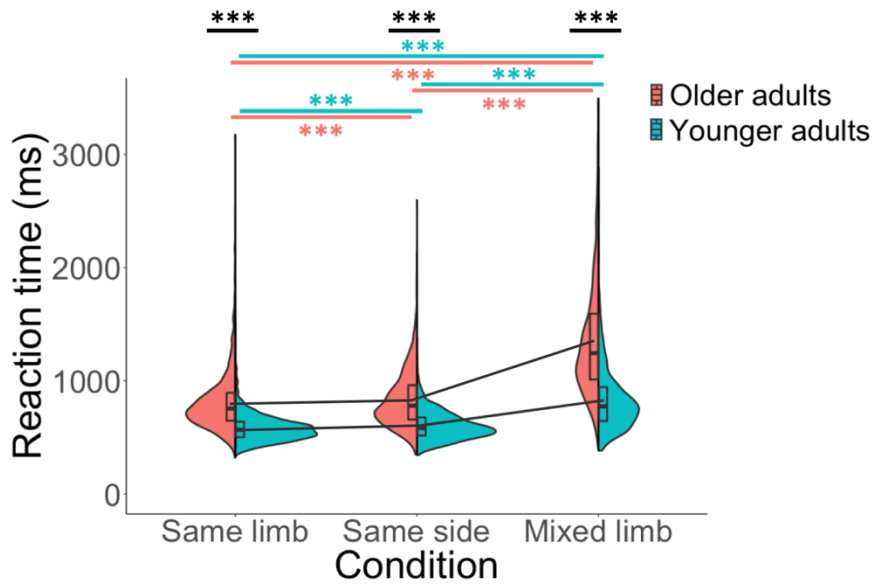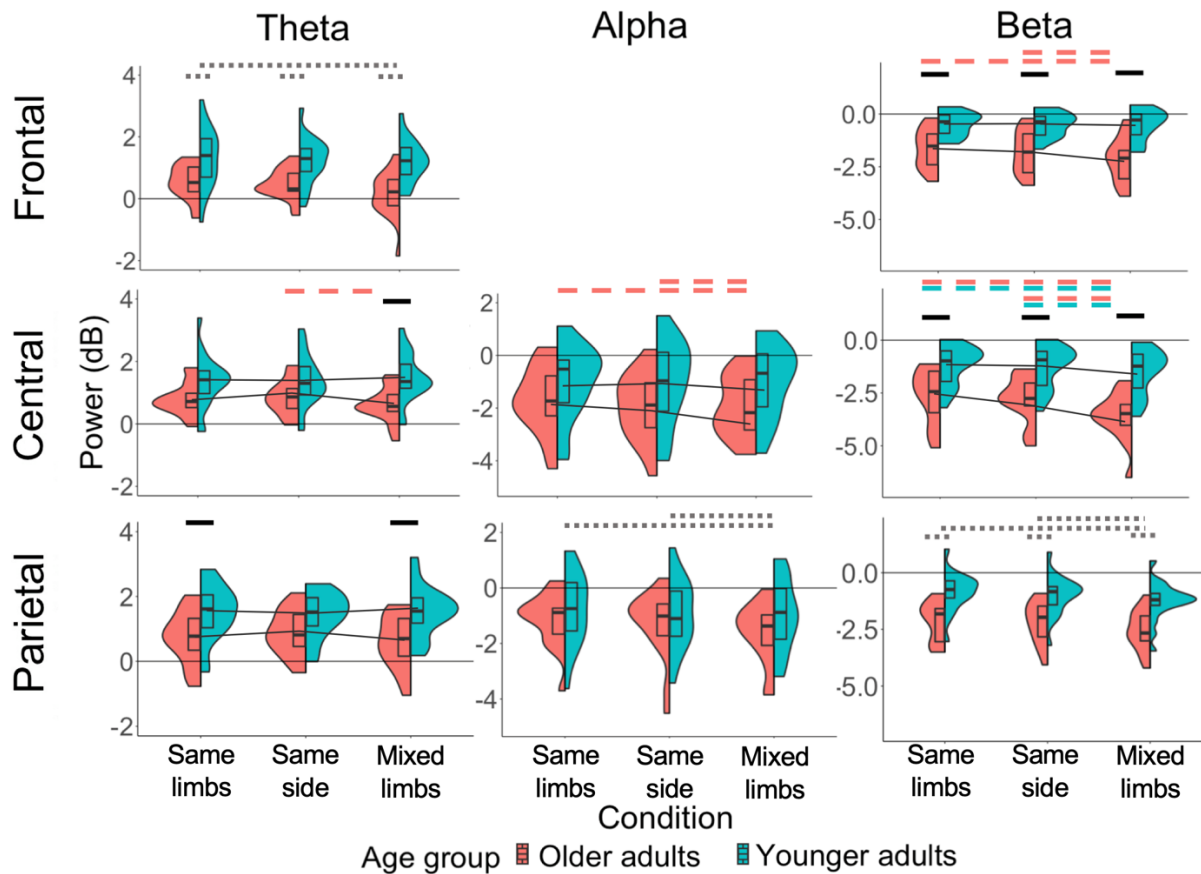
Figure 4. *Multi-limb reaction time task performance. Within each violin plot, box plots are shown. Lines connecting the average values are used to accentuate the significant age group * condition interaction effects. Black (between-group) and colored (within-group) lines show significant contrasts (p < 0.001).*

Spectral results

Time-frequency plots are shown in Fig. 5. Quantitative results are shown in Fig. 6.
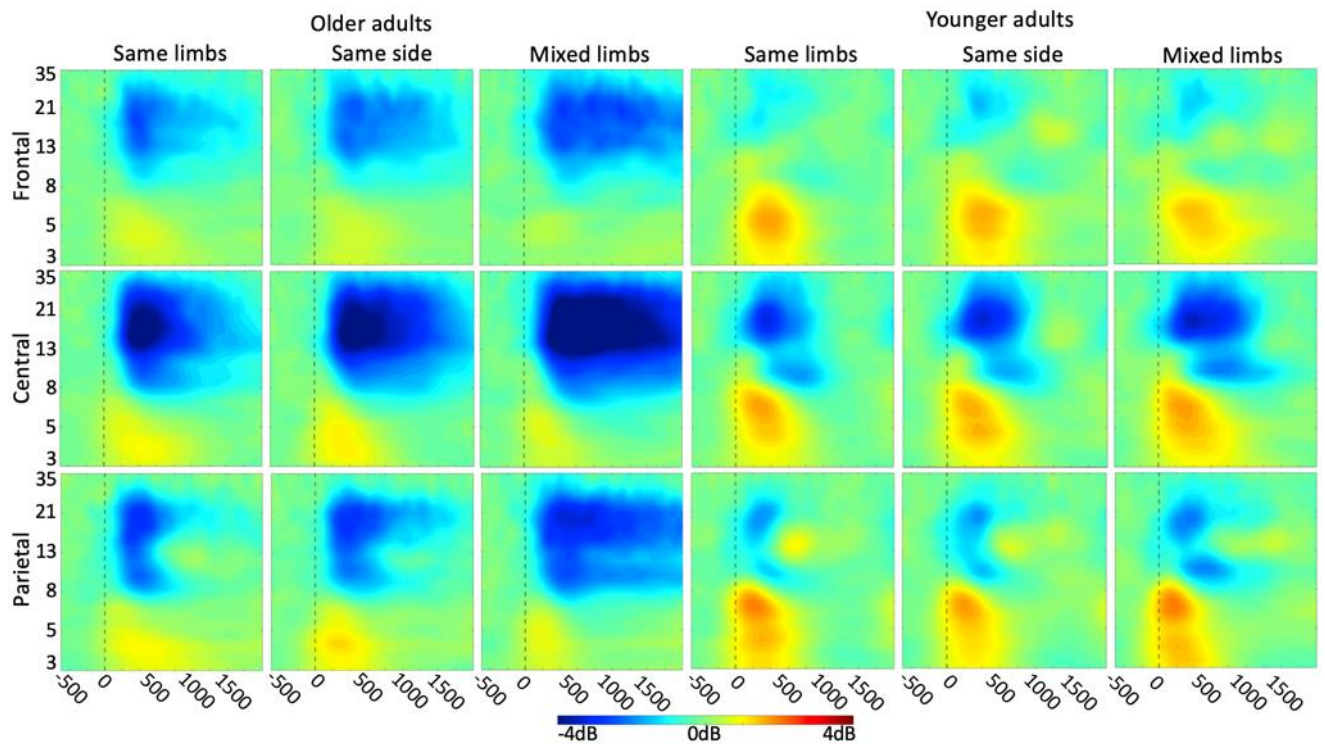
Figure 6. Mean power (dB) per frequency band and region. Within each violin plot, box plots are shown. Black and dashed colored lines denote significant between-group and -condition contrasts, respectively. Lines connecting the average values are used to accentuate significant age group * condition interaction effects. Grey dotted lines denote significant contrasts when no interaction between AGE GROUP and CONDITION was present.

Frontal spectral dynamics

Theta ERS was related to CONDITION ($F_{2,76}$ = 5.72, p = 0.005) and GROUP ($F_{1,37}$ = 16.75, p < 0.001). Theta ERS was lower during mixed (0.69 $\pm$ 0.87 dB) versus same limb movements (0.94 $\pm$ 0.86 dB) (t = 3.29, p = 0.005), and was lower in older (0.39 $\pm$ 0.61 dB) versus younger adults (1.25 $\pm$ 0.78 dB) (t = 4.09, p < 0.001).

Beta ERD was related to CONDITION * GROUP ($F_{2,74}$ = 9.34, p < 0.001). In older adults, beta ERD was higher during mixed (-2.21 ± 1.03 dB) versus same limb (-1.63 ± 0.93 dB) (t = 6.15, p < 0.001) and same side (-1.79 ± 1.00 dB) (t = 4.51, p < 0.001) movements. Beta ERD was higher in older versus younger adults (same limb: -0.49 ± 0.56 dB, same side: -0.50 ± 0.57 dB, mixed limb: -0.52 ± 0.73 dB) (same limb: t = -4.36, p < 0.001, same side: t = -4.92, p < 0.001, mixed limbs: t = -6.45, p < 0.001). The CONDITION * GROUP effect seemed to be mainly driven by beta ERD increases along with task complexity in older adults which were not present in younger adults.

Central spectral dynamics

Theta ERS was related to CONDITION * GROUP ($F_{2,74}$ = 6.63, p = 0.002). Theta ERS was lower in older adults during mixed limb (0.62 ± 0.54 dB) versus same side (0.97 ± 0.73 dB) (t = 3.86, p = 0.002) movements. Theta ERS was higher in younger (1.49 ± 0.76 dB) versus older adults during mixed limbs movements (t = -3.82, p = 0.004). The CONDITION * GROUP effect seemed to be driven by the mixed limb condition, where the difference between both age groups was most apparent.

Alpha ERD was related to CONDITION * GROUP ($F_{2,74}$ = 4.95, p = 0.001). Alpha ERD was higher in older adults during mixed (-2.53 ± 1.79 dB) versus same limb (-1.87 ± 1.49 dB) (t = 5.54, p < 0.001) and same side (-2.05 ± 1.59 dB) (t = 4.01, p = 0.001) movements. The CONDITION * GROUP was driven by the complexity-modulated ERD changes in older adults, that were absent in younger adults.

Beta ERD was related to CONDITION * GROUP ($F_{2,74}$ = 17.96, p > 0.001). In older adults, beta ERD was higher during mixed (-3.9 ± 1.4 dB) versus same limb (-2.56 ± 1.28 dB) (t = 12.87, p < 0.001) and same side (-3.05 ± 1.42 dB) (t = 8.22, p < 0.001) movements, and during same side versus same limb (t = 4.65, p < 0.001) movements. In younger adults, beta ERD was higher during mixed (-1.64 ± 1.27 dB) versus same limb (-1.17 ± 0.91 dB) (t = 4.62, p < 0.001) and same side (-1.24 ± 0.98 dB) (t = 3.95, p < 0.001) movements. Across all conditions, beta ERD was higher in older versus younger adults (same limbs: t = -3.57, p = 0.009, same side: t = -4.63, p < 0.001, mixed limbs: t = -5.79, p < 0.001). The CONDITION * GROUP effect seemed to be driven by beta ERD increases along with task complexity (namely in the mixed limb condition) which were more apparent in older adults.

Parietal spectral dynamics

Theta ERS was related to CONDITION * GROUP ($F_{2,74}$ = 4.3, p = 0.017). Theta ERS decreased in older versus younger adults during the same limb (older adults: 0.75 ± 0.81 dB, younger adults: 1.52 ± 0.85

dB) (t = -1.91, p = 0.032) and mixed limb (older adults: 0.63 ± 0.82 dB, younger adults: 1.6 ± 0.8 dB, t = -3.87, p = 0.003) movements. The CONDITION * GROUP interaction effect was driven by the absence of significant differences across both age groups in the same side movement versus the same and mixed limb movements.

Alpha ERD was related to CONDITION ($F_{2,76}$ = 20.05, p < 0.001). Alpha ERD was higher during mixed (-1.52 ± 1.51 dB) versus same limb (-1.12 ± 1.42 dB) (t = 5.71, p < 0.001) and same side (-1.16 ± 1.44 dB) (t = 5.23, p < 0.001) movements.

Beta ERD was related to CONDITION ($F_{2,76}$ = 22.98, p < 0.001) and GROUP ($F_{1,37}$ = 22.66, p < 0.001). Beta ERD was higher during mixed (-1.92 ± 1.14 dB) versus same limb (-1.47 ± 1.07 dB) (t = 6.58, p < 0.001) and same side (-1.6 ± 1.09 dB) (t = 4.7, p < 0.001) movements. It was higher in older (-2.33 ± 0.93 dB) versus younger adults (-1.03 ± 0.86 dB) (t = -4.76, p < 0.001).

Relationship between behavioral performance and spectral activity.

Reaction time was related to FRONTAL THETA POWER ($F_{1,89}$ = 6.34, p = 0.014). A 1 dB increase was linked to a 61.51 ms reaction time decrease, irrespective of group and condition.

Reaction time was related to PARIETAL BETA POWER * GROUP * CONDITION ($F_{2,70}$ = 4.67, p = 0.012) (see Fig. 7). While a 1 dB increase was linked to a 113.54 ms reaction time decrease during the mixed limb condition, it was associated with a 8.92 ms increase during the same side condition (t = 3.4, p = 0.010). Increased beta ERD was associated with better performance in older adults during mixed limb movements, but worse performance in younger adults (i.e., a 1 dB increase was linked to a 40.75 ms reaction time increase) (t = 2.97, p = 0.034).
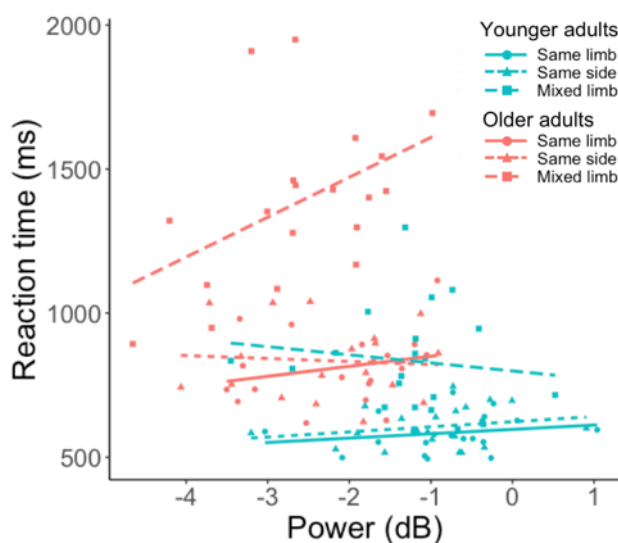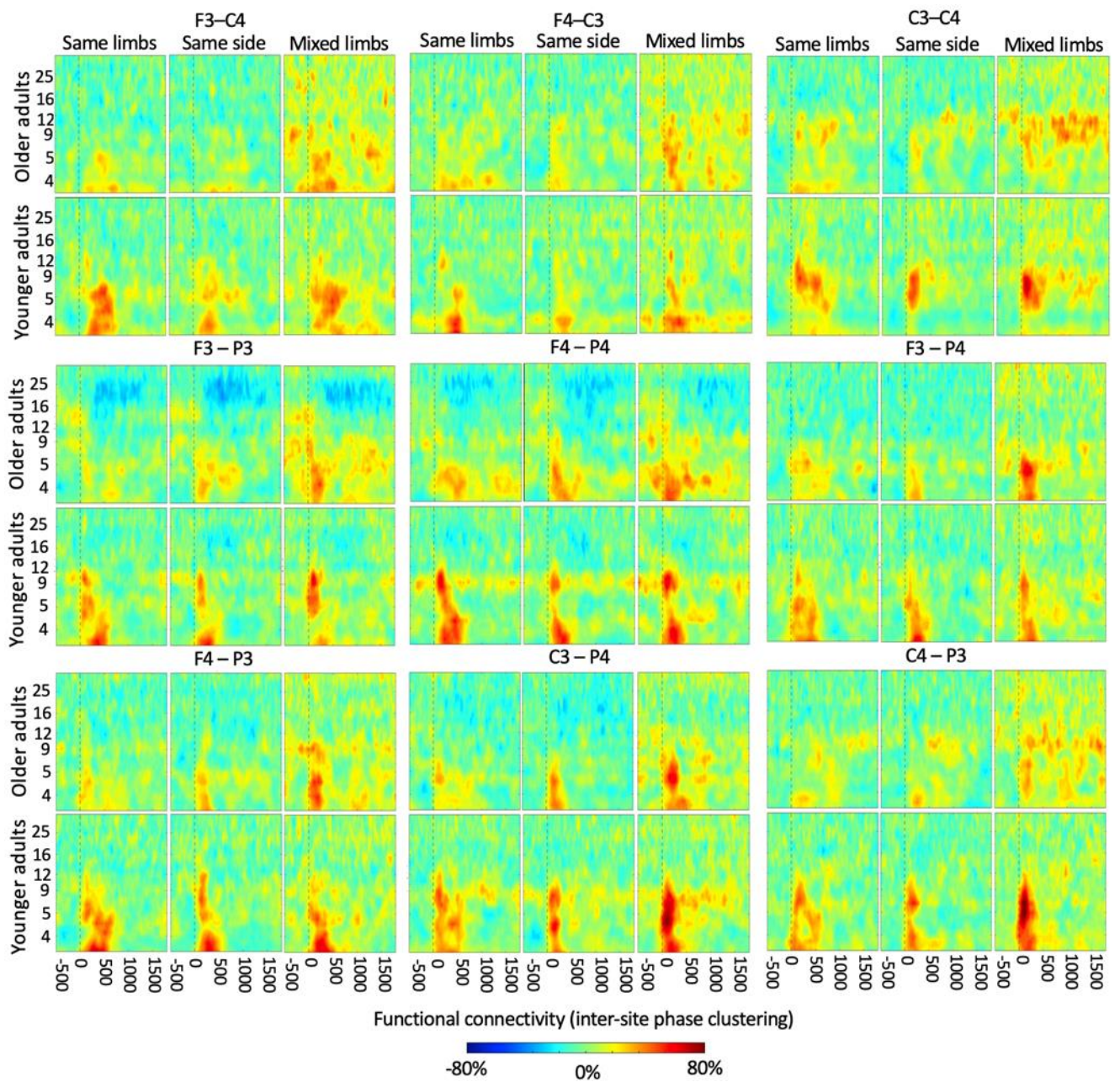
Figure 7. Relationship between parietal beta event-related desynchronization for younger and older adults per task condition.

Functional connectivity

Time-frequency plots are shown in Fig. 8, quantitative results are shown in Fig. 9 and Fig. 10 provides an overview of all connectivity results.

Figure 9. Functional connectivity (inter-site phase clustering) per electrode pair, frequency band and condition. Within each violin plot, box plots are shown. Dashed (within-group) lines denote significant contrasts (p < 0.05). No group * condition contrasts were significant after multiple comparison correction. Thus, all results are on the group- or condition-averaged level.
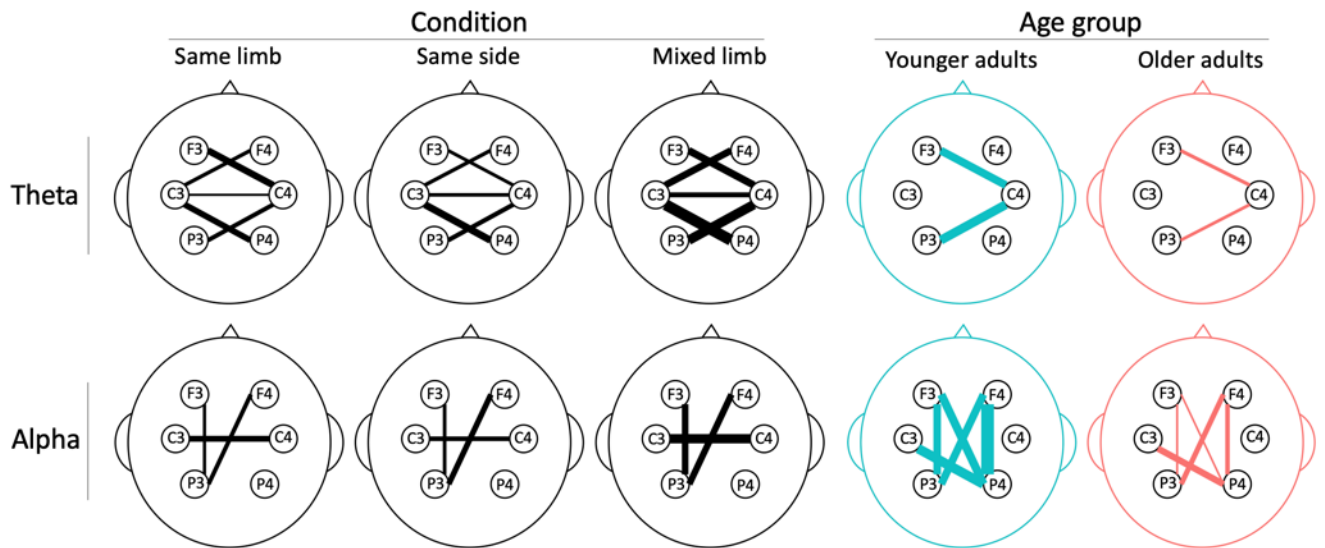
Figure 10. *Functional connectivity results for the theta and alpha band. Only electrode pairs containing a significant condition or age group effect are shown. Line thickness is based on the functional connectivity magnitude in the specific condition or age group.*

Interhemispheric central functional connectivity (C3–C4)

Theta central (C3–C4) connectivity was related to CONDITION ($F_{2,76}$= 6.09, p = 0.004). Connectivity was higher during mixed (23.26 ± 26.03%) versus same limb (10.98 ± 17.74%) (t = -3.49, p = 0.018) movements.

Alpha C3–C4 connectivity was related to CONDITION ($F_{2,76}$= 6.43, p = 0.003). Connectivity was higher during mixed (43.66 ± 41.07%) versus same side (22.11 ± 25.69%) (t = -3.45, p = 0.025) movements.

Frontocentral functional connectivity

Theta left frontal – right central connectivity (F3–C4) was related to CONDITION ($F_{2,76}$= 9.16, p < 0.001) and GROUP ($F_{1,37}$= 6.03, p = 0.019). Connectivity was lower during same side (16.37 ± 26.90%) versus mixed limb (34.91 ± 30.65%) (t = -3.98, p = 0.005) movements. No GROUP contrasts survived correction for the multiple electrode pairs.

Theta right frontal – left central connectivity (F4–C3) was related to CONDITION ($F_{2,67}$ = 6.73, p = 0.002). No contrasts survived multiple comparison correction.

Frontoparietal functional connectivity

Alpha left frontoparietal (F3–P3) connectivity was related to CONDITION ($F_{2,76}$ = 4.9, p = 0.01) and GROUP ($F_{1,37}$ = 7.06, p = 0.012). No contrasts survived multiple comparison correction.

Alpha right frontoparietal connectivity (F4–P4) was related to GROUP ($F_{1,37}$ = 6.78, p = 0.013). No contrasts survived multiple comparison correction.

Alpha left frontal – right parietal connectivity (F3–P4) was related to GROUP ($F_{1,37}$ = 5.3, p = 0.027). No contrasts survived multiple comparison correction.

Alpha right frontal – left parietal connectivity (F4–P3) was related to GROUP * CONDITION ($F_{2,74}$ = 5.83, p = 0.005). No contrasts survived multiple comparison correction.

Centroparietal functional connectivity

Theta left central – right parietal connectivity (C3–P4) was related to CONDITION ($F_{2,76}$ = 14.15, p < 0.001). Connectivity was higher during the mixed (53.04 ± 58.47%) versus same limb (29.23 ± 46.16%) (t = 5.03, p < 0.001) and same side (34.03 ± 63.30%) (t = 4.02, p = 0.004) movements.

Alpha left central – right parietal connectivity (C3–P4) was related to GROUP ($F_{1,37}$ = 14.15, p < 0.001). No contrasts survived multiple comparison correction.

Theta right central – left parietal connectivity (C4–P3) was related to CONDITION ($F_{2,76}$ = 18.75, p < 0.001) and GROUP ($F_{1,37}$ = 6.2, p = 0.017). Connectivity was higher in the mixed (45.08 ± 48.67%) versus same limb (20.74 ± 32.48%) (t = 5.47, p < 0.001) and same side (22.25 ± 38.77%) (t = 5.13, p < 0.001) movements. No other contrasts survived multiple comparison correction.

Relationship between behavioral performance and functional connectivity.

Reaction time was related to alpha interhemispheric central FUNCTIONAL CONNECTIVITY (C3–C4) * GROUP ($F_{1,105}$ = 5.25, p = 0.216). In older adults, a 1% connectivity increase was related to a 1.62 ms reaction time decrease, while it was associated to a 0.16 ms reaction time increase in younger adults. However, this effect did not survive multiple comparison correction.

Reaction time was related to theta right frontal – left central FUNCTIONAL CONNECTIVITY (F4–C3) * GROUP ($F_{1,100}$ = 12.73, p = 0.009). A 1% connectivity increase in older adults was associated with a 3.047 ms reaction time increase, while it was associated with a 0.184 ms reaction time decrease in younger adults (t = 3.52, p = 0.009).

Here, we demonstrated that aging negatively impacts interlimb coordination involving all four limbs, and that the discrepancy between younger and older adults is most apparent in the most complex interlimb movements. We identified several oscillatory spectral and functional connectivity dynamics that are associated with age-related changes in interlimb coordination performance and/or interlimb movement complexity.

Motor performance

Mixed limb movements are the most demanding interlimb movements and same limb movements are the least demanding. These results are in line with the functional space model (Kinsbourne and Hicks, 1978), which portrays the brain as a functional space, wherein functional distance dictates inter-regional collaboration/interference (Boisgontier et al., 2014). According to this model, interhemispheric, homologous areas are functionally closest to another due to callosal connections, followed by intrahemispheric regions. Finally, non-homologous interhemispheric regions, which are responsible for mixed limb movements, are furthest from each other. An interaction between age group and movement condition was present. Qualitative inspection of figure 4 indicates that this interaction was likely attributable to the most difficult mixed limb condition. During the same limb and same side conditions, the difference between younger and older adults in reaction times remained mostly consistent (± 225 ms), while the difference doubled in the mixed limb conditions (± 550 ms). As such, an age-complexity effect seemed to be present. Although primarily described in the cognitive field (Bashore et al., 2014; Smulders et al., 1999), Boisgontier et al. (2016) also reported an age-complexity effect using the multi-limb reaction time task, attributing it to a decline of the inhibitory neural pathways (Levin et al., 2014).

Although not within the direct scope of the current work, analyses of the task accuracy (Supplementary materials 2) substantiate the observation that mixed limb movements are the most demanding movements. Moreover, no between age-group accuracy contrasts remained significant after multiple comparison correction. This, together with the finding that distinct differences in reaction times were present across both groups, seems to suggest that older adults prioritized accuracy over speed, which is in line with previous research (Starns and Ratcliff, 2010).

Beta ERD was consistently higher in older adults. As a certain beta power level seems required for movement execution and resting beta levels are elevated in older adults, the age-related beta ERD increase seems to reflect a compensational mechanism to enable older adults to reach movement execution (Heinrichs-Graham and Wilson, 2016; Heinrichs-Graham et al., 2018; Toledo et al., 2016). Our findings indicate that also in complex interlimb coordination, beta ERD serves this compensational role. Moreover, we found that enhanced beta ERD is linked to better task performance in older adults during mixed limb movements. This further points in the direction of beta ERD serving as a successful compensatory mechanism in older adults (Goble et al., 2010; Heuninckx et al., 2005; Heuninckx et al., 2008; Rueda-Delgado et al., 2019). In all three neural regions, movement complexity significantly affected beta ERD. An interaction between task complexity and age group was even present in the frontal and central regions. Based on the post-hoc contrasts and Figure 4, this interaction effect seemed to be driven by changing beta ERD levels along with task complexity in older adults, whereas beta ERD remained much more consistent across movement conditions in younger adults. A similar effect was present for central alpha ERD.

Overall, our results indicate that beta ERD is modulated by task complexity especially in older adults and in younger adults to a lesser extent. This implies that beta ERD not only acts as a rigid mechanism to reach a movement execution threshold but also reflects characteristics of the executed motor behavior, with increased beta ERD being reflective of more complex motor behavior (Heinrichs-Graham and Wilson, 2016; Kilavik et al., 2013). As such, our observation can be reconciled by a wealth of studies demonstrating that beta modulations are not merely involved in motor execution but also reflect motor demands (Boonstra et al., 2007; Daffertshofer et al., 2007; Nakayashiki et al., 2014; Tzagarakis et al., 2010).

Beta and alpha ERD was spatially widespread in older adults, while more bound to the central region in younger adults. As ERD in these frequencies has been linked to increased fMRI blood oxygenated level dependent signal (Formaggio et al., 2008; Stevenson et al., 2011), this observation is in agreement with various studies indicating that older adults recruit additional regions (i.e., prefrontal areas) during the preparation and execution of interlimb movements (Maes et al., 2017). Although one might associate this diffuse spatial distribution to an age-related dedifferentiation process where brain activity becomes increasingly non-specific as a result of dysfunctional inhibitory mechanisms (Koen and Rugg, 2019), this does not seem to be the case here. Indeed, increased parietal activation (i.e., increased beta ERD) was associated with better behavioral performance in older adults during the most difficult mixed limb movements

Theta ERS was generally lower in older adults, which is consistent with previous work reporting the same phenomenon during a sensorimotor four-choice reaction time task and a memory task (Karrasch et al., 2004; Yordanova et al., 2020). Both for the central and parietal regions, an interaction between age group and movement condition was present. Theta ERS decreased with task complexity in older adults, while it remained consistent across all movement conditions in younger adults. Based on the age-related decline of theta ERS and behavioral performance, and on the role of theta in motor regulatory and sensorimotor processing (Cruikshank et al., 2012; Karrasch et al., 2004; Pellegrino et al., 2018; Yordanova et al., 2020), it seems plausible that the reduction of theta ERS in older adults is reflective of dysfunctional motor regulatory and sensorimotor processes. This is further substantiated by the finding that higher frontal theta ERS was associated with better behavioral performance across both age groups.

Future work should use noninvasive brain stimulation to provide causal evidence for these hypotheses. For instance, beta transcranial alternating current stimulation (tACS) could be administered in older adults during complex interlimb movements. If this would improve interlimb coordination performance and increase beta ERD, this could serve as causal evidence in favor of the compensational function of beta ERD. Alternatively, future work could use a closed-loop EEG-tACS protocol to alter state-dependent beta levels during performance of different interlimb movements. This way, protocols could take the observation of increased beta ERD during more complex movements into account. Enhancement of frontal theta ERS through tACS or repetitive transcranial magnetic stimulation, could provide causal evidence for the importance of theta ERS for adequate motor control.

Functional connectivity dynamics

Functional connectivity dynamics were solely situated in the theta and alpha bands. While the effect of age group on spectral dynamics was mostly dependent on the interlimb movement condition, this was not the case for functional connectivity.

Although no age group related post-hoc contrasts survived multiple comparison correction, task-related functional connectivity tended to be reduced in older adults, suggesting the presence of a generalized age-related phenomenon [e.g., due to a reduction of white matter integrity or gray matter atrophy (Andrews-Hanna et al., 2007)]. In contrast, age-related increases in event-related functional connectivity have also been reported (Heitger et al., 2013; Kiyama et al., 2014; Loehrer et al., 2016). However, as these studies used bimanual tasks and different functional connectivity measures (i.e.,

EEG dynamic causal modelling, fMRI graph analysis and fMRI structural equation modelling), it is difficult to directly compare results. Furthermore, the scale of the investigated networks differed substantially across studies. While the aforementioned studies mostly focused on small-scale connectivity (i.e., primary motor cortex, dorsal premotor cortex and supplementary motor area), we investigated large-scale intra- and interhemispheric connectivity. Notably, Rowe et al. (2006) demonstrated a differential aging effect on small- versus large-scale motor networks during a motor task. While local motor regional connectivity increased as a result of aging, large-scale connectivity (i.e., interhemispheric and frontoparietal connectivity) decreased. Thus, the work of Rowe et al. (2006) seems to partially integrate our work with the results of Heitger et al. (2013); Kiyama et al. (2014); Loehrer et al. (2016).

Results pertaining to frontoparietal functional connectivity seemed to be mostly situated in the alpha band, although no contrasts survived multiple comparison correction. The observation that frontoparietal connectivity was characterized by alpha band dynamics is supported by previous literature designating a critical role to alpha oscillations in the frontoparietal network (Sauseng et al., 2005; van Schouwenburg et al., 2017). Moreover, frontoparietal connectivity was prone to age-related changes as the variable age group was significant in all frontoparietal functional connectivity mixed models. Thus, our work is in agreement with previous studies stating that frontoparietal functional connectivity, which plays a vital role in attentional control, visuomotor integration and motor learning, deteriorates as a result of aging (Campbell et al., 2012; Marek and Dosenbach, 2018; Reuter-Lorenz and Cappell, 2008; Sauseng et al., 2005; Scolari et al., 2015). However, as no significant link between frontoparietal connectivity and behavioral performance was present, it is currently impossible to attribute the age-related decrease in frontoparietal connectivity to the decreased behavioral performance of older adults.

Mainly theta band functional connectivity increased along with movement complexity (see Fig. 10). Given the role of theta oscillations in sensorimotor integration (Caplan et al., 2003; Cruikshank et al., 2012; Huang and Sereno, 2018), increased connectivity in this frequency band could serve as a mechanism to cope with the increased motor demands associated with more complex movements. However, only in younger adults, theta band connectivity increases were associated with increased behavioral performance. In older adults, the opposite was true. To resolve this conflicting finding, future work could use noninvasive brain stimulation techniques capable of altering neural oscillations (e.g., in-phase dual site tACS, repetitive transcranial magnetic stimulation) to enhance functional theta connectivity and investigate the behavioral and neural effects. Altering right frontal - left central connectivity might be a promising starting point, given the presence of a significant relationship with behavioral performance.

Our work is subject to several limitations and/or recommendations that could be addressed in future work. First, we only included two age groups. A longitudinal study design or the inclusion of a middle-aged group would have provided more nuanced insights into the deterioration of interlimb coordination across the lifespan. Second, our study does not allow to draw conclusions regarding the causality of the observed relationship between neural dynamics and behavior. While the analyses linking behavior to neural dynamics provide some insight into this matter, it is by no means of causal nature. Future studies should combine EEG with noninvasive brain stimulation to overcome this limitation. Third, our behavioral analyses included the factor BLOCK as a random intercept to account for motor learning effects. We chose to refrain from further analyses of BLOCK to ensure consistency across the analyses of the behavioral and neural data. As motor learning processes influence neural oscillations, it might be interesting for future work to also take BLOCK into account. To do so, more trials per block should be included to ensure a good signal-to-noise-ratio of the EEG data. Fourth, we are currently unable to determine which observed neural dynamics are reflective of action selection versus preparation. Future work should further investigate this, and could do so via investigation of the oscillatory dynamics underlying simple versus choice reaction time tasks including multiple end-effectors. Fifth, we did not include a variable intertrial interval which implies that temporal anticipation could have taken place. Nevertheless, only a small percentage of the data was identified as anticipatory behavior (0.04%) and, on the other hand, inclusion of varying intertrial intervals could introduce unwanted nonlinear temporal prediction into the neural data (Egner et al., 2010; Gonsalvez and Polich, 2002).

Conclusion

In this study, we set out to unravel the oscillatory dynamics underlying the age-related deterioration of interlimb coordination involving all four limbs. On a behavioral level, older adults performed worse than younger adults in all movement conditions and were disproportionally affected by interlimb coordination complexity, indicating an age-complexity effect. Beta ERD was higher in older adults compared to younger adults, across all conditions and brain regions and increased along with task complexity mainly in older adults. Exploratory analyses and previous literature indicate that this age-related increase in beta ERD serves as a successful compensational mechanism to cope with increased motor demands. Concerning

functional connectivity, frontoparietal alpha band connectivity results suggested an age-related decrease, although post-hoc contrasts did not survive multiple comparison corrections. Large-scale theta band connectivity increased along with movement complexity, irrespective of the age group.

Declaration of interest

Declarations of interest: none

References

Andrews-Hanna, J.R., et al., 2007. Disruption of Large-Scale Brain Systems in Advanced Aging. Neuron. 56**,** 924-935.

Banerjee, A., et al., 2012. Spatiotemporal re-organization of large-scale neural assemblies underlies bimanual coordination. NeuroImage. 62**,** 1582-1592.

Bashore, T.R., Jr., et al., 2014. Response-specific slowing in older age revealed through differential stimulus and response effects on P300 latency and reaction time. Neuropsychol Dev Cogn B Aging Neuropsychol Cogn. 21**,** 633-73.

Bates, D., et al., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software. 67**,** 1 - 48.

Berger, A., et al., 2018. Brain Oscillatory and Hemodynamic Activity in a Bimanual Coordination Task Following Transcranial Alternating Current Stimulation (tACS): A Combined EEG-fNIRS Study. Frontiers in behavioral neuroscience. 12**,** 67-67.

Boisgontier, M.P., et al., 2014. Complexity of Central Processing in Simple and Choice Multilimb Reaction-Time Tasks. PLOS ONE. 9**,** e90457.

Boisgontier, M.P., et al., 2016. Nucleus accumbens and caudate atrophy predicts longer action selection times in young and old adults. Human Brain Mapping. 37**,** 4629-4639.

Boonstra, T.W., et al., 2007. Multivariate time-frequency analysis of electromagnetic brain activity during bimanual motor learning. Neuroimage. 36**,** 370-7.

Brovelli, A., et al., 2004. Beta oscillations in a large-scale sensorimotor cortical network: directional influences revealed by Granger causality. Proc Natl Acad Sci U S A. 101**,** 9849-54.

Campbell, K.L., et al., 2012. Age differences in the frontoparietal cognitive control network: implications for distractibility. Neuropsychologia. 50**,** 2212-23.

Caplan, J.B., et al., 2003. Human θ Oscillations Related to Sensorimotor Integration and Spatial Learning. The Journal of Neuroscience. 23**,** 4726.

Cohen, M.X., 2014. Analyzing neural time series data : theory and practice.

Cohen, M.X., 2015. Effects of time lag and frequency matching on phase-based connectivity. Journal of Neuroscience Methods. 250**,** 137-146.

Cruikshank, L.C., et al., 2012. Theta oscillations reflect a putative neural mechanism for human sensorimotor integration. J Neurophysiol. 107**,** 65-77.

Daffertshofer, A., Boonstra, T.W., Beek, P.J., 2007. Cortical beta synchronization is related to low-order motor parameters. International Congress Series. 1300**,** 329-332.

Debaere, F., et al., 2001. Brain Areas Involved in Interlimb Coordination: A Distributed Network. NeuroImage. 14**,** 947-58.

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods. 134**,** 9-21.

Delorme, A., 2021. Clean Rawdata version 2.0. Vol., ed.^eds.

Egner, T., Ely, S., Grinband, J., 2010. Going, going, gone: characterizing the time-course of congruency sequence effects. Front Psychol. 1**,** 154.

Engel, A.K., Fries, P., 2010. Beta-band oscillations—signalling the status quo? Current Opinion in Neurobiology. 20**,** 156-165.

Esposito, F., et al., 2008. Independent component model of the default-mode brain function: combining individual-level and population-level analyses in resting-state fMRI. Magnetic Resonance Imaging. 26**,** 905-913.

Formaggio, E., et al., 2008. EEG and FMRI coregistration to investigate the cortical oscillatory activities during finger movement. Brain Topogr. 21**,** 100-11.

Fujiyama, H., et al., 2016. Performing two different actions simultaneously: The critical role of interhemispheric interactions during the preparation of bimanual movement. Cortex. 77**,** 141-154.

Goble, D.J., et al., 2010. The neural control of bimanual movements in the elderly: Brain regions exhibiting age-related increases in activity, frequency-induced neural modulation, and task-specific compensatory recruitment. Human Brain Mapping. 31**,** 1281-1295.

Gonsalvez, C.L., Polich, J., 2002. P300 amplitude is determined by target-to-target interval. Psychophysiology. 39**,** 388-96.

Gulbinaite, R., Rijn, H., Cohen, M., 2014. Fronto-parietal network oscillations reveal relationship between working memory capacity and cognitive control. Frontiers in Human Neuroscience. 8.

Heinrichs-Graham, E., Wilson, T.W., 2016. Is an absolute level of cortical beta suppression required for proper movement? Magnetoencephalographic evidence from healthy aging. NeuroImage. 134**,** 514-521.

Heinrichs-Graham, E., et al., 2018. The lifespan trajectory of neural oscillatory activity in the motor system. Developmental cognitive neuroscience. 30**,** 159-168.

Heitger, M.H., et al., 2013. Bimanual Motor Coordination in Older Adults Is Associated with Increased Functional Brain Connectivity – A Graph-Theoretical Analysis. PLOS ONE. 8**,** e62133.

Heuninckx, S., et al., 2005. Neural basis of aging: the penetration of cognition into action control. J Neurosci. 25**,** 6787-96.

Heuninckx, S., Wenderoth, N., Swinnen, S.P., 2008. Systems Neuroplasticity in the Aging Brain: Recruiting Additional Neural Resources for Successful Motor Performance in Elderly Persons. The Journal of Neuroscience. 28**,** 91-99.

Huang, R.-S., Sereno, M.I., 2018. Chapter 7 - Multisensory and sensorimotor maps. In: Handbook of Clinical Neurology. Vol. 151, G. Vallar, H.B. Coslett, ed.^eds. Elsevier, pp. 141-161.

Karrasch, M., et al., 2004. Effects of normal aging on event-related desynchronization/synchronization during a memory task in humans. Neuroscience Letters. 366**,** 18-23.

Kilavik, B.E., et al., 2013. The ups and downs of beta oscillations in sensorimotor cortex. Experimental Neurology. 245**,** 15-26.

Kinsbourne, M., Hicks, R., 1978. Functional cerebral space: A model for overflow, transfer and interference effects in human performance: A tutorial review. In Requin J, (Ed.). Attention and Performance VII.**,** pp. 345–362.

Kiyama, S., et al., 2014. Distant functional connectivity for bimanual finger coordination declines with aging: an fMRI and SEM exploration. Frontiers in Human Neuroscience. 8.

Kline, J.E., et al., 2016. Cortical Spectral Activity and Connectivity during Active and Viewed Arm and Leg Movement. Frontiers in Neuroscience. 10.

Koen, J.D., Rugg, M.D., 2019. Neural Dedifferentiation in the Aging Brain. Trends in cognitive sciences. 23**,** 547-559.

Krause, V., et al., 2016. Beta Band Transcranial Alternating (tACS) and Direct Current Stimulation (tDCS) Applied After Initial Learning Facilitate Retrieval of a Motor Sequence. Frontiers in Behavioral Neuroscience. 10.

Lenth, R.V., 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. . Vol., ed.^eds.

Levin, O., et al., 2014. Aging and motor inhibition: A converging perspective provided by brain stimulation and imaging approaches. Neuroscience & Biobehavioral Reviews. 43**,** 100-117.

Liuzzi, G., et al., 2011. Coordination of Uncoupled Bimanual Movements by Strictly Timed Interhemispheric Connectivity. The Journal of Neuroscience. 31**,** 9111.

Lo, S., Andrews, S., 2015. To transform or not to transform: using generalized linear mixed models to analyse reaction time data. Frontiers in Psychology. 6.

Loehrer, P.A., et al., 2016. Ageing changes effective connectivity of motor networks during bimanual finger coordination. NeuroImage. 143**,** 325-342.

Maes, C., et al., 2017. Two hands, one brain, and aging. Neurosci Biobehav Rev. 75**,** 234-256.

Marek, S., Dosenbach, N.U.F., 2018. The frontoparietal network: function, electrophysiology, and importance of individual precision mapping. Dialogues in clinical neuroscience. 20**,** 133-140.

Moezzi, B., et al., 2019. Characterization of Young and Old Adult Brains: An EEG Functional Connectivity Analysis. Neuroscience. 422**,** 230-239.

Nakayashiki, K., et al., 2014. Modulation of event-related desynchronization during kinematic and kinetic hand movements. Journal of neuroengineering and rehabilitation. 11**,** 90.

Nasreddine, Z.S., et al., 2005. The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. J Am Geriatr Soc. 53**,** 695-9.

Neuper, C., Pfurtscheller, G., 2001. Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. International Journal of Psychophysiology. 43**,** 41-58.

Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia. 9**,** 97-113.

Pellegrino, G., et al., 2018. Theta Activity in the Left Dorsal Premotor Cortex During Action Re-Evaluation and Motor Reprogramming. Frontiers in Human Neuroscience. 12.

Perrin, F., et al., 1989. Spherical splines for scalp potential and current density mapping. Electroencephalography and Clinical Neurophysiology. 72**,** 184-187.

Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin Neurophysiol. 110**,** 1842-57.

Protzak, J., Gramann, K., 2021. EEG beta-modulations reflect age-specific motor resource allocation during dual-task walking. Scientific Reports. 11**,** 16110.

R Core Team, 2021. R: A language and environment for statistical computing., Vol., ed.^eds. R Foundation for Statistical Computing, Vienna, Austria.

Rasooli, A., et al., 2021. Prefronto-Striatal Structural Connectivity Mediates Adult Age Differences in Action Selection. The Journal of Neuroscience. 41**,** 331-341.

Reuter-Lorenz, P.A., Cappell, K.A., 2008. Neurocognitive Aging and the Compensation Hypothesis. Current Directions in Psychological Science. 17**,** 177-182.

Rosjat, N., et al., 2018. Aging-associated changes of movement-related functional connectivity in the human brain. Neuropsychologia. 117**,** 520-529.

Rowe, J.B., et al., 2006. Aging is associated with contrasting changes in local and distant cortical connectivity in the human motor system. NeuroImage. 32**,** 747-760.

RStudio Team, 2020. RStrudio: Integrated Development for R. Vol., ed.^eds. Rstudio, PBC, Boston, MA.

Rueda-Delgado, L.M., et al., 2017. Coordinative task difficulty and behavioural errors are associated with increased long-range beta band synchronization. Neuroimage. 146**,** 883-893.

Rueda-Delgado, L.M., et al., 2019. Age-related differences in neural spectral power during motor learning. Neurobiol Aging. 77**,** 44-57.

Sauseng, P., et al., 2005. Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. Int J Psychophysiol. 57**,** 97-103.

Schmiedt-Fehr, C., et al., 2016. Aging differentially affects alpha and beta sensorimotor rhythms in a go/nogo task. Clinical Neurophysiology. 127**,** 3234-3242.

Scolari, M., Seidl-Rathkopf, K.N., Kastner, S., 2015. Functions of the human frontoparietal attention network: Evidence from neuroimaging. Current opinion in behavioral sciences. 1**,** 32-39.

Seidler, R., et al., 2015. Associations between age, motor function, and resting state sensorimotor network connectivity in healthy older adults. NeuroImage. 108**,** 47-59.

Shih, P.-C., et al., 2021. Alpha and beta neural oscillations differentially reflect age-related differences in bilateral coordination. Neurobiology of Aging. 104**,** 82-91.

Sisti, H.M., et al., 2011. Testing Multiple Coordination Constraints with a Novel Bimanual Visuomotor Task. PLOS ONE. 6**,** e23619.

Smit, D.J.A., et al., 2012. The Brain Matures with Stronger Functional Connectivity and Decreased Randomness of Its Network. PLOS ONE. 7**,** e36896.

Smulders, F.T.Y., et al., 1999. Effects of task complexity in young and old adults: Reaction time and P300 latency are not always dissociated. Psychophysiology. 36**,** 118-125.

Srinivasan, R., et al., 2007. EEG and MEG coherence: measures of functional connectivity at distinct spatial scales of neocortical dynamics. J Neurosci Methods. 166**,** 41-52.

Starns, J.J., Ratcliff, R., 2010. The effects of aging on the speed-accuracy compromise: Boundary optimality in the diffusion model. Psychology and aging. 25**,** 377-390.

Stevenson, C.M., Brookes, M.J., Morris, P.G., 2011. β-Band correlates of the fMRI BOLD response. Human brain mapping. 32**,** 182-197.

Swinnen, S.P., 2002. Intermanual coordination: From behavioural principles to neural-network interactions. Nature Reviews Neuroscience. 3**,** 348-359.

Thomann, A.E., et al., 2020. Enhanced diagnostic accuracy for neurocognitive disorders: a revised cut-off approach for the Montreal Cognitive Assessment. Alzheimer's Research & Therapy. 12**,** 39.

Toledo, D.R., et al., 2016. Cortical correlates of response time slowing in older adults: ERP and ERD/ERS analyses during passive ankle movement. Clin Neurophysiol. 127**,** 655-663.

Tzagarakis, C., et al., 2010. Beta-band activity during motor planning reflects response uncertainty. The Journal of neuroscience : the official journal of the Society for Neuroscience. 30**,** 11270-11277.

Van der Lubbe, R.H.J., et al., 2021. Frontal brain areas are more involved during motor imagery than during motor execution/preparation of a response sequence. International Journal of Psychophysiology. 164**,** 71-86.

van Driel, J., Ridderinkhof, K.R., Cohen, M.X., 2012. Not all errors are alike: theta and alpha EEG dynamics relate to differences in error-processing dynamics. J Neurosci. 32**,** 16795-806.

van Schouwenburg, M.R., Zanto, T.P., Gazzaley, A., 2017. Spatial Attention and the Effects of Frontoparietal Alpha Band Stimulation. Frontiers in human neuroscience. 10**,** 658-658.

Verstraelen, S., et al., 2021. Dissociating the causal role of left and right dorsal premotor cortices in planning and executing bimanual movements – A neuro-navigated rTMS study. Brain Stimulation. 14**,** 423-434.

von Stein, A., Sarnthein, J., 2000. Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. Int J Psychophysiol. 38**,** 301-13.

Vysata, O., et al., 2014. Age-related changes in EEG coherence. Neurologia i Neurochirurgia Polska. 48**,** 35-38.

Whelan, R., 2008. Effective Analysis of Reaction Time Data. The Psychological Record. 58**,** 475-482.

Winter, W.R., et al., 2007. Comparison of the effect of volume conduction on EEG coherence with the effect of field spread on MEG coherence. Stat Med. 26**,** 3946-57.

Yordanova, J., Falkenstein, M., Kolev, V., 2020. Aging-related changes in motor response-related theta activity. International Journal of Psychophysiology. 153**,** 95-106.