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Interlimb coordination is required for adequate execution of most daily life activities. Yet, aging negatively affects interlimb coordination, impacting the quality of life in older people. Therefore, disentangling the underlying age-related neural mechanisms is of utmost importance. Here, we investigated neurophysiological processes of an interlimb reaction time task, including both simple and complex coordination modes. Midfrontal theta power, measured using electroencephalography (EEG), was analysed as a marker for cognitive control. In total, 82 healthy adults participated, with 27 younger, 26 middle-aged, and 29 older adults. On a behavioural level, reaction time increased across the adult lifespan, and error rate was higher in older adults. Notably, aging disproportionately affected reaction times in the complex coordination modes, with larger reaction time increases from simple to complex movements than in younger adults, starting already at middle age. On the neurophysiological level, EEG showed that only younger adults had significantly increased levels of midfrontal theta power during complex relative to simple coordination modes, while no significant differences were found between simple and complex movements in middle-aged and older adults. The absence of this theta power upregulation with regard to movement complexity with increasing age might reflect a premature saturation of the available mental resources.

Keywords: aging; electroencephalography; frequency band analysis; motor control; reaction time

Introduction

The ability to coordinate movements between all four limbs deteriorates with increasing age (Maes et al., 2017; Rasooli et al., 2021; Seidler et al., 2010; Van Hoornweder et al., 2022). This age-related deterioration can jeopardize mobility, independence, and by extension quality of life, since interlimb coordination is required in most daily life activities, such as walking, carrying objects, texting, dressing oneself, or driving a car. Along with accurate interlimb coordination, a quick response is also of importance (e.g., recovering balance to avoid falling or engaging in traffic). Yet, aging is accompanied with slowing of movements, especially with increasing movement complexity (Rasooli et al., 2021; Seidler et al., 2010; Van Hoornweder et al., 2022), and this slowing is already present in middle-aged adults (McEvoy et al., 2001; Rasooli et al., 2021).

Along with these behavioural findings, age-related differences in brain activity have been found. Functional brain research shows that older adults recruit additional brain regions when performing even the simplest of motor tasks. The additional recruited brain regions are situated in frontal areas and parietal areas, which are associated with cognitive control and sensorimotor processing, respectively (Heuninckx et al., 2005; Heuninckx et al., 2008; Reuter-Lorenz & Cappell, 2008; Wu & Hallett, 2005). This increased activation has been observed to be associated with both better (Cabeza et al., 2018; Cabeza et al., 2002; Heuninckx et al., 2005; Heuninckx et al., 2008; Reuter-Lorenz & Cappell, 2008) and worse performance (Bernard & Seidler, 2012; Seidler et al., 2010; Zapparoli et al., 2022) leading to two theories.

The former observation is in accordance with the compensation hypothesis, which hypothesizes that additional recruitment reflects an increased reliance on cognitive control, encompassing a shift from automatic movement processing in younger adults, to more cognitively controlled processing in older adults (Heuninckx et al., 2005; Heuninckx et al., 2008; Seidler et al., 2010). This less automatic processing in older adults may result in an increased cognitive workload in order to execute motor behaviour, as an increased amount of the available capacity in cognitive resources is required to meet task demands (Rauffet et al., 2020). The latter observation of worse performance is in line with the dedifferentiation hypothesis, whereby the overactivation does not lead to behavioural improvement, and sometimes even to performance worsening, and could be the result of a non-functional spread in brain activity and/or deficiencies in inhibitory neurotransmission (Bernard & Seidler, 2012; Seidler et al., 2010; Zapparoli et al., 2022).

While changes in movement speed are already apparent in middle-aged adults (McEvoy et al., 2001; Rasooli et al., 2021), this age group is only sparsely included in cognitive and motor studies, especially considering neural changes in interlimb coordination (Rasooli et al., 2021). However, inclusion of a middle-aged group is key to improve our understanding of neural changes across the adult lifespan in a more nuanced manner. To illustrate, Berchicci et al. (2012) implemented a reaction time task using a button pressing paradigm, in which the performance of middle-aged adults better resembled that of younger adults, while brain activity looked more similar to that of older adults, who demonstrated similar, albeit larger, activations in the prefrontal brain regions (Berchicci et al., 2012). The authors suggested that the additional brain activity reflected compensatory activity, likely reflecting increased cognitive involvement. Hence, this compensation mechanism seemed to be successfully used by middle-aged adults to maintain behavioural performance, whereas as in older adults, it seemed to lose its effectiveness leading to performance declines (Berchicci et al., 2012).

In cognitive tasks, midfrontal theta power (4-8 Hz), as measured by electroencephalography (EEG), has been put forward as a neural marker of cognitive control and workload (Borghini et al., 2014; Cavanagh & Frank, 2014; Cruikshank et al., 2012; Duprez et al., 2020; Klimesch, 1999). Theta power in midfrontal regions tends to increase in uncertain and/or more difficult circumstances, such as during the presentation of novel stimuli or erroneous execution, indicating a need for more control (Cavanagh & Frank, 2014). Moreover, theta activity has been positively associated with task accuracy and task difficulty (Kardos et al., 2014; Klimesch, 1999). Regarding the latter, it has been observed that performing multiple concurrent visuomotor and cognitive tasks also leads to increased midfrontal theta power (Borghini et al., 2014; Puma et al., 2018). Remarkably, theta power plateaued when the number of simultaneous tasks became excessive, and concurrent performance started to decline. Also, in younger adults who were less capable in multitasking, theta power plateaued sooner. Thus, it seems that this plateau effect reflects a saturation of available mental resources (Hamann & Carstengerdes, 2022; Puma et al., 2018).

Interestingly, older adults tend to lack an increase in theta power with higher task difficulty in cognitive working memory tasks (Cummins & Finnigan, 2007; Kardos et al., 2014; McEvoy et al., 2001). This lack in theta upregulation when tasks become more difficult might be explained by an early saturation of mental resources. Likely, maximal theta upregulation is already reached by older people when task demands are relatively low, perhaps due to a premature saturation of mental resources and/or decreased neural efficiency (Cabeza et al., 2018).

This study explored age-related changes in midfrontal theta, as a marker for cognitive control and recruitment of mental resources, in simple and complex movement combinations during a continuously demanding interlimb motor coordination reaction time task in younger (25-35 years), middle-aged (50-60 years) and older (65 years and over) adults (Boisgontier et al., 2014; Van Hoornweder et al., 2022). The younger age group was based on the complete maturation of the prefrontal cortex by the age of 25 years old (Arain et al., 2013). The other age cut-offs were based on previous research, which found that motor and cognitive functioning deteriorated linearly between 45 and 65 years, followed by a steeper decline after the age of 65 years (van der Willik et al., 2020). The classification into simple and complex movement conditions was based on previous research considering both the number of involved limbs (i.e., the recruitment principle), and differences in processing complexity due to which limbs are involved and their inhibitory and excitatory interactions (i.e., the selection principle) (Boisgontier et al., 2016; Boisgontier et al., 2014; Rasooli et al., 2021; Van Hoornweder et al., 2022). In order to interpret possible age-related neurophysiological changes, it is needed that all participants perform the task with a similar level of accuracy, so that these changes are not the result of differences in effort or motor output (Heuninckx et al., 2005; Ward, 2006; Wu & Hallett, 2005). Therefore, we implemented a novel adaptive version of the interlimb task, in which the intertrial time varied based on task accuracy. First, we hypothesized that the complex movements would result in slower reaction times and higher error rates relative to simple movements for all age groups. Second, we expected that reaction time would gradually increase with higher age, across all conditions. Also, we expected that increasing age would affect the complex movements to a larger extent relative to simple movements, in line with previous research, i.e., the "age-complexity effect" (Boisgontier et al., 2016; Rasooli et al., 2021; Van Hoornweder et al., 2022). Finally, we hypothesized that more complex movements, as reflected by increased reaction times (Boisgontier et al., 2014; Wickens, 1981), would require more cognitive controlled and less automatic processing with higher age. Thus, performing complex movements in older adults likely requires more mental resources than in younger adults. This could be reflected by one of the following, mutually exclusive, mechanisms. It could be reflected by a greater complexity-related increase in midfrontal theta power with age, as increased theta is associated with an increased need for cognitive control (Borghini et al., 2014; Cavanagh & Frank, 2014; Klimesch, 1999). It could also be reflected by a lack in midfrontal theta upregulation with aging, indicating a premature saturation of the limited capacity in mental resources (Anguera et al., 2013; Cummins & Finnigan, 2007; Kardos et al., 2014; McEvoy et al., 2001).

Materials and Methods

Participants

A total of 82 healthy adults were recruited via social media, local newsletters, and the university of Hasselt, and were either part of the younger adult (YA: 25-35 years), middle-aged adult (MAA: 50-60 years) or older adult group (OA: 65 years and over) (cf., Table 1). Participants reported (corrected to) normal vision and hearing and did not suffer from mild cognitive impairment, as evaluated by a score of ≥ 23 on the Montreal Cognitive Assessment (MoCA) (cf., Table 1) (Carson et al., 2018; Nasreddine et al., 2005). Participants were excluded if they reported a history of neuropsychiatric conditions, or the current use of medication affecting the central nervous system. All participants signed a written informed consent. The study protocol was approved by the local ethics committee of the University of Hasselt (B9115202043058), according to the declaration of Helsinki and its amendments (World Medical Association, 1964, 2008).

Table 1. Participant demographics

Age group	Group size (♀)	Age (mean ± standard deviation)	MoCA score
Younger adults	27 (12)	27.15 ± 2.67 years	28.07 ± 1.27
Middle-aged adults	26 (15)	55.08 ± 3.06 years	27.15 ± 1.31
Older adults	29 (12)	68.76 ± 3.02 years	27.28 ± 1.28

Interlimb Task

The multi-limb reaction time task was used to evaluate interlimb coordination (Boisgontier et al., 2014; Van Hoornweder et al., 2022). Participants were seated in front of a PC monitor, with hands and forefeet resting on tablets containing capacitive proximity switches (Pepperl Fuchs CBN5-F46-E2, sampling frequency: 1000 Hz). Four squares representing the four limbs were displayed on the PC monitor. After each fixed time interval (see Procedure), some of the squares turned white. This stimulus instructed the participant to release contact with the corresponding tablets as quickly and as accurate as possible by lifting the corresponding limbs simultaneously.

Eleven different movements conditions, divided into two complexity categories based on previous research (Boisgontier et al., 2016; Boisgontier et al., 2014; Rasooli et al., 2021), were included in this task (see Figure 1A). These studies found that not only recruitment principles affect reaction times, but selection principles also play a role. For each trial, reaction time was recorded as the time between visual cue onset and lift-off of the slowest limb. Error rate (i.e., number of erroneous trials divided by all trials) was evaluated as well.

EEG Recording & Processing

The BioSemi ActiveTwo system (BioSemi, The Netherlands, sampling rate 2048Hz) was used to record EEG data with 64 scalp electrodes, placed according to the international 10-20 system. EEG data were recorded at 2048 Hz and preprocessed offline via MATLAB (v2021a, The MathWorks, MA, USA), using the EEGLAB plugin (v2021.1) (Delorme & Makeig, 2004). Data were down-sampled to 256 Hz, bandpass filtered between 1-35 Hz and referenced to common average reference. Noisy channels and bad data segments were identified and subsequently removed using the Clean Rawdata plugin. To avoid spatial bias, removed channels were interpolated prior to Independent Component Analysis (ICA). Oculomotor, muscle, heart, and channel noise artefacts were automatically identified and removed using the ICLabel plugin (Pion-Tonachini et al., 2019).

Finally, spectral analyses were performed over four electrodes in the midfrontal region (F1, F2, Fz, FCz) to calculate the absolute midfrontal theta power. Spectral theta power was calculated using a Fast-Fourier transform to 2-second epochs with 50% overlap for data segments spanning from stimulus onset for “simple” trials until the next “complex” trial stimulus onset, and vice versa for the execution of complex movement combinations. Considering age- and interindividual variations in spectral properties, theta band frequency range was determined for each participant using the Individual Alpha Frequency (IAF) from the one-minute eyes closed EEG recording (Corcoran et al., 2018). Theta range was defined as IAF - 6 Hz to IAF - 4 Hz (Klimesch, 1999).

Procedure

In the beginning of the experiment, EEG data were recorded during a two-minute eyes open and a one-minute eyes closed rest period. Participants first performed a familiarization block, in which each movement condition was repeated five times consecutively. During this familiarization block, a trial started every 3.5 seconds, regardless of whether the limbs were (re)placed on the tablets. Next, participants performed a difficulty determination block to ensure a sufficiently challenging but not too challenging task for all participants (see Figure 1B) (Anguera et al., 2013; Heuninckx et al., 2005; Ward, 2006; Wu & Hallett, 2005). During the determination block, the time between each trial changed based on the participant's performance. Each participant started with an intertrial time of 2 seconds. Every five trials, accuracy was evaluated, and the intertrial time was either maintained, lowered, or raised. When all five trials were correct, intertrial time was lowered with 250 milliseconds. When three or four trials were correct, the intertrial time was maintained. When only two or less trials were correct, the intertrial time was increased with 250 milliseconds. The individualized intertrial time was determined as the shortest intertrial time that was maintained by the participant for at least 15 trials in the determination block. Ultimately, EEG was recorded during four experimental blocks lasting two and a halve minutes using the individualized intertrial time (see Figure 1C). Movement conditions were randomized across the four blocks, so that participants could not predict movement order. At the end of the experiment, participants were asked to report their experienced subjective load, using the NASA Task Load Index (NASA-TLX) (Hart & Staveland, 1988). This index evaluates perceived demands on six dimensions: mental, physical, and temporal demand, performance, overall effort, and frustration. Participants rated each dimension from 0 (low/poor) to 10 (high/good). All dimensions were then compiled into a single, composite score.

INSERT FIGURE 1 HERE

Figure 1. Multi-limb reaction time task. (A) Simple and complex movement conditions. (B) Difficulty determination block. After 5 trials, intertrial time was adapted based on task accuracy. Intertrial time remained constant in case 3 or 4 trials were correct. When all 5 trials were correct, intertrial time decreased by 250 ms, when less than 2 trials were correct, intertrial time increased by 250 ms. (C). Exemplar course of one experimental block with an individualized intertrial time of 2250 ms, lasting a total of 2 and a halve minutes.

Data Analysis

All statistical analyses were performed in RStudio (version 3.6.0) (RStudio Team, 2021). Behavioural and EEG data from the four experimental blocks were combined and statistically analysed. Extreme outliers, defined as data points exceeding the 25th or 75th percentile by 3 times the interquartile range, were removed for each age group. The level of significance was set at $\alpha = 0.05$.

Behavioural (reaction time and error rate) and EEG data (midfrontal theta power) were analysed using a linear mixed model (nlme package, version 3.1-153), with PARTICIPANT added as a random intercept and TASK COMPLEXITY added as a random slope (simple versus complex) (Pinheiro et al., 2007). AGE GROUP (YA, MAA or OA), TASK COMPLEXITY (Simple vs Complex) and AGE GROUP*TASK COMPLEXITY were added as fixed effects. Tukey-corrected post hoc tests were conducted to further evaluate significant main effects and interactions (Lenth et al., 2018).

For subjective data, differences between age groups were evaluated using One-Way ANOVA, and further examined using Tukey's honestly significant different (HSD) post hoc tests to account for multiple comparisons.

Finally, the association between behavioural and EEG data was evaluated by computing the Spearman rank correlation coefficient for each age group between (1) midfrontal theta power and error rate, (2) midfrontal theta power and reaction time, (3) midfrontal theta power and individualized intertrial time, and (4) error rate and individualized intertrial time. A Bonferroni correction was applied to account for multiple testing.

Results

Reaction Time

The linear mixed model yielded a significant main effect of AGE GROUP ($F_{2,78} = 39.86$, $p < 0.01$) and of TASK COMPLEXITY ($F_{1,78} = 49.35$, $p < 0.01$), as well as an AGE GROUP*TASK COMPLEXITY interaction ($F_{2,78} = 24.21$, $p < 0.01$) (see Figure 2). Tukey-corrected post-hoc tests indicated that reaction time increased significantly from simple to complex movement conditions in all age groups (all $p < 0.01$). Reaction time for simple conditions was slower in OA [922.54 ± 171.02 (mean ± standard deviation) ms] compared to YA (624.37 ± 57.04 ms) and MAA (772.09 ± 108.40 ms), and slower in MAA compared to YA (all $p < 0.01$). For complex conditions, reaction time was slower in OA (1555.52 ± 381.97 ms) compared to YA (898.51 ± 153.35 ms; $p < 0.01$), and in MAA (1328.13 ± 269.42 ms) compared to YA ($p < 0.01$), but not in OA compared to MAA ($p = 0.06$). The significant interaction suggests a steeper increase in reaction time between the simple movements and complex movements with higher age than in younger adults.

INSERT FIGURE 2 HERE

Figure 2. Reaction time for simple and complex movement conditions during interlimb task performance, for younger adults (YA – dark blue dots), middle-aged adults (MAA – blue triangles) and older adults (OA – light blue squares). Data are presented in raincloud plots containing boxplots. Significant within-group and between-group Tukey-corrected pairwise comparisons are indicated by horizontal coloured and black lines, respectively.

Error Rate

The linear mixed model yielded no significant interaction between AGE GROUP and TASK COMPLEXITY ($F_{2,76} = 1.42$, $p = 0.25$) (see Figure 3). A significant main effect of AGE GROUP ($F_{2,76} = 9.72$, $p < 0.01$) and TASK COMPLEXITY ($F_{1,76} = 12.84$, $p < 0.01$) was found. Tukey-corrected post-hoc tests indicated that error rate increased significantly from simple (0.19 ± 0.11) to complex (0.27 ± 0.13) movement conditions overall ($p < 0.01$). Error rate was lower in YA (0.18 ± 0.10) and MAA (0.20 ± 0.11) compared to OA (0.31 ± 0.13; both $p < 0.01$). No difference was found between YA and MAA ($p = 0.69$).

INSERT FIGURE 3 HERE

Figure 3. Error rate for simple and complex movement conditions during interlimb task performance, for younger adults (YA – dark blue dots), middle-aged adults (MAA – blue triangles) and older adults (OA – light blue squares). Data are presented in raincloud plots containing boxplots. A significant main effect of age group indicated that error rate was higher in OA compared to both YA and MAA. The significant main effect of task complexity indicated that error rate was higher in complex relative to simple movements.

Midfrontal Theta Power

The linear mixed model yielded a significant main effect of AGE GROUP ($F_{2,76} = 8.64$, $p < 0.01$) and of TASK COMPLEXITY ($F_{1,76} = 10.06$, $p < 0.01$), as well as a significant interaction between AGE GROUP and TASK COMPLEXITY ($F_{2,76} = 6.18$, $p < 0.01$) (see Figure 4). Tukey-corrected post-hoc tests indicated that theta power significantly increased from simple to complex interlimb conditions in YA (simple = 0.87 ± 0.42: complex = 0.98 ± 0.51; $p = 0.02$), but not in MAA (simple = 0.53 ± 0.32; complex = 0.55 ± 0.30; $p > 0.99$) or OA (simple = 0.51

± 0.31; complex = 0.45 ± 0.28; $p = 0.54$). Midfrontal theta power was higher in YA compared to both MAA and OA during simple and complex movement conditions (all $p < 0.01$). No differences were found between MAA and OA for either movement conditions (both $p > 0.98$).

INSERT FIGURE 4 HERE

Figure 4. Midfrontal theta power for simple and complex movement conditions during interlimb task (MLT) performance, for younger adults (YA – dark blue dots), middle-aged adults (MAA – blue triangles) and older adults (OA – light blue squares). Data are presented in raincloud plots containing boxplots. Significant within-group and between-group Tukey-corrected pairwise comparisons are indicated by horizontal coloured and black lines, respectively.

Subjective Data

No significant differences in subjective load were determined between age groups (YA = 4.08 ± 1.56; MAA = 4.57 ± 2.20; OA = 4.97 ± 1.93) according to the One-Way ANOVA ($F_{2,79} = 1.53$, $p = 0.22$) (see Figure 5).

INSERT FIGURE 5 HERE

Figure 5. Subjective load after interlimb task performance, for younger adults (YA – dark blue dots), middle-aged adults (MAA – blue triangles) and older adults (OA – light blue squares). Data are presented in raincloud plots containing boxplots.

Correlation Analysis

The results from the correlation analysis are presented in Table 2. For YA and MAA, there were no significant associations between midfrontal theta power and error rate, midfrontal theta power and reaction time, midfrontal theta power and individualized intertrial time and between error rate and individualized intertrial time (all adjusted p = 1.00). However, significant associations were found for OA between midfrontal theta power and reaction time (Spearman's ρ = -0.48, p < 0.01), midfrontal theta power and individualized intertrial time (Spearman's ρ = -0.57, p < 0.01), and for error rate and individualized intertrial time (Spearman's ρ = 0.41, p = 0.01) (see Figure 6). Results for simple and complex movements separately can be found in the Supplementary Material.

Overall		**Spearman' s ρ**	**p-value**	**adjusted p-value**
YA	Theta Power - Error Rate	0.04	0.78	1.00
	Theta Power - Reaction Time	-0.06	0.69	1.00
	Theta Power - Intertrial Time	-0.12	0.41	1.00
	Error Rate - Intertrial Time	-0.23	0.10	1.00
MAA	Theta Power - Error Rate	-0.08	0.59	1.00
	Theta Power - Reaction Time	-0.02	0.88	1.00
	Theta Power - Intertrial Time	-0.07	0.65	1.00
	Error Rate - Intertrial Time	0.25	0.07	1.00
OA	Theta Power - Error Rate	-0.28	*0.05	0.57
	Theta Power - Reaction Time	-0.48	*<0.01	*<0.01
	Theta Power - Intertrial Time	-0.57	*<0.01	*<0.01
	Error Rate - Intertrial Time	0.41	*<0.01	*0.02

Table 2. Correlation analysis. YA = Younger Adults, MAA = Middle-Aged Adults, OA = Older Adults, *p<0.05.

INSERT FIGURE 6 HERE

Figure 6. Correlation between reaction time and midfrontal theta power (A), error rate and midfrontal theta power (B), midfrontal theta power and individualized intertrial time (C) and between error rate and individualized intertrial time (D) for younger adults (YA – dark blue dots), middle-aged adults (MAA – blue triangles) and older adults (OA – light blue squares). ρ = Spearman's rho, $^{*}p < 0.05$.

Discussion

The goal of this study was to assess age-related changes in midfrontal theta across the adult lifespan during a novel continuously demanding interlimb coordination task. Unlike previous studies, our study is the first that captured overall theta power during continuous motor task performance, contrary to focusing solely on a cognitive task, and motor planning or motor execution during interlimb coordination. As hypothesized, complex movements resulted in longer reaction times and higher error rates for all age groups. Also, reaction time increased along with age, and age disproportionately affected reaction time in the complex movements, i.e., the reaction time increases from simple to complex movement combinations were more substantial with higher age. Furthermore, older adults demonstrated an overall higher error rate than both younger and middle-aged adults. Along with these age-related behavioural changes, differences in midfrontal theta power were found. Remarkably, only younger adults displayed increased theta in complex relative to simple movements. Significant associations between midfrontal theta and interlimb coordination were only found for older adults.

Interlimb Performance

In line with previous literature, an age-complexity effect was present, evidenced by the larger increase in reaction time during complex movements in older relative to younger adults (Boisgontier et al., 2016; Rasooli et al., 2021; Van Hoornweder et al., 2022). Importantly, this age-complexity effect was already present in middle-aged adults, as reaction time increased significantly from simple to complex movements, and there was no longer a significant difference in reaction time between the middle-aged and older adults for the more complex movements. This finding corroborates previous research, which also found that reaction time in interlimb coordination, and in a button-pressing paradigm is already compromised at middle-age (McEvoy et al., 2001; Rasooli et al., 2021). Yet, Berchicci et al. (2012) found that reaction time was maintained in middle-aged relative to younger adults in a button pressing task

(Berchicci et al., 2012). This discrepancy might be explained by differences in the nature of the implemented tasks. One key difference lies in the involvement of one limb, often only one finger for the button pressing tasks, versus the involvement of multiple limbs in the interlimb tasks. Also, McEvoy et al. (2001) employed a choice reaction task, while Berchicci et al. (2012) employed a go/no-go task (Berchicci et al., 2012; McEvoy et al., 2001).

In contrast to previous findings (Boisgontier et al., 2016; Rasooli et al., 2021; Van Hoornweder et al., 2022), error rate varied between age groups, with older adults performing worse than the younger and middle-aged adults. Previously, this lack of differences in error rate was attributed to the speed-accuracy trade-off (Starns & Ratcliff, 2010). The speed-accuracy trade-off states that older adults prioritize accuracy over speed, thus increasing reaction time as to preserve accuracy (Starns & Ratcliff, 2010). Possibly, this conflicting result stems from the individualisation procedure. More specifically, individualization of the intertrial interval might have led to all participants, irrespective of age group, feeling a similar time pressure, which mitigated the accuracy over speed prioritization for older adults. Also, in the other studies, an ensuing trial only started if the participant had correctly replaced all limbs on the contact tablets, which was not the case here. It could be that the longest intertrial time in this study was insufficiently long for some older adults, so that accuracy could not be preserved based on the speed-accuracy trade-off (Starns & Ratcliff, 2010). This is in agreement with the significant positive correlation between individualized intertrial time and error rate in older adults that was established. The fact that middle-aged adults did demonstrate a trade-off between speed and accuracy in the complex movement conditions, as movement slowed down to a similar level as older adults to maintain a similar error rate as younger adults, further argues in favour of the assumption that the longest intertrial time was insufficiently long for some older adults (Starns & Ratcliff, 2010).

Midfrontal Theta Power

In accordance with previous literature, younger adults demonstrated higher midfrontal theta power than older adults (Anguera et al., 2013; Cummins & Finnigan, 2007; McEvoy et al., 2001; Polich, 1997). The age-related theta power decrease was already present in middle-aged adults (Berchicci et al., 2012). Interestingly, only younger adults demonstrated theta power upregulation from simple to more complex movement combinations. This increased oscillatory power is in line with previous research on cognitive tasks which found increased power when tasks become more demanding, thus requiring more cognitive control (Borghini et al., 2014; Cavanagh & Frank, 2014; Cruikshank et al., 2012; Duprez et al., 2020; Kardos et al., 2014; Klimesch, 1999; Puma et al., 2018). Yet, this increased need for cognitive control reflected by increased theta power in the more complex movements was not present in middle-aged and older adults, while behavioural results indicated that the complex movements were more demanding. The absence of theta upregulation might reflect a saturation of mental resources, as performance in the complex movements deteriorated significantly, and reaction time increases were more substantial in middle-aged and older adults versus younger adults (Cummins & Finnigan, 2007; Kardos et al., 2014; McEvoy et al., 2001). Correspondingly, this probably indicates that the maximum amount of theta power upregulation has already been reached when performing the simple movement combinations in middle-aged and older adults, thus prematurely reaching the limit in mental resource capacity (Cabeza et al., 2018; Reuter-Lorenz, 2002). This finding is in accordance with the Compensation-Related Utilization of Neural Circuit Hypothesis (CRUNCH), which takes into consideration task complexity and task demands (Reuter-Lorenz & Cappell, 2008). CRUNCH states that recruitment of additional mental resources might be sufficient in less demanding situations, but a limit in resource capacity might be reached when task demands progressively increase, thus leading to performance decrements (Reuter-Lorenz & Cappell, 2008).

Also in support of a limitation in mental resource capacity is that there was a significant overall association between lesser individualized intertrial time and higher theta power only in older adults, along with a negative association between reaction time and midfrontal theta. This could signify that older adults who were capable of faster reaction times for both simple and complex movement combinations, and thus had a lesser individualized intertrial time, i.e., ability to respond faster, had a larger capacity in theta power, and thus, mental resources, than those adults who required more processing time to perform the correct interlimb movement (Park & Reuter-Lorenz, 2009; Puma et al., 2018; Reuter-Lorenz & Cappell, 2008). On the other hand, these significant correlations could also signify that older adults who were required to respond quicker than those adults with a greater individualized intertrial time, required increased cognitive control in order to perform the task (Cavanagh & Frank, 2014; Cruikshank et al., 2012; Duprez et al., 2020; Klimesch, 1999). Yet, the significant association between higher error rate and longer individualized intertrial time in older adults contradicts this interpretation, since adults that had more time to perform the correct movement still had a higher error rate.

Finally, in line with the findings of Berchicci et al. (2012), middle-aged adults did indeed demonstrate midfrontal theta power dynamics that were more similar to that in older adults. Also, on a behavioural level, the performance was more similar to that of younger adults, as there was no difference in error rate, although middle-aged adults did react more slowly than younger adults, especially in more complex movements. Hence, it is plausible to consider the reduced theta power with aging as a compensatory brain strategy in order to preserve task accuracy (Cabeza et al., 2018; Cabeza et al., 2002; Heuninckx et al., 2005; Heuninckx et al., 2008; Reuter-Lorenz & Cappell, 2008). Yet, this compensation mechanism might have become less effective with increasing age, as task accuracy deteriorated in older adults relative to the middle-aged adults (Berchicci et al., 2012).

Limitations and conclusions

One important methodological constraint is the fact that the longest intertrial time might still have been insufficiently long for the older adults, even though the determination of the intertrial time was based on previous research (Boisgontier et al., 2016; Rasooli et al., 2021; Van Hoornweder et al., 2022). This might also be due to the fact there was no pause in between trials when a participant did not correctly replace all limbs on the contact tablets, in contrast to the previous research (Boisgontier et al., 2016; Rasooli et al., 2021; Van Hoornweder et al., 2022). Therefore, the individualisation of task difficulty might be considered unsuccessful, and thus complicating the interpretation of the age-related neurophysiological changes due to differences in effort. However, no differences between age groups were found in experienced subjective load based on the results from the NASA-TLX.

Also, this study did not analyse all of the movement combinations separately, yet clustered them in simple and complex movements, thus no conclusions can be drawn regarding differences between upper- or lower-limb movements, between movements on either side of the body, or between movements requiring the involvement of two, three or four limbs. Yet, this classification into simple and complex movements was based on considerable evidence from previous studies implementing the interlimb task (Boisgontier et al., 2016; Boisgontier et al., 2014; Rasooli et al., 2021; Van Hoornweder et al., 2022). Also, this classification ensured that there was a sufficient amount of EEG data for the power analysis.

A final limitation of the study was that simple and complex trials were intermixed, which could have resulted in overlap in the EEG signal for movement complexity when transitioning between the two complexity levels. However, the sequence of simple and complex trials was balanced across the task blocks, establishing a similar level of overlap in the EEG signal for both movement conditions.

In conclusion, aging negatively impacts interlimb coordination, and disproportionately affects performance in more complex movement combinations. On a neurophysiological level, the lack of theta power upregulation with higher age might reflect a premature limitation in the mental resource capacity, as the simple movements possibly already require the maximal amount of resources available. Notably, these age-related neurophysiological changes are already present in middle-age. Hence, interventions targeting the preservation of mental resource capacity, possibly by inducing increased midfrontal theta power using none-invasive brain stimulation in older adults, could aid the preservation of interlimb coordination, and by extension quality of life.

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The authors report there are no competing interests to declare.

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