Frontal Theta Oscillations and Cognitive Flexibility: Age-Related Modulations in EEG Activity

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Abstract

Cognitive flexibility, the ability to adapt one's behaviour in changing environments, declines during aging. Electroencephalography (EEG) studies demonstrate that the P300 and midfrontal theta oscillations are sensitive to attentional set-shifting – a measure of cognitive flexibility. Few is known about the electrocortical modulations underlying set-shifting in healthy older adults. Here, we investigated aging effects on set-shifting performance by analysing the P300 and theta power in 20 young (mean age: 22.5 ± 2.9 years) and 19 older (mean age: 69.4 ± 6.1 years) adults. While increasing shift difficulty (e.g. intra- vs. extra-dimensional shifts) led to increased reaction times (RTs) and higher error rates in both age groups, older adults showed an additional increase in RT variability. Older adults showed higher P300 latencies and P300 amplitude decreased during set-shifting in both groups. Young adults exhibited amplified midfrontal theta power with increasing shift difficulty whereas older adults showed an overall decrease. This study suggests that set-shifting in healthy older adults occurs without midfrontal theta modulation indicating that different neural substrates are recruited compared to young adults.

Keywords

Theta power; cognitive flexibility; set-shifting; Electroencephalography (EEG); healthy aging; P300

1. Introduction

Cognitive flexibility refers to an individual's ability to adapt their behaviour in a changing environment (Braem and Egner, 2018; Dajani and Uddin, 2015; Diamond, 2013). Cognitive flexibility is commonly investigated using task-switching and set-shifting paradigms, which require to flexibly adapt to repeated changes of stimulus-response mappings. In such paradigms, participants typically show switch costs, defined as the increase in reaction time and errors when a mapping rule is changed compared to trials (or blocks) in which the rule does not change (Monsell, 2003; Wylie and Allport, 2000). Deficits in cognitive flexibility have been reported in healthy older adults in several paradigms (Reynolds et al., 1995; Richter et al., 2023; Wecker et al., 2005), often evident in increased switch costs compared to young adults (Cepeda et al., 2001; Kray and Lindenberger, 2000). Older adults commonly commit more preservative errors in tasks of cognitive flexibility (Haaland et al., 1987; Zelazo et al., 2004) and often fail to shift when a previously irrelevant dimension becomes relevant (Owen et al., 1991).

The Attentional Set-Shifting Task (ASST) is a task commonly used to assess cognitive flexibility (Sahakian and Owen, 1992). In the ASST, set-shifts with increasing difficulty are presented in a consecutive manner starting from reversal learning, going to intra-dimensional (ID) shifts, and finishing with an extra-dimensional (ED) shift. During an ID shift a change to a different feature-value within the current dimension is made, whereas in ED shifts, the set rule is changed to a different feature dimension. The shift from one dimension to another is expected to be more difficult than within one dimension and thereby engages more neural resources (Watson et al., 2006). The ASST can also be conducted as a learning paradigm, in which a new stage is started as soon as the participant successfully learned a rule. The paradigm is stopped when a participant cannot successfully discern the rule of a specific stage. This task is particularly well-suited for the evaluation of an individual's cognitive

flexibility since set-shifting demands gradually increase from stage to stage. Previous studies have shown that older adults show deficits and commonly fail in the last stage, namely the ED shift (De Luca et al., 2003; Zelazo et al., 2004). Besides these well-replicated behavioural differences between young and older adults during set-shifting, little is known about their neural underpinnings.

Using electroencephalography (EEG), the P300 component has been investigated as prominent event-related potential (ERP) in set-shifting. The P300 component that usually peaks around 350 to 600 ms at parietal electrode sites, sometimes also referred to as P3b, has been associated with set-shifting as it is lower in shift trials compared to repeat trials (Barceló, 2003; Fernandes et al., 2015). Aging studies have reported a delayed P300 latency in older adults (Fernandes et al., 2015; Van Dinteren et al., 2014), which has also been related to lower performance in executive function tasks (Duncan et al., 2009).

Time-frequency analyses of task-related EEG have shown that midfrontal theta oscillations (4-8 Hz) are associated with cognitive control processes (Cavanagh and Shackman, 2015; Domic-Siede et al., 2021; Stolz et al., 2023) and cognitive flexibility, as switch trials elicit increased theta power compared to repeat trials (Cooper et al., 2017; Cunillera et al., 2012). Additionally, theta phase-coupling between prefrontal and posterior (i.e., occipital and temporo-parietal) regions has been shown to increase during switch versus repeat trials (Sauseng et al., 2006). This has been attributed to activity in the medial prefrontal cortex (PFC) when switches take place as suggested by a study using magnetoencephalography (MEG) by Oh et al. (2014). Recognizing the importance of separating ID and ED set-shifting conditions from each other, Oh et al. (2014) observed in young adults that theta band activity in the inferior frontal gyrus was higher in ED compared to ID trials.

Based on this work, we asked whether set-shifting deficits in healthy older adults might be reflected by shift-type (ID vs. ED) related differences in midfrontal theta oscillations. To this end, we applied the EEG-compatible ID/ED set-shifting (IDED) task, which is based on the

ASST used in Oh et al. (2014). We expected midfrontal theta power to be overall decreased in older participants (Dias et al., 2015) and a theta power increase in ED as compared to ID in young individuals, with the question remaining open, how this modulation would appear in the older participant group. To uncover ERP correlates of increasing cognitive challenge, we also investigated the posterior P300 component. Here, we expected to observe reduced P300 amplitudes when set-shifting takes place and anticipated an increased P300 latency in healthy older adults.

2. Material and Methods

2.1 Participants

Participants were between 18 and 35 years old or at least 60 years old to be assigned to the young or the older age groups, respectively. All participants gave written informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013) and received financial compensation for participation. The study was approved by the Ethics Committee of the Faculty of Medicine at the Otto von Guericke University of Magdeburg. Exclusion criteria for participation were manifested neurological or psychiatric disorders or history thereof, past or present substance dependence or abuse, use of neurological or psychiatric medication, and serious medical conditions (e.g., heart failure NYHA stage III or IV, metastatic cancer, or diabetes mellitus with complications) as assessed by a routine neuropsychiatric interview and a health questionnaire. All participants were right-handed and had fluent German language skills. Crystallized intelligence was estimated with the “Mehrfachwahl-Wortschatz-Intelligenztest B” (MWT-B) (Lehrl, 1999; Lehrl et al., 1995). Older participants also completed the Mini Mental State Examination (MMSE; Folstein et al., 1975) to evaluate their cognitive status.

The experiment was performed by a total of 41 participants, 20 young (mean age: 22.5 ± 2.9 years) and 21 older. This sample size was chosen based on previous research (e.g. da Costa et al., 2015; Oh et al., 2014; Yeung et al., 2016) and according to the minimum sample size required (N = 34) to achieve 80% power for a medium effect size (η_p^2= 0.05) at a significance criterion of α = .05 for a within-between interaction in an analysis of variance (ANOVA) (G*Power version 3.1.9.1 (Faul et al., 2009)). Two older participants were excluded from further analysis due to high noise in the EEG signal due to muscle artefacts or high error rates (>50%) resulting in 19 older participants included in the final study sample (mean age: 69.4 ± 6.1 years; Table 1).

Table 1: Participant summary statistics

	Young participants	**Older participants**	**Statistics**
N	20	19	
Age	22.5 ± 2.9	69.4 ± 6.1	t (25.51) = 30.392, p < .001
Gender	15 F, 5 M	13 F, 6 M	$X^2(1)$ = 0.010, p = 0.920
Education years	14.9 ± 2.4	15.2 ± 2.7	W = 172, p = .747
MWT-B	27.1 ± 4.0	31.7 ± 3.0	W = 294, p < .001
MMSE	-	28.3 ± 1.2 (Lowest score: 26)	-

Note. The values are presented as Mean ± Standard Deviation. F = female. M = male. t = Welch two-sample t-test. X^2 = Pearson's Chi-squared test. W = Wilcoxon rank sum test. MMSE: 3 values missing. MWT-B: 1 value missing. Education: 1 value missing.

2.2 Cognitive Flexibility Tasks

To assess participants' cognitive flexibility, all participants first completed the ASST (Dickson et al., 2014; Sahakian and Owen, 1992). The task consisted of eight stages with increasing shift difficulty termed as simple discrimination (SD), compound discrimination

(CD), compound discrimination reversal (CDR), intra-dimensional shift 1 (IDS1), intra-dimensional shift 1 reversal (IDS1R), intra-dimensional shift 2 (IDS2), intra-dimensional shift 2 reversal (IDS2R) and extra-dimensional shift (EDS). Eight consecutive correct responses signalled that the sorting rule was recognized and led to the advancement to the following stage. The task was terminated when a participant successfully completed all stages or when they reached 50 trials in one stage without successfully recognizing the sorting rule.

In order to investigate the set-shifting ability with EEG, we used an adapted version of the ASST, previously established and used with MEG and referred to as the intra-dimensional/extra-dimensional set-shifting task (IDED).

The IDED is a trial-based paradigm in which participants are asked to match one of two stimuli above a single target presented below the fixation cross. During each trial, only one of the two stimuli matches the target in one of two possible dimensions: colour or shape. From trial to trial, the target may remain the same or may change, thereby entailing a shift of the matching rule. The shifts can be a) intra-dimensional (ID), meaning that the dimension remains the same but a different feature value needs to be attended (match colour-to-colour or shape-to-shape) (C) or b) extra-dimensional (ED). In ED trials, the previously irrelevant dimension becomes relevant (colour-to-shape or shape-to-colour) (D).

Each trial always had the following structure (A). First, a fixation cross was presented on a black background signalling the start of a new trial. After a pseudorandomized interval of 800 to 1300 ms, which was generated using uniformly distributed pseudorandom numbers in MATLAB (The MathWorks Inc., 2021; https://www.mathworks.com; Version 9.11.0.1809720 (R2021b)), the stimuli were presented above the fixation cross together with the target, which appeared below the fixation cross. The participant had a total of 4 seconds to respond via button press. Pressing the left versus right button meant that the left versus right stimulus matched the target in its colour or shape, respectively. If no button was pressed after four seconds the trial was terminated and counted as an error trial. After button press or trial

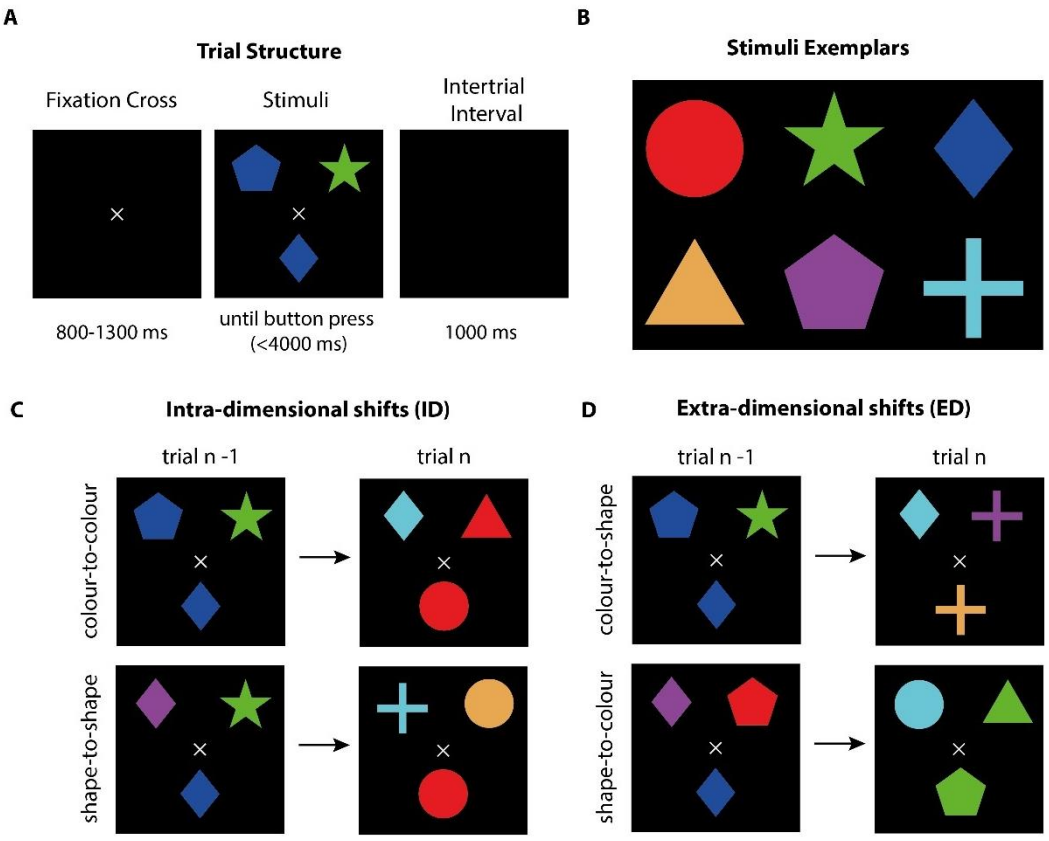

Figure 1: The IDED Task. **A:** Trial structure. After the presentation of the fixation cross the stimuli appear. These disappear after button press or after a time of 4000 ms; **B:** Stimuli exemplars showcasing the six possible colour (red, green, blue, beige, magenta, cyan) and shape combinations (circle, star, diamond, triangle, pentagon, cross). All shapes could have any of the six colours creating a total of 36 possible stimuli; **C:** Types of intra-dimensional shifts (ID). ID shifts could either be colour-to-colour (e.g. blue-to-red, top row) or shape-to-shape (e.g diamond-to-circle, bottom row); **D:** Types of extra-dimensional shifts (ED). ED shifts could either be colour-to-shape (e.g. blue-to-cross, top row) or shape-to-colour (e.g. diamond-to-green, bottom row). Each set-shifting condition was presented the same number of times.

termination, a black screen was presented for 1000 ms, followed by the fixation cross, which signalled the beginning of the next trial.

Six possible colours (red, green, blue, beige, magenta and cyan) and six possible shapes (circle, star, diamond, triangle, pentagon and cross) were combined to create 36 distinct stimuli (B). Before the start of the experiment, all participants were shown the six colours in the form of squares to ensure that they could successfully differentiate the six colours from each other. Participants then completed a set of 20 practice trials, in which all conditions were included and feedback was given, as part of task preparation. The practice trials were not included in the analysis.

Participants were not aware in advance; which dimension was relevant in each trial. In total 50 ED (25 colour-to-shape and 25 shape-to-colour) and 50 ID (25 colour-to-colour and 25 shape-to-shape) trials were presented. Shift trials were followed by 3 to 8 trials in which the target remained the same. Trials were presented in a pseudorandomized order that was established by shuffling the type of shifts (ID or ED) and the number of repeat trials after them (3 to 8) in MATLAB using the Toolbox Psychtoolbox (Brainard and Vision, 1997; http://psychtoolbox.org/; Version 3.0.18). Only the second trial after a shift was used as a control trial in the analysis (Oh et al., 2014). These trials will be referred to as repeat trials. The participants completed the task in 6 blocks with 5 self-paced breaks. After a break all trials that occurred before the first shift were excluded from the analysis. The task duration was approximately 30 to 40 min.

Recordings took place in a dimmed electrically shielded room. Stimuli were presented on a 32" presentation monitor with a refresh rate of 120 Hz and a resolution of 1920 x 1280 pixels. The participants were seated at a distance of 110 cm away from the monitor. Responses were recorded as mouse clicks with the right hand. The MATLAB Toolbox Psychtoolbox (Brainard and Vision, 1997; http://psychtoolbox.org/; Version 3.0.18) was used for stimulus presentation and port event signalling was performed with the Mex-File Plug-in IO64 (http://apps.usd.edu/coglab/psyc770/IO64.html).

2.3 EEG Acquisition and Pre-processing

EEG was recorded at a sampling rate of 1000 Hz from 64 active electrodes (Brain Products GmbH, Gilching, Germany) of the actiCAP layout (EASYCAP) and additional reference and ground electrodes (online reference: FCz; ground: AFz) using BrainRecorder from Brain Products. Electrode impedance was kept below 10 kΩ by applying electrolyte gel onto each electrode location. Four additional passive electrodes were used to record the Electrooculogram (EOG) with the positions: hEOGL (horizontal EOG left), hEOGR

(horizontal EOG right), vEOGi (vertical EOG inferior, below the left eye) and vEOGs (vertical EOG superior, above the left eye).

Data were pre-processed in Brain Vision Analyzer (Brain Products GmbH, Gilching, Germany). The continuous EEG data of the remaining electrodes were first re-referenced to the average of the TP9 and TP10 channels, representing virtually linked mastoids. The data were then filtered with zero phase shift Butterworth filters and a 1 Hz to 100 Hz band-pass second-order filter (Winkler et al., 2015). Artefacts were detected semi-automatically by defining subject-specific criteria based on the gradient (mean maximum allowed voltage step: 50 μV, marked time window: 400 ms before and after an event), maximum difference of values in an interval length of 200 ms (mean maximal allowed absolute difference: 600 μV, marked time window: 1000 ms before and after an event) and low activity in intervals of 100 ms (lowest allowed activity: 0.5 μV, marked time window: 200 ms before and after an event; Supplementary Table 1). Here, channels with more than 20% rejected data points were interpolated using spline interpolation (order 2, degree 10 and $\lambda = 1e^{-5}$). Channel interpolation had to be conducted in four participants for one channel each (Supplementary Table 2). Next, Independent Component Analysis (ICA) was performed to detect components of blinks and saccades. ICA weight matrices were saved and applied to the data with the same pre-processing steps as described above but using filters: A 0.1 to 30 Hz band-pass second order filter was applied for ERP analysis and a 0.1 to 100 Hz band-pass second order filter for wavelet analysis, respectively. The previously detected blink and saccade ICA components were removed by a trained observer (author MD). A second artefact detection was performed here to ensure the detection of artefacts that may have been missed prior to the ICA (the maximum difference of values in an interval length of 200 ms was set to 400 μV; the other criteria remained the same). The continuous data sets were then down-sampled to 500 Hz and exported for further processing in MATLAB using Fieldtrip (Oostenveld et al., 2011; http://fieldtriptoolbox.org; Version 20211122).

In Fieldtrip, custom scripts were used for ERP analysis including the following steps: a) extraction of stimulus-locked epochs (from -1250 ms until 3000 ms) from the trials of interest: repeat, ID and ED trials that were followed by correct responses. b) baseline correction using the average of -250 to 0 ms pre-stimulus, c) calculation of time-locked averages of each participant for each condition. P300 latency was defined as the time point of maximum peak found between 300 and 600 ms post-stimulus of the averaged electrodes Pz, P1, P2, POz, PO3 and PO4 (Hirayasu et al., 2000). Individual grand average peak latencies of each age group were used to define the time window for mean amplitude calculation (Stolz et al., 2019). The time window for mean amplitude calculation was defined as the time period 100 ms before and after the P300 maximum for each age group. This was between 308 and 508 ms for the young participants (maximum: 408 ms) and from 408 to 608 ms for the older participants (maximum: 508 ms).

Additional ERP analyses on difference waves and response-locked trials were performed to control for different aspects of the dataset (see supplementary material S1.3, S2, S3).

For wavelet analysis, the continuous EEG data was imported into MATLAB and cut into stimulus-locked epochs as described above. Frequency power from 1 to 60 Hz in steps of 1 Hz was calculated using Morlet wavelets with a width of 7 cycles and length equal to 3 standard deviations of the implicit Gaussian kernel. The time window used was sliding between -1250 ms and +3000 ms in steps of 50 ms, where 0 was defined as the onset of stimulus presentation. A baseline of -400 ms to -200 ms of the common average of each participant was used for normalization of all trials within each frequency bin separately. Normalization into *dB* was performed as follows:

$$activity_{dB} = 10 * \log_{10}(activity/baseline)$$

Averages for each participant and condition were calculated and used for spectral analysis. Midfrontal theta power was calculated as the mean theta power (4-8 Hz) at electrode sites F1, F2, Fz, FC1, FC2, FCz in the post-stimulus time period between 250 and 500 ms. These

electrodes were chosen based on the observed distribution of theta activity on the grand average of all participants and all conditions (Stolz et al., 2023). For the purposes of single-trial analysis, the mean theta power obtained from the frontocentral electrodes in the time period between 250 and 500 ms after target presentation, was calculated for each trial before normalization with baseline subtraction. Single-trial correlations were calculated separately for each participant and each condition using Shepherd's Pi correlation (Schwarzkopf et al., 2012), which enables unbiased outlier removal by bootstrapping based on the Mahalanobis distance. The obtained correlation coefficients were then transformed in z-space using the Fisher z-transformation to make them approach normal distribution for further statistical analysis.

2.4 Statistical Analysis

All statistical analyses were performed in RStudio (R version 4.2.2; R Core Team, 2022; R Studio Team, 2020).

Behavioural performance in the ASST was evaluated by estimating a survival curve using the Kaplan-Meier method. Each stage of the paradigm was evaluated as an event and the probability of "survival" was defined as the probability of successfully completing all stages of the paradigm. The estimated probability of survival is reported together with the standard error. Additionally, spearman correlations of completed ASST stages with IDED reaction times were performed.

IDED reaction time (RT) was defined as the time taken to correctly respond after stimulus presentation. For each condition and each participant, median RTs were used as dependent variables in the statistical analysis. The median was chosen because of the right-skewed distribution of RTs (mean skewness: 2.30 ± 0.75) due to high inter- and intra-individual variability. To investigate possible differences in RT variance across age groups and

conditions, we also evaluated the individual standard deviations of RTs. The error rate was computed as the percentage of trials with incorrect or no responses in each condition.

Alpha significance level was set to p = .05. ANOVA results are reported with the obtained F value, p value and partial eta squared (η_p^2) as a measure of effect size. Whenever ANOVAs were significant, post-hoc two-tailed t-tests were performed to uncover specific differences between the means. Cohen's d is reported as effect size. Statistical significance is reported in the graphs as followed: * for $p \leq .05$, ** for $p \leq .005$ and *** for $p \leq .001$. In graphs the error bars represent the 95% confidence interval around the mean. Average values in text are being reported with standard deviations in the form: mean ± standard deviation, unless otherwise specified.

The following variables were tested as dependent variables in separate two-factorial mixed ANOVAs with the between-subjects factor age group (young vs. older adults) and the within-subjects factor condition (repeat vs. ID vs. ED): median RT, standard deviation of RT, error rate, P300 latency, P300 amplitude, midfrontal theta power, and the z-transformed single-trial correlation coefficients. Sphericity for ANOVAs was tested using Mauchly's Test for Sphericity. When sphericity assumptions were not met, Greenhouse-Geisser correction was used on the degrees of freedom. All dependent variables were tested for non-normality and inhomogeneity of variances with the Shapiro-Wilk test and Levene test respectively. Both tests were non-significant across all variables, conditions, and age groups (Shapiro-Wilk: all p > 0.10; Levene: all p > 0.07) except for the following. For error rate non-normality was given (highest value: ED within young participants: W = 0.85, p = 0.005). For RTs, there was an inhomogeneity of variances in the ID and ED condition between the two age groups (ID: F(1,37) = 8.75, p = .005; ED: F(1,37) = 10.7, p = .002). Therefore, RTs and errors were additionally assessed with a robust ANOVA. The results of the robust ANOVAs did not qualitatively differ from the results of the ANOVAs and are reported in the supplementary material (S1.2).

The Fisher z-transformed single-trial correlation coefficients were tested against zero using one-sample t-tests. These were corrected for multiple comparisons with the False Discovery Rate (FDR; Benjamini and Hochberg, 1995).

3. Results

3.1 Behavioural Results of the ASST Task

Out of 20 young participants, only one failed to complete the ASST, whereas 14 of 19 older participants did not finish the task. The majority of them failed in the ED shift stage (n=9). A survival analysis revealed significant differences in task completion between the two groups (X^2(1, N = 39) = 17.20, p < .001) with young participants completing the task at an estimated probability of 0.95 ± 0.05 (Standard Error) at the last stage (2). Conversely, the estimated completion probability in the older age group at the last stage was 0.29 ± 0.10 (Standard Error).

3.2 Behavioural Results of the IDED Task

Across the three conditions, all participants had an overall median RT of 718 ± 199 ms. RTs were significantly longer in older compared to young participants in all conditions (F (1, 37) = 58.30, p < .001, η_p^2= 0.61) (Figure 3A). Regardless of age group, a significant condition effect on RTs was found (F (1.14, 42.11) = 81.94, p < .001, η_p^2= 0.69). As expected, we observed significantly longest RTs in the ED condition, followed by the ID condition, and shortest RTs in the repeat condition (ED vs repeat: $t(38)$ = 10.20, p < .001, d = 1.63; ED vs ID: $t(38)$ = 6.67, p < .001, d = 1.07; ID vs repeat: $t(38)$ = 11.50, p < .001, d = 1.85). The interaction between condition and age group did not reach significance (F (1.14, 42.11) = 3.48, p = .064, η_p^2= 0.09).

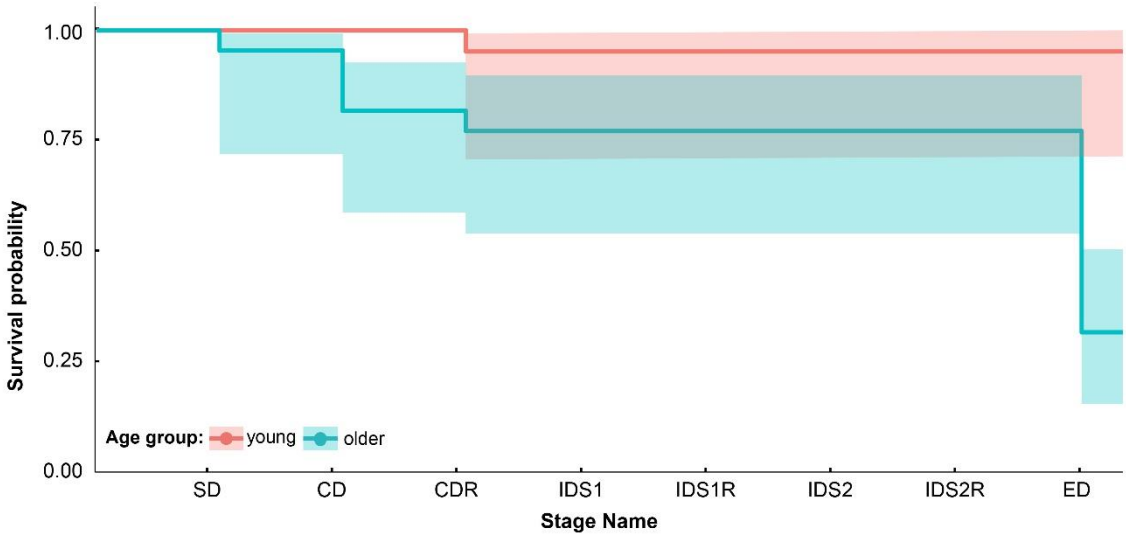

Figure 2: ASST Task Completion Curve. Survival probability in the ASST for the two age groups. There is a significant difference in task completion rates between the two age groups ($X^2(1, N = 39) = 17.20$, $p < .001$). The majority of older individuals fail to complete the ASST at the ED stage. The shaded areas represent Standard Errors of the survival curves.

In a mixed ANOVA with the standard deviations of RTs, we found a significant interaction effect between age group and condition (F (2, 74) = 4.94, p = .010, η_p^2= 0.12) and a main effect of condition (F (2, 74) = 19.66, p < .001, η_p^2= 0.347). Closer investigations of the interaction revealed a smaller effect size of condition within the group of younger participants (F (1.48, 28.1) = 5.05, p = .021, η_p^2= 0.075) compared to the older participants (F (2, 36) = 14.10, p < .001, η_p^2= 0.141). Overall, the ED condition resulted in the highest standard deviations, followed by the ID and the repeat condition (ED vs repeat: t(38) = 5.59, p < .001, d = 0.90; ED vs ID: t(38) = 2.86, p = .007, d = 0.46; ID vs repeat: t(38) = 3.36, p = .002, d = 0.54). Additionally, a main effect of age group was found (F (1, 37) = 25.86, p < .001, η_p^2= 0.41), where older participants had overall higher standard deviations of the RTs compared to the younger participants (Figure 3B).

Within the group of older participants, we found a correlation of mean IDED reaction times with the number of stages that were completed in the ASST (ρ= -0.56, p = .013) (Figure 3C). This correlation could not be carried out in the group of young participants as almost all of them successfully completed all stages of the ASST.

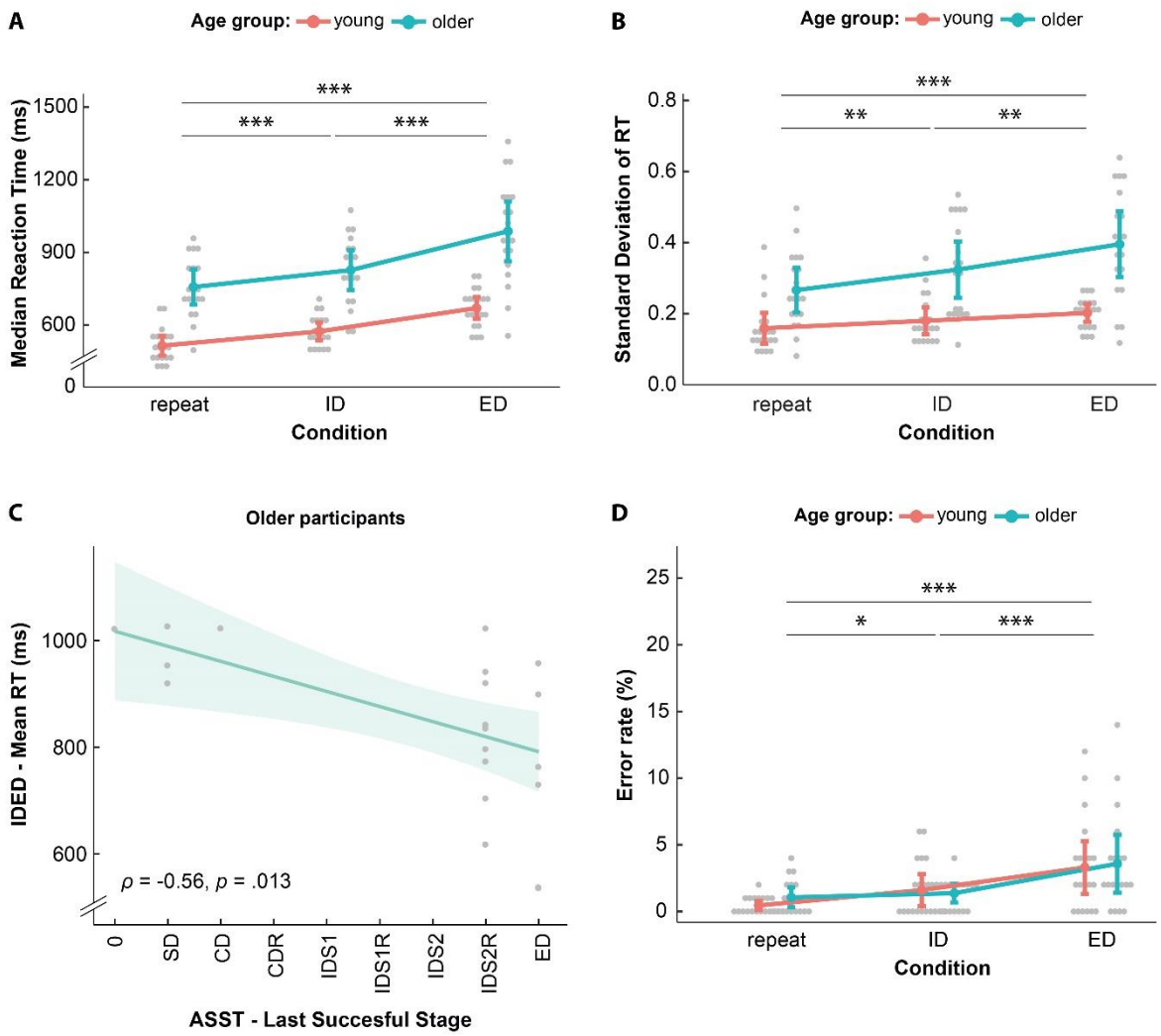

Figure 3: Behavioural results in the IDED task. A: Median reaction times of each participant depending on condition. Older participants had longer RTs than younger participants (F (1, 37) = 58.30, p < .001, η_p^2= 0.61). There is a significant difference in reaction time between all conditions in both age groups in ED trials reaching the longest RTs followed by ID and repeat (F (1.14, 42.11) = 81.94, p < .001, η_p^2= 0.69). **B:** Standard deviation of RTs of each participant depending on condition and age group. There was a significant interaction effect between age group and condition (F (2, 74) = 4.94, p = .010, η_p^2= 0.12), a significant effect of age group (F (1, 37) = 25.86, p < .001, η_p^2= 0.41) and a significant effect of condition (F (2, 74) = 19.66, p < .001, η_p^2= 0.347). **C:** Negative correlation of mean RT and last successful stage in ASST in older adults (R = -0.56, p = .013). **D:** Individual error rates for each condition. In both age groups there is a gradual increase in error rate from repeat to ID and ED (F (1.32, 48.91) = 17.27, p < .001, η_p^2= 0.32).

Average error rates were low (1.90% ± 2.60%, see Figure 3D). There was neither a significant difference in error rates between the age groups (*F* (1, 37) = 0.17, *p* = .68, η_p^2= 0.01), nor a significant interaction of age group and condition (*F* (1.32, 48.91) = 0.40, *p* =.59, η_p^2= 0.01), but a significant main effect of condition was found (*F* (1.32, 48.91) = 17.27, *p* < .001, η_p^2=

0.32; Figure 3B). Again, significantly worst performance with most errors was observed in the ED trials followed by ID trials, and best performance in the repeat trials (ED vs repeat: *t(38)* = 5.07, *p*< .001, *d* = 0.81; ED vs ID: *t(38)* = 3.50, *p* = .001, *d* = 0.56; ID vs repeat: *t(38)* = 2.87, *p* = .007, *d* = 0.46).

3.3 The P300 Component in the EEG

P300 latencies significantly differed between age groups (*F* (1, 37) = 18.70, *p* < .001, η_p^2= 0.34) (Figure 4A, B & C). Older individuals showed significantly longer P300 latencies (514 ms ± 49 ms) compared to young individuals (440 ms ± 74 ms; Figure 4C). A significant main effect of condition (*F* (1.63, 60.46) = 4.30, *p* =.024, η_p^2= 0.10) was found. Multiple post-hoc comparisons revealed a significant difference in latency between the repeat and ID condition (*t(38)* = -3.71, *p* < .001, *d* = -0.56) and between repeat and ED condition (*t(38)* = -2.21, *p* = .033, *d* = -0.35). There was no latency difference between the ID and ED condition (*t(38)* = 0.23, *p* = .823, *d* = -0.04). The interaction between age group and condition was not significant (*F (*1.63, 60.46*)* = 1.46, *p* =.24, η_p^2= 0.04).

We took the latency differences into consideration when computing the mean amplitudes of the P300 for each age group by using shifted time windows centred around the mean P300 latencies mentioned above. A significant main effect of condition was found for the amplitude of the P300 component (*F* (2, 74) = 10.59, *p* <.001, η_p^2= 0.22) (Figure 4D). The ED condition elicited a P300 with the significantly lowest amplitude, followed by the ID trials and the repeat trials, which showed the highest amplitudes (ED vs repeat: *t* (38) = -4.49, *p* < .001, *d* = -0.72; ED vs ID: *t* (38) = -2.36, *p* = .023, *d* = -0.38; ID vs repeat: t (38) = -2.42, *p* = .020, *d* = -0.39). There were no significant differences in the P300 amplitude between the two age

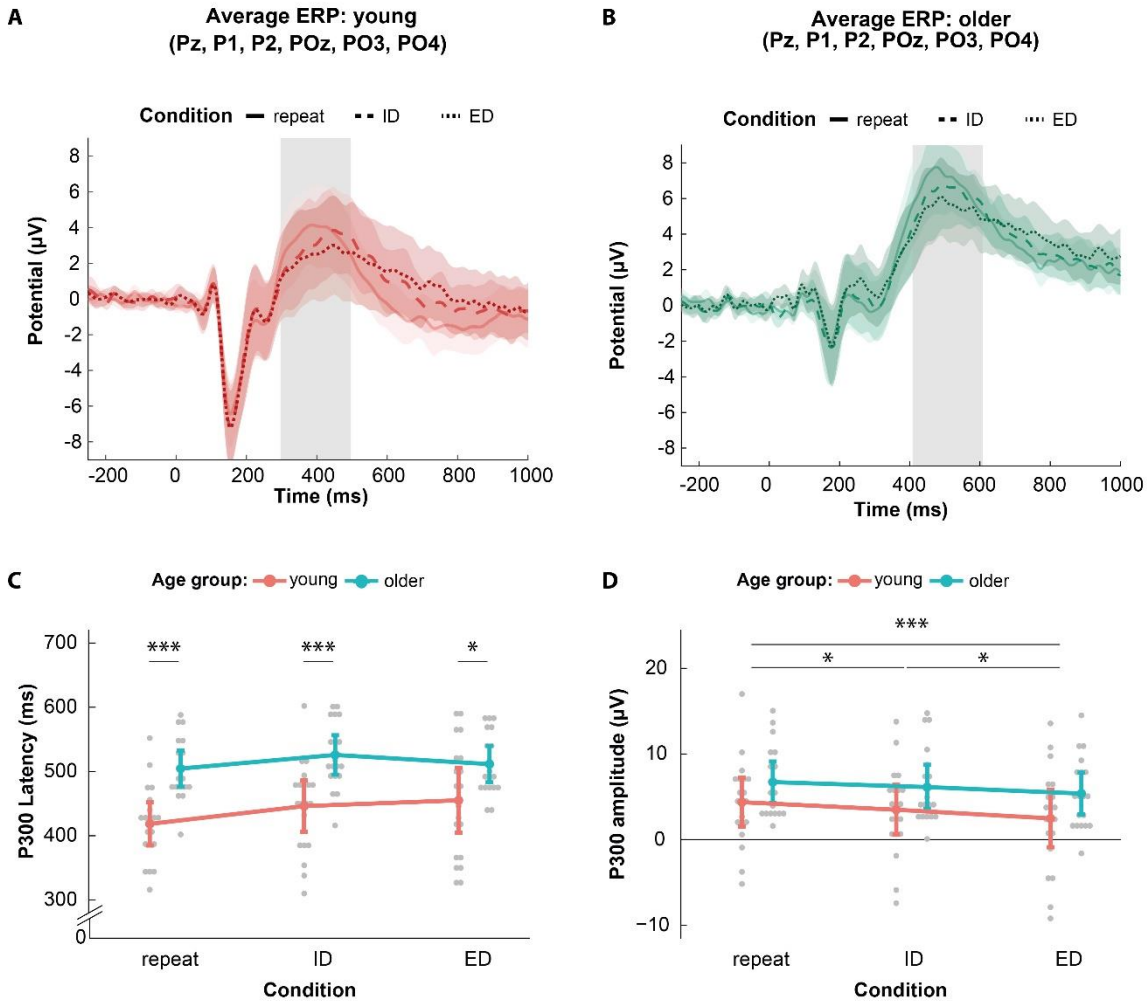

Figure 4: Analysis of the P300 component. **A:** Average stimulus-locked ERP obtained from young participants. Mean P300 amplitude was calculated within the time range of 308 - 508 ms (shaded area); **B:** Average stimulus-locked ERP obtained from old participants. Mean P300 amplitude was calculated within the time range of 408 - 508 ms (shaded area); **C:** P300 latency for each condition and age group. There is a significant difference in component latency between age groups (F (1, 37) = 18.70, p < .001, η_p^2= 0.34) and between conditions (F (1.63, 60.46) = 4.30, p =.024 η_p^2= 0.10). **D:** P300 amplitude within the time frame shaded in A or B. P300 amplitude is significantly different between all three conditions, with repeat trials eliciting the highest P300 amplitude followed by ID and ED (F (2, 74) = 10.59, p <.001, η_p^2= 0.22).

groups (*F* (1, 37) = 3.14, *p* =.085, η_p^2= 0.08) and no significant interaction (*F* (2, 74) = 0.31, *p* = .74, η_p^2= 0.01).

3.4 Midfrontal Theta Activity

During the post-stimulus interval, theta oscillations showed the expected timing and topography in the group average, as compared to a previous study (Oh et al., 2014). Theta

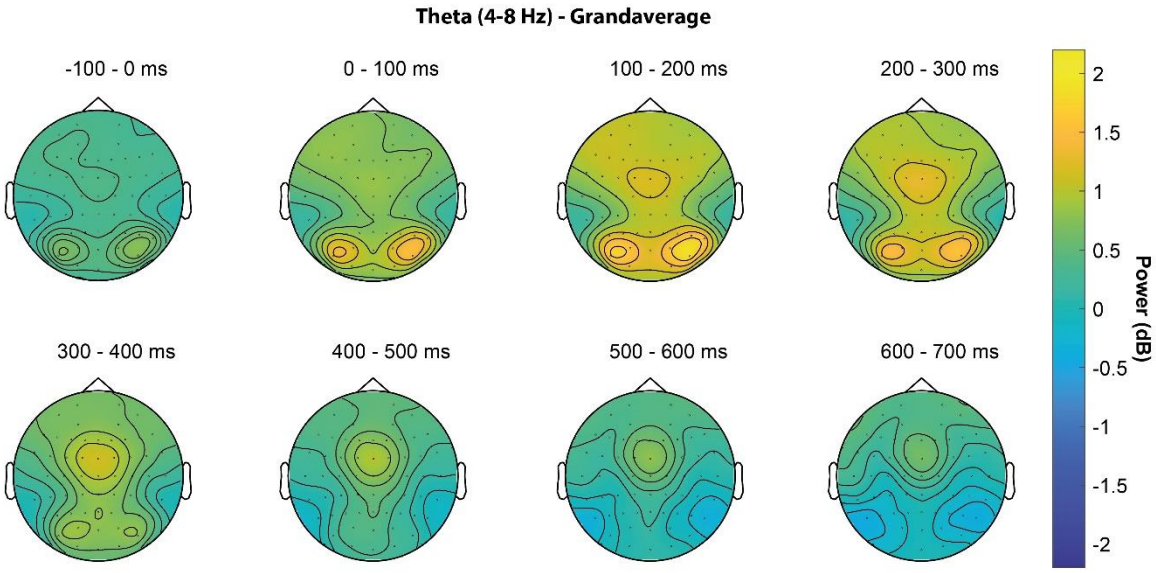

Figure 5: Mean theta power (dB) across all conditions and all participants. Occipital theta activations are followed by frontocentral theta activations in the time window between 200 to 500 ms after target presentation.

first appeared over posterior occipital electrodes between 0 and 200 ms (Figure 5), which can be attributed to the visual evoked response after stimulus presentation, followed by midfrontal activations in the area of the electrodes F1, F2, Fz, FC1, FC2 and FCz. Midfrontal theta power gradually increased from 250 to 500 ms and reached a maximum around 300 ms after stimulus presentation (Figure 6 A&B).

Mean midfrontal theta power in the interval between 250 and 500 ms after stimulus presentation differed significantly between age groups (F (1, 37) = 15.18, $p < .001$, $\eta_p^2 = 0.29$), with 1.63 *dB* ± 1.29 *dB* in young vs. 0.34 *dB* ± 0.87 *dB* in older individuals. The latter values did not differ significantly from zero (t *(18)* = 1.78, $p = .091$, $d = 0.41$), in contrast to the young adults (t *(19)* = 6.04, $p < .001$, $d = 1.35$). We also observed significant differences in theta power across conditions within the young group, which were largely absent in the older participants (age group by condition interaction: F (2, 74) = 14.51, $p < .001$, $\eta_p^2 = 0.28$) (Figure 6 A, B & C). Specifically, in young adults, ED and ID trials elicited an average theta power of 2.03 *dB* ± 1.31 *dB* and 1.73 *dB* ± 1.18 *dB*, respectively. Both the ED and ID conditions elicited significantly higher theta power than the repeat condition, which reached

an average of 1.13 *dB* ± 1.26 *dB* (ED vs repeat: *t(19)* = 9.46, *p* < .001, *d* = 2.11; ID vs repeat: *t(19)* = 4.24, *p* < .001, *d* = 0.95; ED vs ID: *t(19)* = 2.06, *p* = .053, *d* = 0.46) (Figure 6C). In older individuals, we found no significant differences between conditions (highest t-value: repeat vs ED: *t (19)* = 0.60, *p* = .78, *d* = 0.14).

We next calculated correlation coefficients between individual RTs and corresponding single-trial theta power, using outlier-robust Shepherd's *Pi* correlations (Schwarzkopf et al., 2012). The correlation coefficients were Fisher-z-transformed and statistically compared with a two-factorial mixed ANOVA with the factors age group and condition. A main effect of age group was found (*F* (1, 37) = 13.73, *p* < .001, η_p^2= 0.27), where young participants had higher z-values than older individuals, reaching values of 0.103 ± 0.176 and -0.025 ± 0.173, respectively. To investigate whether the mean z-value of each age group and condition significantly differed from zero we performed one-sample t-tests of values obtained from each condition and each age group. The Z-values for both the ED and ID conditions among the young individuals significantly differed from zero (ED: *t*(19) = 2.70, p_{adj} = .043, *d* = 0.60; ID *t*(19) = 3.31, p_{adj} = .022, *d* = 0.74) in the positive direction (Figure 6D). In the older adults, none of the values obtained at any condition significantly differed from zero (highest absolute t-value: ID: *t (19)* = -2.23, p_{adj} = .078, *d* = -0,51).

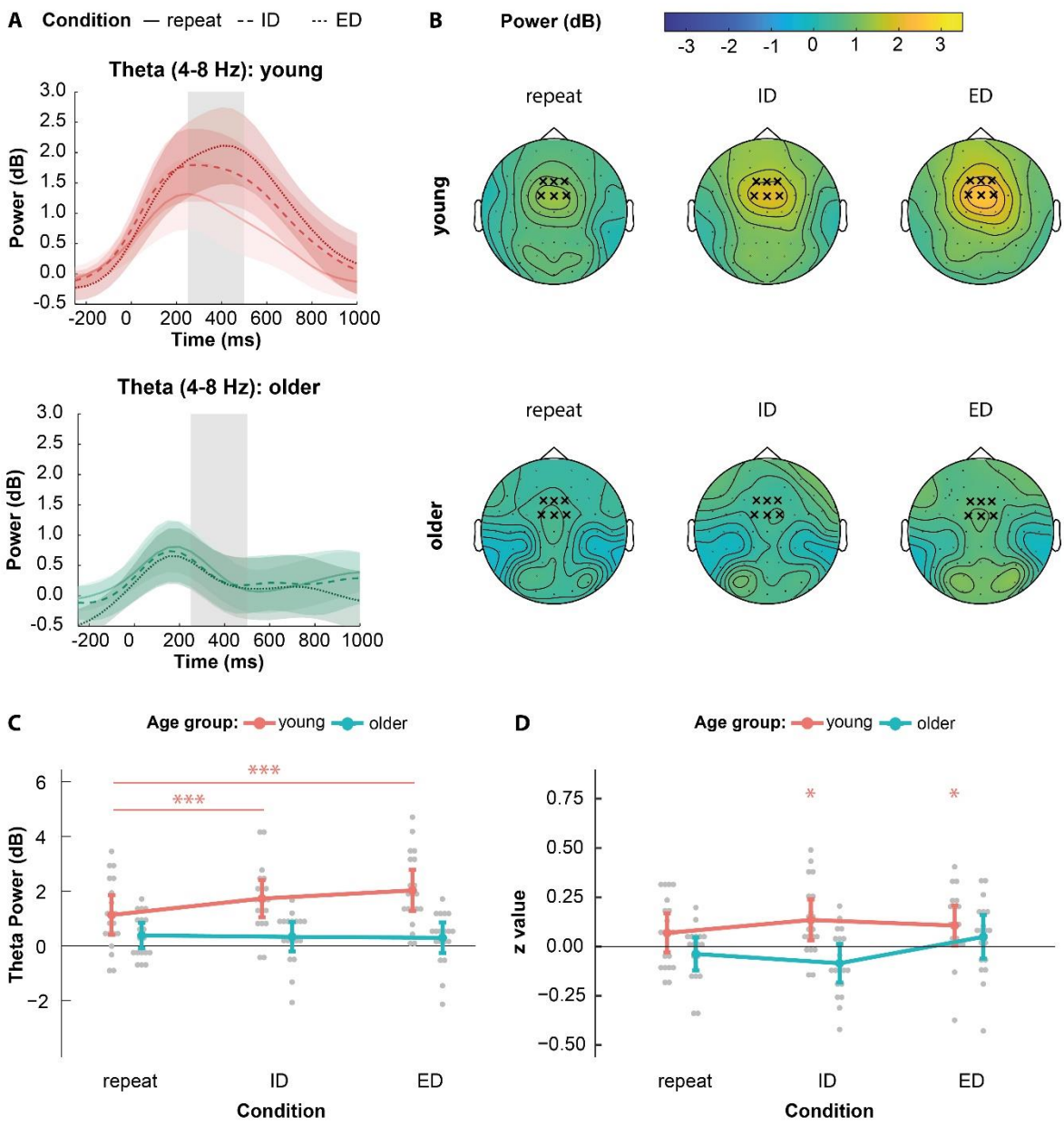

Figure 6: Condition-dependent modulation of frontocentral theta power within the two age groups. A: Frontocentral theta power after target presentation in the young (top) and old (bottom) age groups, depending on condition. The grey shaded area indicates the time period used to calculate mean theta power; **B:** Average topographical distribution of mean theta power in the young (top) and old (bottom) age groups 250-500 ms after target presentation for each condition; **C:** Average theta power in the frontocentral electrodes for each individual depending on condition. Here, only young individuals show an increase in theta power when set-shifting takes place compared to the repeat condition (interaction term of age group and condition F (2, 74) = 14.51, p < .001, η_p^2= 0.28); **D:** z-values obtained from single trial correlations of theta power and reaction time for each condition and age group. Young participants have highest z-values overall (F (1, 37) = 13.73, p < .001, η_p^2= 0.27). One-sample t-tests revealed that within the young individuals both the ED and ID conditions significantly differ from zero in the positive direction (ED: t(19) = 2.70, p_{adj} = .043, d = 0.60; ID t(19) = 3.31, p_{adj} = .022, d = 0.74).

4. Discussion

In this study, we observed differences in performance and neural processing during set-shifting between young and older adults using two different tasks. In the ASST, we investigated group differences at the behavioural level and observed that older adults often fail to successfully solve the ED stage, a finding which is in line with other studies (De Luca et al., 2003; Owen et al., 1991; Zelazo et al., 2004). In the IDED task, we investigated participants' RTs, error rates, P300 characteristics, and theta band power in relation to age group and set-shift condition. In this paradigm, older participants were slower than young participants, and had a higher RT variability but showed comparable error rates. Across all participants, RTs and error rates increased with higher set-shifting demands. As to the brain activity measures, the P300 peaked earlier in young versus old adult groups, with its amplitude being modulated by the conditions, such that the highest values were elicited in repeat trials and the lowest values in ED trials. Most notably, older adults differed from young adults by a lack of significant midfrontal theta modulation during set-shifting.

4.1 Switch costs and age-related changes in cognitive flexibility

As expected, we observed age effects in both of our cognitive flexibility tasks. Compatible with previous investigations (for a review, see Monsell, 2003), switch costs (ED > ID > repeat) manifested as increasing error rates, longer reaction times, and bigger RT variability in young and older adults. Older adults showed increased switch costs, especially regarding the RT variability. The majority of older participants in our study failed to complete the ASST, with particular difficulty at the ED stage. Difficulties in extradimensional shifts have been observed in older adults in previous studies (De Luca et al., 2003; Owen et al., 1991; Zelazo et al., 2004). A decline in cognitive flexibility with normal aging has also been shown in task

switching (Cepeda et al., 2001; Kray and Lindenberger, 2000) and other tasks that require cognitive flexibility (Ridderinkhof et al., 2002; Zelazo et al., 2004).

Set-shifting relies heavily on prefrontal activity as evident from MEG (Periáñez et al., 2004), positron emission tomography (Nagahama et al., 1998) and functional magnetic resonance imaging (fMRI) studies in humans (Konishi et al., 2002; Konishi et al., 1998; Lie et al., 2006; Liu et al., 2015; Monchi et al., 2001; Nagahama et al., 2001; Pa et al., 2010; Smith et al., 2004). Aging-related prefrontal cortical volume loss has been associated with increased response latencies in task switching (Hakun et al., 2015) and reduced memory (Nordahl et al., 2006). Hence, one possible explanation for the decline of cognitive flexibility in older adults can be prefrontal cortical volume loss.

4.2 P300 modulations and set-shifting: insights from IDED paradigm

In the IDED task, P300 amplitudes were modulated by the conditions, reaching the highest values in the repeat trials and lowest in the ED trials in both age groups. This modulation of the P300 amplitude has been observed before in tasks such as the Wisconsin Card Sorting Task (WCST) and has been attributed to the confirmation of established rules (Barceló, 2003; Fernandes et al., 2015) and the allocation of attentional resources (Kopp and Lange, 2013; Lange et al., 2015). fMRI studies support this notion by relating parietal activity during set-shifting to the reorganization of stimulus-response associations (Nagahama et al., 2001; Smith et al., 2004). Notably, the P300 modulations observed here, could also be attributed to selection negativity (Hillyard and Anllo-Vento, 1998). This is a negative component, which modulates the P300 and scales depending on the amount (and complexity) of features and/or dimensions that are being attended and discriminated (Keil and Müller, 2010). In its nature, a set-shift involves the selection of more than one feature-value in the ID condition and of a new dimension and feature value in the ED condition. This increases the amount of selection

steps and gives rise to a stronger and/or longer lasting selection negativity that attenuates the P300, and makes it appear smaller in the set-shifting conditions.

In older participants, we observed longer P300 latencies compared to young adults. Our results complement a previous study in which an increase in P300 latency but not in P300 amplitude was observed in older healthy adults during the WCST (Fernandes et al., 2015). Considering the possibility that the P300 reduction observed here reflects the superimpositionof selection negativity, it is to be expected that no aging effects are present, since early visual selective attention is typically not disturbed in healthy older adults performing a visual selection task (Alperin et al., 2013; de Jong et al., 1988).

In regards to the P300 latency, irrespective of the task used, higher P300 latencies are commonly observed in healthy older adults (Gajewski and Falkenstein, 2014; Polich, 1997). These prolonged latencies can be attributed to the decline in processing speed and efficiency that occurs in the aging brain (for a comprehensive review, see: Van Dinteren et al., 2014).

4.3 Age-related differences in midfrontal theta modulations and cognitive control in set-shifting

In the young group, we observed a notable modulation of theta oscillatory activity by shift type. Prefrontal theta has been linked to cognitive control (Cavanagh and Frank, 2014), and increased theta power has been associated with better performance in tasks that demand cognitive flexibility (Cooper et al., 2017; Cunillera et al., 2012; Dias et al., 2015; Sauseng et al., 2006). In line with these findings, we found an increase in midfrontal theta power during shifts compared to repeat trials, aligning with the heightened demand for cognitive control during shifting. Remarkably, single-trial performance correlated with theta power, with average z-values within both set-shifting conditions being consistently above zero, indicating a positive correlation between midfrontal theta power and reaction time in individual trials. In other words, increased theta power in single trials corresponded to longer reaction times

during set-shifting. Moreover, this pattern was condition-specific and not evident within the repeat dimension, underscoring the role of midfrontal theta during set-shifting, where substantial cognitive control is required (Cavanagh and Shackman, 2015; Domic-Siede et al., 2021; Stolz et al., 2023).

In the older age group, there appeared to be little midfrontal theta, which is in line with previous studies that have investigated cognitive flexibility (Dias et al., 2015), short term memory (Cummins and Finnigan, 2007) and working memory (Gajewski and Falkenstein, 2014) in older adults. One may ask why older adults exhibited consistently lower midfrontal theta power during task execution, which did not increase with demands on cognitive flexibility. Prefrontal theta oscillations reflect the activity of the PFC. The prefrontal cortex is one of the main regions that exhibit atrophy within the age range used in this study (Fjell et al., 2009; Grothe et al., 2013; Jernigan et al., 2001; Raz et al., 1997; Salat et al., 2001).

4.4 Limitations of the study

A notable limitation of our current study is that participants had a generous four-second time window to respond in each trial. This extended time frame may not have put enough pressure on participants to respond as quickly as possible. This aspect is also reflected in the exceptionally low error rates observed. It is possible that these factors may have concealed increased switch costs that were expected in older participants. Dias et al. (2015) assessed in the WCST the performance differently by examining completed categories and the number of perseverative and non-perseverative errors. In the IDED, we encountered very few errors, rendering this type of evaluation impossible due to floor effects. We assume that, if we had employed a narrower time window for reactions, we might have observed overall faster response times and a higher frequency of errors, making the heightened switch costs in the older population more conspicuous. We further propose that such an adjustment might

additionally accentuate the theta power differences between the two set-shifting conditions, with ED shifts eliciting higher theta power than ID shifts in the young participants.

4.5 Conclusions

In summary, this study contributes insights into age-related differences in set-shifting performance and neural processing, emphasizing the role of midfrontal theta oscillations and P300 modulations. Our findings suggest that midfrontal theta oscillatory activity is not necessary for successful set-shifting in older age, indicating that different neural substrates are being recruited for set-shifting. Conversely, the mechanisms that drive the P300 amplitude modulations due to set-shifting appear to be preserved although with a longer latency in older age. Nevertheless, further research is needed to explore the alterations of the underlying mechanism and to investigate potential interventions for preserving the neural substrates of cognitive flexibility in older adults.

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Author Contribution

MD: conceptualization, data curation, methodology, software, formal analysis, investigation, writing – original draft, writing – review and editing, visualization

CS: methodology, writing – original draft, writing – review and editing

HSJ: investigation

HS: methodology

JMH: methodology, writing – original draft, writing – review and editing

BHS: conceptualization, supervision, funding acquisition, writing – original draft, writing – review and editing

CIS: conceptualization, supervision, funding acquisition, writing – review and editing

AR: conceptualization, supervision, methodology, writing – original draft, writing – review and editing

Data Availability Statement

Experimental Code, MATLAB Scripts, RStudio Scripts and averages of dependent variables are provided in a GitHub repository (https://github.com/margdarna/IDED).

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