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

Margarita Darna[1], Christopher Stolz[1,2], Hannah-Sophia Jauch[1], Hendrik Strumpf [1,3], Jens-Max Hopf [1,2,3], Constanze I. Seidenbecher[1,4,7,8], Björn H. Schott[1,4,5,6], Anni Richter[1,7,8]

[1] Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

[2] Institute of Psychology, Otto-von-Guericke University Magdeburg, Magdeburg, Germany

[3] Clinic for Neurology, Otto-von-Guericke University Magdeburg, Magdeburg, Germany

[4] Center for Behavioral Brain Sciences (CBBS), Magdeburg, Germany

[5] German Center for Neurodegenerative Diseases (DZNE), Göttingen, Germany

[6] Department of Psychiatry and Psychotherapy, University Medical Center Göttingen, Göttingen, Germany

[7] German Center for Mental Health (DZPG), partner site Halle-Jena-Magdeburg

[8] Center for Intervention and Research on adaptive and maladaptive brain Circuits underlying mental health (C-I-R-C), Halle-Jena-Magdeburg

Abstract

Cognitive flexibility, the ability to adapt one's behaviour in changing environments, declines during aging. Electroencephalography (EEG) studies have implicated midfrontal theta oscillations in attentional set-shifting, a measure of cognitive flexibility. Little is known about the electrocortical underpinnings of set-shifting in aging. Here, we investigated aging effects on set-shifting performance by analysing 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 (i.e., intra- vs. extra-dimensional shifts) elicited increased reaction times (RTs) and higher error rates in both age groups, older adults additionally showed an increase in RT variability. Young adults exhibited amplified theta power increases with higher shift difficulty whereas older adults showed overall lower theta power and no task-related power modulation. Our results suggest that set-shifting in older adults occurs without midfrontal theta modulation, indicating potentially distinct underlying neural mechanisms compared to young adults.

Keywords

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

1. Introduction

Cognitive flexibility refers to an individual's ability to adapt one's behaviour in a changing environment (e.g. Braem and Egner, 2018; Dajani and Uddin, 2015; Diamond, 2013). As an executive function (Diamond, 2013), cognitive flexibility relies on more basic cognitive functions, such as attention, selection processes and performance monitoring (Cavanagh and Frank, 2014; Diamond, 2013). Cognitive flexibility is commonly investigated using task-switching and set-shifting paradigms, which require to flexibly adapt one's response to repeatedly changing stimulus-response mappings. Such paradigms typically elicit switch costs, defined as increased reaction times (RTs) and error rates when a mapping rule is changed compared to trials (or blocks) without rule change (Monsell, 2003; Wylie and Allport, 2000). Many studies of set-shifting have distinguished between intra-dimensional (ID) and extra-dimensional (ED) shifts. 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 ED shift is expected to be more difficult than the ID shift and, consequently, to engage more neural resources (Watson et al., 2006).

Results regarding alterations of cognitive flexibility in older age are somewhat inconsistent. Some studies report deficits in cognitive flexibility in healthy older adults (Reynolds et al., 1995; Richter et al., 2023; Wecker et al., 2005), mostly evident in increased switch costs (Cepeda et al., 2001; Kray et al., 2002; Meiran et al., 2001), more perseverative errors (Haaland et al., 1987; Zelazo et al., 2004) and failure to perform ED shifts (De Luca et al., 2003; Owen et al., 1991; Zelazo et al., 2004). However, some other studies report that switch costs are not altered (Falkenstein et al., 2001; Karayanidis et al., 2011; Kolev et al., 2005; Kray and Lindenberger, 2000; Mayr and Liebscher, 2001; Salthouse et al., 1998) or are even diminished (Kray, 2006) in older adults. Besides these inconsistent behavioural results during set-shifting in older adults, little is known about their neural underpinnings.

Task-related analyses of electroencephalography (EEG) data, such as event-related time-frequency analysis can help to decipher the neural mechanisms underlying alterations of cognitive flexibility in old age. For the present study, we focused on one EEG parameter previously discussed in the context of cognitive flexibility.

Time-frequency analyses of task-related EEG have implicated midfrontal theta oscillations (4-8 Hz) in cognitive control processes (Cavanagh and Shackman, 2015; Domic-Siede et al., 2021; Stolz et al., 2023), action adjustment (van de Vijver et al., 2011), maintenance of working memory content (Ratcliffe et al., 2022) and cognitive interference (Nigbur et al., 2011). In fact, medial theta has been characterized as a hallmark neural signature of cognitive control (Cavanagh and Frank, 2014; Cohen, 2011a, 2014; Duprez et al., 2020) and its source has been localized in the anterior cingulate cortex and adjacent medial prefrontal cortex (Cavanagh and Shackman, 2015; Mitchell et al., 2008; Tsujimoto et al., 2006), a core structure of the brain's salience network (Seeley, 2019; Seeley et al., 2007).

As aging has been associated with altered functioning of the prefrontal cortex (Cabeza, 2002; Cabeza et al., 2002; Harada et al., 2013; Zanto and Gazzaley, 2019), it can be assumed that cognitive deficits in old age may result from an age-dependent functional reorganization of medial frontal regions (Mukli et al., 2024; Nyberg et al., 2010; Yao and Hsieh, 2022; Zhu et al., 2015). Assuming that midfrontal theta oscillations reflect information transmission from the midfrontal cortex to other brain areas in contexts requiring cognitive control (e.g. lateral prefrontal cortex, motor cortex and sensory cortex; for review see: Cavanagh and Frank, 2014), the reduced midfrontal theta power observed in older adults (e.g. Cummins and Finnigan, 2007; Dias et al., 2015; van de Vijver et al., 2014) might constitute a neural signature of such age-related cognitive decline.

However, in the context of cognitive flexibility, studies on midfrontal theta in aging are scarce. In young adults, switch trials have been associated with 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). Recognizing the importance of separating ID and ED set-shifting conditions from each other due to their different needs for cognitive resources, Oh et al. (2014) observed in young adults' theta activity in the inferior frontal gyrus to be higher in ED compared to ID trials. In older adults, Dias et al. (2015) observed lower theta power during baseline activity, lower theta coherence across brain regions and worse set shifting performance in older adults (Dias et al., 2015).

Here we investigated midfrontal theta power as a measure of cognitive control in the frontal cortex To this end, we applied the EEG-compatible ID/ED set-shifting (IDED) task (Oh et al., 2014) in which we assessed whether set-shifting deficits in healthy older adults might be reflected by the modulation of theta by shift-types (ID vs. ED). We expected midfrontal theta power to be overall decreased in older participants and increased in ED as compared to ID shifts in young individuals, reflecting the need for higher cognitive control with increasing set-shifting demands. In older adults we expected theta modulation in set-shifting to differ from young adults.

2. Materials 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).

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, $p < .001$
Sex	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. N = number of participants. F = female. M = male. t = Welch two-sample t-test. X^2 = Pearson's Chi-squared test. W = Wilcoxon rank sum test. MMSE (Mini Mental State Examination): 3 values missing. MWT-B (Mehrfachwahl-Wortschatz-Intelligenztest B): 1 value missing. Education: 1 value missing.

Older participants also completed the Mini Mental State Examination (MMSE; Folstein et al., 1975) to evaluate their cognitive status. None of the participants scored below 26, and thus well above the level of 24, which has been suggested as a value indicative for dementia in a comprehensive meta-analysis (e.g. Creavin et al., 2016)).

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 resulting from muscle artifacts, 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).

2.2 Cognitive Flexibility Task

To assess participants' cognitive flexibility, all participants first completed the Attentional Set Shifting Task (ASST; Dickson et al., 2014; Sahakian and Owen, 1992). The results and a brief discussion are provided in the supplementary material (Supplementary Material S3).

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; Oh et al., 2014).

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. The matching rule stays the same for at least three consecutive trials, indicated by the fact that the target also remains unchanged. When a new target appears a change of the matching rule occurs, initiating a set shift. 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) (Figure 1C) or b) extra-dimensional (ED). In ED trials, the previously irrelevant dimension becomes relevant (colour-to-shape or shape-to-colour) (Figure 1D).

Each trial always had the following structure (Figure 1A). 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 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 (Figure 1B). 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. After practice, no further feedback on response correctness was given.

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 and matching rule remained the same (e.g., in case of a colour match the target remained a red square and one of the stimuli was red). 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 using 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). We opted for individual thresholds for the gradient criterion as this accounts for individual variability in the EEG signal and differences in noise level (Luck, 2014). 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 100 Hz band-pass second order filter was applied for wavelet analysis. 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 and wavelet 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 (a lengthy stimulus-locked epoch was chosen to account for the relatively low frequency of theta oscillations, as at least 7 full theta cycles were required for the wavelet analysis and to enable a better investigation of response trials), b) baseline correction using the average of -250 to 0 ms pre-stimulus.

Frequency power from 1 to 60 Hz in steps of 1 Hz was then 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. The baseline window was chosen to not overlap the stimulus presentation to avoid temporal smearing (Morales and Bowers, 2022), as done in previous studies (e.g. Panitz et al., 2019). Normalization into *dB* was performed using the following equation:

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

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 and time period were chosen based on the observed distribution of theta activity on the grand average of all participants and all conditions (Stolz et al., 2023). The same time window was chosen for both age groups, as the onset of theta power increase after stimulus presentation did not differ between the two age groups (see supplementary material S2). These locations also correspond to the positions used for analysis of midfrontal theta power in other studies, in particular the FCz (e.g. Kolev et al., 2024; Ratcliffe et al., 2022; Yordanova et al., 2020).

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 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).

IDED reaction time (RT) was defined as the time taken to correctly respond after stimulus presentation. Participants' RTs exhibited a right-skewed distribution (mean skewness of all trials: 2.30 ± 0.75) and were therefore first log-transformed. The mean and standard deviation of the distribution of the logarithmic RTs (log_RTs) were used as dependent variables in statistical analyses. Error rates were computed as 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 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): mean log_RT, standard deviation of log_RT, error rate, 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, degrees of freedom were adjusted using the

Greenhouse-Geisser correction. All dependent variables were tested for non-normality and inhomogeneity of variances with the Shapiro-Wilk test and Levene's test respectively. Both tests were non-significant across all variables, conditions, and age groups (Shapiro-Wilk: all $p > 0.10$; Levene: all $p > 0.05$) except for the error rate. Here, non-normality was given (highest value: ED within young participants: $W = 0.85$, $p = 0.005$). Therefore, error rates were additionally compared with a robust ANOVA. The results of the robust ANOVA did not qualitatively differ from the results of the ANOVA and are reported in the supplementary material (S4).

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).

Whenever accepting the null hypothesis – rather than merely not rejecting it – was appropriate for the interpretation of our results, we employed Bayesian statistics using JASP (version 0.18.3; JASP Team, 2024). Specifically, we computed Bayesian repeated measures ANOVAs of mean midfrontal theta power within each age group for the factor condition followed by Bayesian paired t-tests. We additionally performed Bayesian one sample t-tests of the single-trial correlation coefficients.

3. Results

3.1 Behavioural Results of the IDED Task

Across the three conditions, all participants had an overall median RT of 718 ± 199 ms. Mean log RTs were significantly longer in older compared to young participants in all conditions (F (1, 37) = 62.00, $p < .001$, $\eta_p^2 = 0.63$) (Figure 2A). Regardless of age group, a significant condition effect on log_RTs was found (F (1.30, 47.94) = 163.57, $p < .001$, $\eta_p^2 = 0.82$). As expected, we observed the longest log_RTs in the ED condition, followed by the ID

condition, and shortest log_RTs in the repeat condition (ED vs repeat: *t(38)* = 14.80, *p* < .001, *d* = 2.37; ED vs ID: *t(38)* = 9.27, *p* < .001, *d* = 1.48; ID vs repeat: *t(38)* = 15.1, *p* < .001, *d* = 2.43). The interaction between condition and age group did not reach significance (*F* (1.3, 47.94) = 0.192, *p* = .727, η_p^2= 0.01).

In a mixed ANOVA with the standard deviations of log_RTs, we found a significant main effect of condition (*F* (2, 74) = 11.49, *p* < .001, η_p^2= 0.237). Overall, the ED condition resulted in the highest standard deviations, followed by the ID and the repeat condition (ED vs repeat: *t*(38) = 4.89, *p* < .001, *d* = 0.78; ED vs ID: *t* (38) = 2.12, *p* = .040, *d* = 0.34; ID vs repeat: *t*(38) = 2.98, *p* = .005, *d* = 0.48). Additionally, a main effect of age group was found (*F* (1, 37) = 4.61, *p* = .038, η_p^2= 0.11), where older participants had overall higher standard deviations of the log_RTs compared to the younger participants (Figure 2B).

Average error rates were low (1.90% ± 2.60%, see Figure 2D). 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 2C). Again, the 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).

3.2 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 first appeared over posterior occipital electrodes between 0 and 200 ms (Figure 3), 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 4A&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, $p < .001$, $\eta_p^2 = 0.29$, $BF_{10} = 52.482$), 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 ($t\ (18) = 1.78$, $p = .091$, $d = 0.41$, $BF_{10} = 0.893$), in contrast to the young adults ($t\ (19) = 6.04$, $p < .001$, $d = 1.35$, $BF_{10} = 2599.162$). 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, $p < .001$, $\eta_p^2 = 0.28$, $BF_{10} = 5.193 * 10^6$) (Figure 4A, 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: $t(19) = 9.46$, $p < .001$, $d = 2.11$, $BF_{10} = 994295.971$; ID vs repeat: $t(19) = 4.24$, $p < .001$, $d = 0.95$, $BF_{10} = 74.724$; ED vs ID: $t(19) = 2.06$, $p = .053$, $d = 0.46$, $BF_{10} = 1.330$) (Figure 4C). In older individuals, we found no significant differences between conditions (highest t-value: repeat vs ED: $t\ (19) = 0.60$, $p = .78$, $d = 0.14$, $BF_{10} = 0.278$).

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, $p < .001$, $\eta_p^2 = 0.27$, $BF_{10} = 18.653$), 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: $t(19) = 2.70$, $p_{adj} = .043$, $d = 0.60$, $BF_{10} = 3.799$; ID $t(19) = 3.31$, $p_{adj} = .022$, $d = 0.74$, $BF_{10} = 11.845$) in the positive direction (Figure 4D). In the older adults, none of the values obtained at any condition significantly differed from zero (highest absolute t-value: ID: $t\ (19) = -2.23$, $p_{adj} = .078$, $d = -0{,}51$, $BF_{10} = 1.722$).

4. Discussion

In this study, we observed differences in performance and neural processing during set-shifting between young and older adults In the IDED task, we investigated participants' log_RTs, error rates and midfrontal theta power in relation to age group and set-shift condition. Older participants were slower than young participants, but showed comparable error rates. Across all participants, log_RTs and error rates increased with higher set-shifting demands. Most notably, older adults differed from young adults by lower overall theta power and a lack of significant modulation of midfrontal theta activity during set-shifting.

4.1 Switch costs and age-related changes in cognitive flexibility

Compatible with previous investigations (for a review, see Monsell, 2003), switch costs (ED > ID > repeat) manifested as increasing error rates and longer reaction times, as well as larger log_RT variability in young and older adults. Older adults showed increased log_RT variability, and the majority of older participants in our study failed to complete the ASST, with particular difficulty at the ED stage (see S2). 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 in other tasks that require cognitive flexibility (Ridderinkhof et al., 2002; Zelazo et al., 2004).

In the IDED task, which is easier to be performed, there was no conclusive evidence for increased behavioural switch costs in older adults. Karayanidis et al. (2011) have argued that increased switch costs might not be attributable to actual set-shifting deficits, but rather reflect increased mixing costs (Kramer et al., 1999; Kray, 2006; Meiran et al., 2001) which result from using blocks with multiple different trial types. In their specific task, proactive preparation eliminated switch costs. According to the authors, increased switch costs in other task-switching paradigms might reflect insufficient preparation and slowing of non-decision processes like target encoding, suppression of irrelevant information, or slower post-decision processes. It should be noted, though, that their study, like other task-switching studies, relied more on proactive preparation resulting from cue presentation preceding the targets, whereas our paradigm largely relied on reactive processes. We can thus not exclude that increased switch costs would have become apparent in the IDED, if the participants had less time to employ alternative processes. This is further discussed in the limitations paragraph.

4.2 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 within the young group 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. This finding is consistent with previous studies on response conflict, in which single trial RTs also positively correlated with theta-band power (Cohen and Cavanagh, 2011; Cohen and van Gaal, 2014; Jiang et al., 2018; Jiang et al., 2015a, b). In our study 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 and adaptive behaviour is required (Cavanagh and Shackman, 2015; Domic-Siede et al., 2021; Stolz et al., 2023).

Our study aligns with previous studies that identified midfrontal theta-band activity as a core neural signature of executive function (Cohen, 2011a, 2014; Duprez et al., 2020). During set-shifting, in particular, midfrontal theta may play a role in updating stimulus-response mappings (van de Vijver et al., 2014), selective attention (McDermott et al., 2017) behaviour re-adjustment (Fusco et al., 2018) and inhibition (Kaiser et al., 2019). Midfrontal theta may also coordinate the interaction between the executive system in frontal areas and the parietally located representational system, as previously reported for working memory (Ratcliffe et al., 2022). In the older age group, there appeared to be little midfrontal theta activity, which is in line with previous studies of cognitive flexibility (Dias et al., 2015), short term memory (Cummins and Finnigan, 2007), and working memory (Gajewski and Falkenstein, 2014) in older adults. These findings provoke the question why older adults exhibited consistently lower midfrontal theta power during task execution, which did not significantly increase with increasing demands on cognitive flexibility.

Converging evidence from MEG (Asada et al., 1999; Periáñez et al., 2004), positron emission tomography (Nagahama et al., 1998) and functional magnetic resonance imaging (fMRI) studies (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) points to a key role of prefrontal activity in set-shifting. Compatibly, aging-related prefrontal cortical volume loss has been associated with increased response latencies in task switching (Hakun et al.,

2015) and lower memory performance (Nordahl et al., 2006). Prefrontal white matter integrity has also been associated with cognitive control (Ziegler et al., 2010) and memory performance (Cohen, 2011b; Kennedy and Raz, 2009; Schott et al., 2011). Notably, prefrontal white matter tract integrity has also been directly linked to theta amplitude during error processing(Cohen, 2011a). Hence, reduced cognitive flexibility in older adults may, at least in part, be attributable to the frequently observed prefrontal cortical volume loss and reduced white matter integrity in aging (Fjell et al., 2009; Grothe et al., 2013; Jernigan et al., 2001; Raz et al., 1997; Salat et al., 2001) (but see: He et al., 2021; Moretti et al., 2007) and/or decreased metabolic activity of the anterior cingulate cortex in older adults (Pardo et al., 2007).

In this study, we aimed to investigate whether older adults exhibit similar set-shifting-related theta modulations as younger adults, despite the well-documented age-related midfrontal theta power decrease (e.g. Cummins and Finnigan, 2007; Dias et al., 2015; van de Vijver et al., 2014)). Our results point to a reduced function of the oscillatory theta system in older age, as no evidence for a set-shifting-related modulation of theta activity was found and theta power was reduced overall. Our study supports previous results that argue for a functional reorganization of frontal networks with aging (Cabeza, 2002; Cabeza et al., 2002; Koen and Rugg, 2019; Li et al., 2001; Reuter-Lorenz, 2002). Recent studies on midfrontal theta have reported a disengagement of the medial frontal lobe during error processing (Kolev et al., 2024) and during motor coordination (Yordanova et al., 2020) in older age. Some past studies have additionally reported a redistribution of medial activity to more frontal areas (van de Vijver et al., 2014; Velanova et al., 2006).

Collectively, this functional rearrangement with aging may play a role in diminished cognitive flexibility in older age. Cognitive flexibility relies on both frontal and posterior areas (Kennedy and Raz, 2009) or, more specifically, the interaction of prefrontal and other cortical systems, as evidenced by fMRI (Imaruoka et al., 2005; Owen et al., 2005) and

oscillation studies (Cohen et al., 2011; Engel et al., 2001; Varela et al., 2001). Diminished midfrontal activity might therefore elicit a shift towards greater resource allocation to late rather than early selection processes (Velanova et al., 2006) and a tendency for more conservative decision making (Forstmann et al., 2011; Karayanidis et al., 2011; Ratcliff et al., 2005). Within the dual model of cognitive control framework (Braver, 2012), there is evidence for an age-related decline of proactive control processes (Ball et al., 2023). Other studies additionally report diminished reactive cognitive control (Karayanidis et al., 2011) or both, depending on the context (Zhang and Wang, 2022). In fact, task-switching ERP investigations suggest that older adults process mixed repeat trials (i.e., repeat trials in blocks with different trial types, as in our study) as if they were switch trials (Karayanidis et al., 2011; Mayr, 2001). Taken together, the absence of set-shifting-related theta modulation in older adults might point to a functional reorganization of cognitive control networks with a disengagement of the midfrontal cortex and recruitment of alternative neural resources, thereby leading to a shift to late selection processes and reactive control.

4.3 Limitations of the study

A notable limitation of our current study is a lack of time-pressure, as 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 by the exceptionally low error rates observed. These factors may have potentially concealed increased switch costs that were expected in older participants. In the study by Dias et al. (2015), the WCST performance was assessed 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. Nevertheless, it should be mentioned here that increased switch costs in older age are not invariably observed in studies of task switching (Falkenstein et al., 2001; Kolev et al., 2005), as discussed above. 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.

Finally, we acknowledge the limitations of the small sample size and the limited cognitive assessment of the older participants. More studies in the future with larger sample sizes and deeper subject phenotyping shall help better interpret the results and answer questions that arose from this investigation.

4.5 Conclusions and future perspectives

In summary, this study contributes insights into age-related differences in set-shifting performance and neural processing, emphasizing the role of midfrontal theta oscillations. Our findings suggest that midfrontal theta oscillatory activity is not necessary for successful set-shifting in older age, indicating that different neural substrates are possibly being recruited for set-shifting as a consequence of functional reorganization of frontal networks. Future research utilizing simultaneous EEG-fMRI or MEG to delineate the functional connectivity changes with subcortical areas is needed to elucidate the underlying mechanism further.

Maintaining cognitive flexibility in older age is essential, particularly in an aging society. Previous studies show that task switching can be trained (Karbach and Kray, 2009; Strobach et al., 2012), even in older individuals (Cepeda et al., 2001; Steyvers et al., 2019; Whitson et al., 2014). Understanding the underlying neural mechanisms may help to develop more targeted training and intervention protocols. Our results suggest that, in this context, EEG oscillations in particular, might constitute a useful readout, potentially not only in

normal aging but also in mild cognitive impairment and Alzheimer's disease (Yener et al., 2022; Yener and Başar, 2013).

Acknowledgments

The authors are grateful to Alexander Dityatev for valuable comments on the manuscript. The authors would like to thank Matthias Deliano and Renate Blobel-Lüer for their expert technical assistance. Finally, we would like to express our sincere gratitude to our study participants for their consent to take part in this research study.

Funding and Conflict of Interest Declaration

We gratefully acknowledge funding from the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) - 425899996/CRC1436 and 362321501/RTG 2413 SynAGE as well as from the German Center for Mental Health and from the State of Saxony-Anhalt and the European Union (Research Alliance "Autonomy in Old Age"). The funding agencies had no role in the design or analysis of the study.

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).

5. References

Asada, H., Fukuda, Y., Tsunoda, S., Yamaguchi, M., Tonoike, M., 1999. Frontal midline theta rhythms reflect alternative activation of prefrontal cortex and anterior cingulate cortex in humans. Neuroscience Letters 274(1), 29-32. https://doi.org/10.1016/S0304-3940(99)00679-5.

Ball, B.H., Peper, P., Bugg, J.M., 2023. Dissociating proactive and reactive control in older adults. Psychol Aging 38(4), 323-332. https://psycnet.apa.org/doi/10.1037/pag0000748.

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. Journal of the Royal Statistical Society: Series B (Methodological) 57(1), 289-300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x.

Braem, S., Egner, T., 2018. Getting a grip on cognitive flexibility. Current directions in psychological science 27(6), 470–476. https://doi.org/10.1177/0963721418787475.

Brainard, D.H., Vision, S., 1997. The psychophysics toolbox. Spatial vision 10(4), 433-436. https://psycnet.apa.org/doi/10.1163/156856897X00357.

Braver, T.S., 2012. The variable nature of cognitive control: a dual mechanisms framework. Trends in Cognitive Sciences 16(2), 106-113. https://doi.org/10.1016/j.tics.2011.12.010.

Cabeza, R., 2002. Hemispheric asymmetry reduction in older adults: The HAROLD model. Psychology and Aging 17(1), 85-100. https://doi.org/10.1037//0882-7974.17.1.85.

Cabeza, R., Anderson, N.D., Locantore, J.K., McIntosh, A.R., 2002. Aging Gracefully: Compensatory Brain Activity in High-Performing Older Adults. NeuroImage 17(3), 1394-1402. https://doi.org/10.1006/nimg.2002.1280.

Cavanagh, J.F., Frank, M.J., 2014. Frontal theta as a mechanism for cognitive control. Trends in cognitive sciences 18(8), 414–421. https://doi.org/10.1016/j.tics.2014.04.012.

Cavanagh, J.F., Shackman, A.J., 2015. Frontal midline theta reflects anxiety and cognitive control: Meta-analytic evidence. Journal of Physiology-Paris 109(1-3), 3-15. https://doi.org/10.1016/j.jphysparis.2014.04.003.

Cepeda, N.J., Kramer, A.F., Gonzalez de Sather, J.C.M., 2001. Changes in executive control across the life span: Examination of task-switching performance. Developmental Psychology 37, 715-730. https://psycnet.apa.org/doi/10.1037/0012-1649.37.5.715.

Cohen, M.X., 2011a. Error-related medial frontal theta activity predicts cingulate-related structural connectivity. NeuroImage 55(3), 1373-1383. https://doi.org/10.1016/j.neuroimage.2010.12.072.

Cohen, M.X., 2011b. Hippocampal-prefrontal connectivity predicts midfrontal oscillations and long-term memory performance. Curr Biol 21(22), 1900-1905. https://doi.org/10.1016/j.cub.2011.09.036.

Cohen, M.X., 2014. A neural microcircuit for cognitive conflict detection and signaling. Trends in Neurosciences 37(9), 480-490. https://doi.org/10.1016/j.tins.2014.06.004.

Cohen, M.X., Cavanagh, J.F., 2011. Single-Trial Regression Elucidates the Role of Prefrontal Theta Oscillations in Response Conflict. Frontiers in Psychology 2. https://doi.org/10.3389/fpsyg.2011.00030.

Cohen, M.X., van Gaal, S., 2014. Subthreshold muscle twitches dissociate oscillatory neural signatures of conflicts from errors. NeuroImage 86, 503-513. https://doi.org/10.1016/j.neuroimage.2013.10.033.

Cohen, M.X., Wilmes, K.A., van de Vijver, I., 2011. Cortical electrophysiological network dynamics of feedback learning. Trends in Cognitive Sciences 15(12), 558-566. https://doi.org/10.1016/j.tics.2011.10.004.

Cooper, P.S., Wong, A.S.W., McKewen, M., Michie, P.T., Karayanidis, F., 2017. Frontoparietal theta oscillations during proactive control are associated with goal-updating and reduced behavioral variability. Biological Psychology 129, 253-264. https://dx.doi.org/10.1016/j.biopsycho.2017.09.008.

Creavin, S.T., Wisniewski, S., Noel-Storr, A.H., Trevelyan, C.M., Hampton, T., Rayment, D., Thom, V.M., Nash, K.J.E., Elhamoui, H., Milligan, R., et al., 2016. Mini-Mental State Examination (MMSE) for the detection of dementia in clinically unevaluated people aged 65 and over in community and primary care populations. Cochrane Database of Systematic Reviews(1). https://doi.org/10.1002/14651858.cd011145.pub2.

Cummins, T.D.R., Finnigan, S., 2007. Theta power is reduced in healthy cognitive aging. International Journal of Psychophysiology 66(1), 10-17. https://doi.org/10.1016/j.ijpsycho.2007.05.008.

Cunillera, T., Fuentemilla, L., Periañez, J., Marco-Pallarès, J., Krämer, U.M., Càmara, E., Münte, T.F., Rodríguez-Fornells, A., 2012. Brain oscillatory activity associated with task switching and feedback processing. Cognitive, Affective, & Behavioral Neuroscience 12(1), 16–33. https://doi.org/10.3758/s13415-011-0075-5.
da Costa, L., Robertson, A., Bethune, A., MacDonald, M.J., Shek, P.N., Taylor, M.J., Pang, E.W., 2015. Delayed and disorganised brain activation detected with magnetoencephalography after mild traumatic brain injury. Journal of Neurology, Neurosurgery & Psychiatry 86(9), 1008. https://doi.org/10.1136/jnnp-2014-308571.
Dajani, D.R., Uddin, L.Q., 2015. Demystifying cognitive flexibility: Implications for clinical and developmental neuroscience. Trends in Neurosciences 38(9), 571-578. https://dx.doi.org/10.1016/j.tins.2015.07.003.
De Luca, C.R., Wood, S.J., Anderson, V., Buchanan, J.-A., Proffitt, T.M., Mahony, K., Pantelis, C., 2003. Normative Data From the Cantab. I: Development of Executive Function Over the Lifespan. Journal of Clinical and Experimental Neuropsychology 25(2), 242-254. https://doi.org/10.1076/jcen.25.2.242.13639.
Diamond, A., 2013. Executive functions. Annual review of psychology 64, 135–168. https://doi.org/10.1146/annurev-psych-113011-143750.
Dias, N.S., Ferreira, D., Reis, J., Jacinto, L.R., Fernandes, L., Pinho, F., Festa, J., Pereira, M., Afonso, N., Santos, N.C., Cerqueira, J.J., Sousa, N., 2015. Age effects on EEG correlates of the Wisconsin Card Sorting Test. Physiological Reports 3(7), e12390. https://doi.org/10.14814/phy2.12390.
Dickson, P.E., Calton, M.A., Mittleman, G., 2014. Performance of C57BL/6J and DBA/2J mice on a touchscreen-based attentional set-shifting task. Behavioural brain research 261, 158–170. https://doi.org/10.1016/j.bbr.2013.12.015.
Domic-Siede, M., Irani, M., Valdés, J., Perrone-Bertolotti, M., Ossandón, T., 2021. Theta activity from frontopolar cortex, mid-cingulate cortex and anterior cingulate cortex shows different roles in cognitive planning performance. NeuroImage 226, 117557. https://doi.org/10.1016/j.neuroimage.2020.117557.
Duprez, J., Gulbinaite, R., Cohen, M.X., 2020. Midfrontal theta phase coordinates behaviorally relevant brain computations during cognitive control. NeuroImage 207, 116340. https://doi.org/10.1016/j.neuroimage.2019.116340.
Engel, A.K., Fries, P., Singer, W., 2001. Dynamic predictions: Oscillations and synchrony in top–down processing. Nature Reviews Neuroscience 2(10), 704-716. https://doi.org/10.1038/35094565.
Falkenstein, M., Hoormann, J., Hohnsbein, J., 2001. Changes of error-related ERPs with age. Experimental Brain Research 138(2), 258-262. https://doi.org/10.1007/s002210100712.
Faul, F., Erdfelder, E., Buchner, A., Lang, A.-G., 2009. Statistical power analyses using G* Power 3.1: Tests for correlation and regression analyses. Behavior research methods 41(4), 1149-1160. https://doi.org/10.3758/BRM.41.4.1149.
Fjell, A.M., Walhovd, K.B., Fennema-Notestine, C., McEvoy, L.K., Hagler, D.J., Holland, D., Brewer, J.B., Dale, A.M., 2009. One-Year Brain Atrophy Evident in Healthy Aging. The Journal of Neuroscience 29(48), 15223-15231. https://doi.org/10.1523/jneurosci.3252-09.2009.
Folstein, M.F., Folstein, S.E., McHugh, P.R., 1975. “Mini-mental state”: A practical method for grading the cognitive state of patients for the clinician. Journal of Psychiatric Research 12(3), 189-198. https://doi.org/10.1016/0022-3956(75)90026-6.
Forstmann, B.U., Tittgemeyer, M., Wagenmakers, E.J., Derrfuss, J., Imperati, D., Brown, S., 2011. The speed-accuracy tradeoff in the elderly brain: a structural model-based approach. J Neurosci 31(47), 17242-17249. https://doi.org/10.1523/JNEUROSCI.0309-11.2011.
Fusco, G., Scandola, M., Feurra, M., Pavone, E.F., Rossi, S., Aglioti, S.M., 2018. Midfrontal theta transcranial alternating current stimulation modulates behavioural adjustment after error execution. European Journal of Neuroscience 48(10), 3159-3170. https://doi.org/10.1111/ejn.14174.
Gajewski, P.D., Falkenstein, M., 2014. Age-related effects on ERP and oscillatory EEG-dynamics in a 2-back task. Journal of Psychophysiology. https://doi.org/10.1027/0269-8803/a000123.
Grothe, M., Heinsen, H., Teipel, S., 2013. Longitudinal measures of cholinergic forebrain atrophy in the transition from healthy aging to Alzheimer's disease. Neurobiology of Aging 34(4), 1210-1220. https://doi.org/10.1016/j.neurobiolaging.2012.10.018.

Haaland, K.Y., Vranes, L.F., Goodwin, J.S., Garry, P.J., 1987. Wisconsin Card Sort Test Performance in a Healthy Elderly Population. Journal of Gerontology 42(3), 345-346. https://doi.org/10.1093/geronj/42.3.345.
Hakun, J.G., Zhu, Z., Brown, C.A., Johnson, N.F., Gold, B.T., 2015. Longitudinal alterations to brain function, structure, and cognitive performance in healthy older adults: A fMRI-DTI study. Neuropsychologia 71, 225-235. https://doi.org/10.1016/j.neuropsychologia.2015.04.008.
Harada, C.N., Natelson Love, M.C., Triebel, K.L., 2013. Normal Cognitive Aging. Clinics in Geriatric Medicine 29(4), 737-752. https://doi.org/10.1016/j.cger.2013.07.002.
He, M., Liu, F., Nummenmaa, A., Hämäläinen, M., Dickerson, B.C., Purdon, P.L., 2021. Age-Related EEG Power Reductions Cannot Be Explained by Changes of the Conductivity Distribution in the Head Due to Brain Atrophy. Frontiers in Aging Neuroscience 13. https://doi.org/10.3389/fnagi.2021.632310.
Imaruoka, T., Saiki, J., Miyauchi, S., 2005. Maintaining coherence of dynamic objects requires coordination of neural systems extended from anterior frontal to posterior parietal brain cortices. NeuroImage 26(1), 277-284. https://doi.org/10.1016/j.neuroimage.2005.01.045.
JASP Team, 2024. JASP. https://jasp-stats.org/. https://jasp-stats.org/.
Jernigan, T.L., Archibald, S.L., Fennema-Notestine, C., Gamst, A.C., Stout, J.C., Bonner, J., Hesselink, J.R., 2001. Effects of age on tissues and regions of the cerebrum and cerebellum. Neurobiology of Aging 22(4), 581-594. https://doi.org/10.1016/S0197-4580(01)00217-2.
Jiang, J., Bailey, K., Xiao, X., 2018. Midfrontal Theta and Posterior Parietal Alpha Band Oscillations Support Conflict Resolution in a Masked Affective Priming Task. Frontiers in Human Neuroscience 12. https://doi.org/10.3389/fnhum.2018.00175.
Jiang, J., Zhang, Q., van Gaal, S., 2015a. Conflict awareness dissociates theta-band neural dynamics of the medial frontal and lateral frontal cortex during trial-by-trial cognitive control. NeuroImage 116, 102-111. https://doi.org/10.1016/j.neuroimage.2015.04.062.
Jiang, J., Zhang, Q., Van Gaal, S., 2015b. EEG neural oscillatory dynamics reveal semantic and response conflict at difference levels of conflict awareness. Scientific Reports 5(1), 12008. https://doi.org/10.1038/srep12008.
Kaiser, J., Simon, N.A., Sauseng, P., Schütz-Bosbach, S., 2019. Midfrontal neural dynamics distinguish between general control and inhibition-specific processes in the stopping of motor actions. Scientific Reports 9(1), 13054. https://doi.org/10.1038/s41598-019-49476-4.
Karayanidis, F., Whitson, L.R., Heathcote, A., Michie, P.T., 2011. Variability in Proactive and Reactive Cognitive Control Processes Across the Adult Lifespan. Frontiers in Psychology 2. https://doi.org/10.3389/fpsyg.2011.00318.
Karbach, J., Kray, J., 2009. How useful is executive control training? Age differences in near and far transfer of task-switching training. Developmental Science 12(6), 978-990. https://doi.org/10.1111/j.1467-7687.2009.00846.x.
Kennedy, K.M., Raz, N., 2009. Aging white matter and cognition: Differential effects of regional variations in diffusion properties on memory, executive functions, and speed. Neuropsychologia 47(3), 916-927. https://doi.org/10.1016/j.neuropsychologia.2009.01.001.
Koen, J.D., Rugg, M.D., 2019. Neural Dedifferentiation in the Aging Brain. Trends in Cognitive Sciences 23(7), 547-559. https://doi.org/10.1016/j.tics.2019.04.012.
Kolev, V., Falkenstein, M., Yordanova, J., 2005. Aging and Error Processing: Time-Frequency Analysis of Error-Related Potentials. Journal of Psychophysiology 19(4), 289-297. https://psycnet.apa.org/doi/10.1027/0269-8803.19.4.289.
Kolev, V., Falkenstein, M., Yordanova, J., 2024. A distributed theta network of error generation and processing in aging. Cognitive Neurodynamics 18(2), 447-459. https://doi.org/10.1007/s11571-023-10018-4.
Konishi, S., Hayashi, T., Uchida, I., Kikyo, H., Takahashi, E., Miyashita, Y., 2002. Hemispheric asymmetry in human lateral prefrontal cortex during cognitive set shifting. Proceedings of the National Academy of Sciences of the United States of America 99(11), 7803-7808. https://doi.org/10.1073/pnas.122644899.
Konishi, S., Nakajima, K., Uchida, I., Kameyama, M., Nakahara, K., Sekihara, K., Miyashita, Y., 1998. Transient activation of inferior prefrontal cortex during cognitive set shifting. Nature Neuroscience 1(1), 80-84. https://doi.org/10.1038/283.

Kramer, A.F., Hahn, S., Gopher, D., 1999. Task coordination and aging: explorations of executive control processes in the task switching paradigm. Acta Psychol (Amst) 101(2-3), 339-378. https://doi.org/10.1016/s0001-6918(99)00011-6.
Kray, J., 2006. Task-set switching under cue-based versus memory-based switching conditions in younger and older adults. Brain Research 1105(1), 83-92. https://doi.org/10.1016/j.brainres.2005.11.016.
Kray, J., Li, K.Z.H., Lindenberger, U., 2002. Age-Related Changes in Task-Switching Components: The Role of Task Uncertainty. Brain and Cognition 49(3), 363-381. https://doi.org/10.1006/brcg.2001.1505.
Kray, J., Lindenberger, U., 2000. Adult age differences in task switching. Psychology and Aging 15(1), 126-147. https://doi.org/10.1037/0882-7974.15.1.126.
Lehrl, S., 1999. Mehrfachwahl-Wortschatz-Intelligenztest: MWT-B. Spitta.
Lehrl, S., Triebig, G., Fischer, B., 1995. Multiple choice vocabulary test MWT as a valid and short test to estimate premorbid intelligence. Acta Neurologica Scandinavica 91(5), 335-345. https://doi.org/10.1111/j.1600-0404.1995.tb07018.x.
Li, S.-C., Lindenberger, U., Sikström, S., 2001. Aging cognition: from neuromodulation to representation. Trends in Cognitive Sciences 5(11), 479-486. https://doi.org/10.1016/S1364-6613(00)01769-1.
Lie, C.-H., Specht, K., Marshall, J.C., Fink, G.R., 2006. Using fMRI to decompose the neural processes underlying the Wisconsin Card Sorting Test. NeuroImage 30(3), 1038-1049. https://doi.org/10.1016/j.neuroimage.2005.10.031.
Liu, Z., Braunlich, K., Wehe, H.S., Seger, C.A., 2015. Neural networks supporting switching, hypothesis testing, and rule application. Neuropsychologia 77, 19-34. https://doi.org/10.1016/j.neuropsychologia.2015.07.019.
Luck, S.J., 2014. An introduction to the event-related potential technique, Second edition ed. The MIT Press, Cambridge.
Mayr, U., 2001. Age differences in the selection of mental sets: the role of inhibition, stimulus ambiguity, and response-set overlap. Psychol Aging 16(1), 96-109. https://doi.org/10.1037/0882-7974.16.1.96.
Mayr, U., Liebscher, T., 2001. Is there an age deficit in the selection of mental sets? European Journal of Cognitive Psychology 13(1-2), 47-69. https://doi.org/10.1080/09541440042000214.
McDermott, T.J., Wiesman, A.I., Proskovec, A.L., Heinrichs-Graham, E., Wilson, T.W., 2017. Spatiotemporal oscillatory dynamics of visual selective attention during a flanker task. NeuroImage 156, 277-285. https://doi.org/10.1016/j.neuroimage.2017.05.014.
Meiran, N., Gotler, A., Perlman, A., 2001. Old Age Is Associated With a Pattern of Relatively Intact and Relatively Impaired Task-Set Switching Abilities. The Journals of Gerontology: Series B 56(2), P88-P102. https://doi.org/10.1093/geronb/56.2.P88.
Mitchell, D.J., McNaughton, N., Flanagan, D., Kirk, I.J., 2008. Frontal-midline theta from the perspective of hippocampal “theta”. Progress in Neurobiology 86(3), 156-185. https://doi.org/10.1016/j.pneurobio.2008.09.005.
Monchi, O., Petrides, M., Petre, V., Worsley, K., Dagher, A., 2001. Wisconsin Card Sorting Revisited: Distinct Neural Circuits Participating in Different Stages of the Task Identified by Event-Related Functional Magnetic Resonance Imaging. The Journal of Neuroscience 21(19), 7733-7741. https://doi.org/10.1523/jneurosci.21-19-07733.2001.
Monsell, S., 2003. Task switching. Trends in Cognitive Sciences 7(3), 134-140. https://doi.org/10.1016/S1364-6613(03)00028-7.
Morales, S., Bowers, M.E., 2022. Time-frequency analysis methods and their application in developmental EEG data. Developmental Cognitive Neuroscience 54, 101067. https://doi.org/10.1016/j.dcn.2022.101067.
Moretti, D.V., Miniussi, C., Frisoni, G.B., Geroldi, C., Zanetti, O., Binetti, G., Rossini, P.M., 2007. Hippocampal atrophy and EEG markers in subjects with mild cognitive impairment. Clinical Neurophysiology 118(12), 2716-2729. https://doi.org/10.1016/j.clinph.2007.09.059.
Mukli, P., Pinto, C.B., Owens, C.D., Csipo, T., Lipecz, A., Szarvas, Z., Peterfi, A., Langley, A., Hoffmeister, J., Racz, F.S., Perry, J.W., Tarantini, S., Nyúl-Tóth, Á., Sorond, F.A., Yang, Y., James, J.A., Kirkpatrick, A.C., Prodan, C.I., Toth, P., Galindo, J., Gardner, A.W., Sonntag, W.E., Csiszar, A., Ungvari, Z., Yabluchanskiy, A., 2024. Impaired Neurovascular Coupling and Increased Functional

Connectivity in the Frontal Cortex Predict Age-Related Cognitive Dysfunction. Adv Sci (Weinh) 11(10), e2303516. https://doi.org/10.1002/advs.202303516.
Nagahama, Y., Okada, T., Katsumi, Y., Hayashi, T., Yamauchi, H., Oyanagi, C., Konishi, J., Fukuyama, H., Shibasaki, H., 2001. Dissociable mechanisms of attentional control within the human prefrontal cortex. Cerebral Cortex 11(1), 85-92. https://doi.org/10.1093/cercor/11.1.85.
Nagahama, Y., Sadato, N., Yamauchi, H., Katsumi, Y., Hayashi, T., Fukuyama, H., Kimura, J., Shibasaki, H., Yonekura, Y., 1998. Neural activity during attention shifts between object features. NeuroReport 9(11), 2633-2638. https://doi.org/10.1097/00001756-199808030-00038.
Nigbur, R., Ivanova, G., Stürmer, B., 2011. Theta power as a marker for cognitive interference. Clinical Neurophysiology 122(11), 2185-2194. https://doi.org/10.1016/j.clinph.2011.03.030.
Nordahl, C.W., Ranganath, C., Yonelinas, A.P., DeCarli, C., Fletcher, E., Jagust, W.J., 2006. White Matter Changes Compromise Prefrontal Cortex Function in Healthy Elderly Individuals. Journal of Cognitive Neuroscience 18(3), 418-429. https://doi.org/10.1162/jocn.2006.18.3.418.
Nyberg, L., Salami, A., Andersson, M., Eriksson, J., Kalpouzos, G., Kauppi, K., Lind, J., Pudas, S., Persson, J., Nilsson, L.-G., 2010. Longitudinal evidence for diminished frontal cortex function in aging. Proceedings of the National Academy of Sciences 107(52), 22682-22686. https://doi.org/10.1073/pnas.1012651108.
Oh, A., Vidal, J., Taylor, M.J., Pang, E.W., 2014. Neuromagnetic correlates of intra- and extra-dimensional set-shifting. Brain and Cognition 86, 90-97. https://doi.org/10.1016/j.bandc.2014.02.006.
Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. Computational Intelligence and Neuroscience 2011, 1-9. https://doi.org/10.1155/2011/156869.
Owen, A.M., McMillan, K.M., Laird, A.R., Bullmore, E., 2005. N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. Human Brain Mapping 25(1), 46-59. https://doi.org/10.1002/hbm.20131.
Owen, A.M., Roberts, A.C., Polkey, C.E., Sahakian, B.J., Robbins, T.W., 1991. Extra-dimensional versus intra-dimensional set shifting performance following frontal lobe excisions, temporal lobe excisions or amygdalo-hippocampectomy in man. Neuropsychologia 29(10), 993-1006. https://doi.org/10.1016/0028-3932(91)90063-E.
Pa, J., Possin, K.L., Wilson, S.M., Quitania, L.C., Kramer, J.H., Boxer, A.L., Weiner, M.W., Johnson, J.K., 2010. Gray matter correlates of set-shifting among neurodegenerative disease, mild cognitive impairment, and healthy older adults. Journal of the International Neuropsychological Society 16(4), 640-650. https://doi.org/10.1017/S1355617710000408.
Panitz, C., Keil, A., Mueller, E.M., 2019. Extinction-resistant attention to long-term conditioned threat is indexed by selective visuocortical alpha suppression in humans. Scientific Reports 9(1), 15809. https://doi.org/10.1038/s41598-019-52315-1.
Pardo, J.V., Lee, J.T., Sheikh, S.A., Surerus-Johnson, C., Shah, H., Munch, K.R., Carlis, J.V., Lewis, S.M., Kuskowski, M.A., Dysken, M.W., 2007. Where the brain grows old: decline in anterior cingulate and medial prefrontal function with normal aging. Neuroimage 35(3), 1231-1237. https://doi.org/10.1016/j.neuroimage.2006.12.044.
Periáñez, J.A., Maestú, F., Barceló, F., Fernández, A., Amo, C., Ortiz Alonso, T., 2004. Spatiotemporal brain dynamics during preparatory set shifting: MEG evidence. NeuroImage 21(2), 687-695. https://doi.org/10.1016/j.neuroimage.2003.10.008.
R Core Team, 2022. R: A Language and Environment for Statistical Computing. https://www.R-project.org/. https://www.R-project.org/.
R Studio Team, 2020. RStudio: Integrated Development Environment for R. http://www.rstudio.com/. http://www.rstudio.com/.
Ratcliff, R., Thapar, A., Smith, P.L., McKoon, G., 2005. 3Aging and response times: a comparison of sequential sampling models, in: Duncan, J., Phillips, L., McLeod, P. (Eds.), Measuring the Mind: Speed, control, and age. Oxford University Press, p. 0. https://doi.org/10.1093/acprof:oso/9780198566427.003.0001.
Ratcliffe, O., Shapiro, K., Staresina, B.P., 2022. Fronto-medial theta coordinates posterior maintenance of working memory content. Current Biology 32(10), 2121-2129.e2123. https://doi.org/10.1016/j.cub.2022.03.045.
Raz, N., Gunning, F.M., Head, D., Dupuis, J.H., McQuain, J., Briggs, S.D., Loken, W.J., Thornton, A.E., Acker, J.D., 1997. Selective aging of the human cerebral cortex observed in vivo: differential

vulnerability of the prefrontal gray matter. Cerebral Cortex 7(3), 268-282. https://doi.org/10.1093/cercor/7.3.268.
Reuter-Lorenz, P.A., 2002. New visions of the aging mind and brain. Trends in Cognitive Sciences 6(9), 394-400. https://doi.org/10.1016/S1364-6613(02)01957-5.
Reynolds, C., James, B., Mayfield, J., 1995. Baseline Performance of Normal Elderly on a Verbal Measurement of Set-Shifting and Executive Function. Archives of Clinical Neuropsychology 4(10), 383. https://doi.org/10.1093/arclin/10.4.383.
Richter, A., Soch, J., Kizilirmak, J.M., Fischer, L., Schütze, H., Assmann, A., Behnisch, G., Feldhoff, H., Knopf, L., Raschick, M., Schult, A., Seidenbecher, C.I., Yakupov, R., Düzel, E., Schott, B.H., 2023. Single-value scores of memory-related brain activity reflect dissociable neuropsychological and anatomical signatures of neurocognitive aging. Human Brain Mapping 44(8), 3283-3301. https://doi.org/10.1002/hbm.26281.
Ridderinkhof, K.R., Span, M.M., van der Molen, M.W., 2002. Perseverative Behavior and Adaptive Control in Older Adults: Performance Monitoring, Rule Induction, and Set Shifting. Brain and Cognition 49(3), 382-401. https://doi.org/10.1006/brcg.2001.1506.
Sahakian, B.J., Owen, A.M., 1992. Computerized assessment in neuropsychiatry using CANTAB: discussion paper. Journal of the Royal Society of Medicine 85(7), 399–402.
Salat, D.H., Kaye, J.A., Janowsky, J.S., 2001. Selective Preservation and Degeneration Within the Prefrontal Cortex in Aging and Alzheimer Disease. Archives of Neurology 58(9), 1403-1408. https://doi.org/10.1001/archneur.58.9.1403.
Salthouse, T.A., Fristoe, N., McGuthry, K.E., Hambrick, D.Z., 1998. Relation of task switching to speed, age, and fluid intelligence. Psychology and Aging 13(3), 445-461. https://doi.org/10.1037/0882-7974.13.3.445.
Sauseng, P., Klimesch, W., Freunberger, R., Pecherstorfer, T., Hanslmayr, S., Doppelmayr, M., 2006. Relevance of EEG alpha and theta oscillations during task switching. Experimental Brain Research 170(3), 295-301. https://doi.org/10.1007/s00221-005-0211-y.
Schott, B.H., Niklas, C., Kaufmann, J., Bodammer, N.C., Machts, J., Schutze, H., Duzel, E., 2011. Fiber density between rhinal cortex and activated ventrolateral prefrontal regions predicts episodic memory performance in humans. Proceedings of the National Academy of Sciences 108(13), 5408-5413. https://doi.org/10.1073/pnas.1013287108.
Schwarzkopf, D., de Haas, B., Rees, G., 2012. Better Ways to Improve Standards in Brain-Behavior Correlation Analysis. Frontiers in Human Neuroscience 6. https://doi.org/10.3389/fnhum.2012.00200.
Seeley, W.W., 2019. The Salience Network: A Neural System for Perceiving and Responding to Homeostatic Demands. J Neurosci 39(50), 9878-9882. https://doi.org/10.1523/jneurosci.1138-17.2019.
Seeley, W.W., Menon, V., Schatzberg, A.F., Keller, J., Glover, G.H., Kenna, H., Reiss, A.L., Greicius, M.D., 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. J Neurosci 27(9), 2349-2356. https://doi.org/10.1523/JNEUROSCI.5587-06.2007.
Smith, A.B., Taylor, E., Brammer, M., Rubia, K., 2004. Neural Correlates of Switching Set as Measured in Fast, Event-Related Functional Magnetic Resonance Imaging. Human Brain Mapping 21(4), 247-256. https://doi.org/10.1002/hbm.20007.
Steyvers, M., Hawkins, G.E., Karayanidis, F., Brown, S.D., 2019. A large-scale analysis of task switching practice effects across the lifespan. Proc Natl Acad Sci U S A 116(36), 17735-17740. https://doi.org/10.1073/pnas.1906788116.
Stolz, C., Pickering, A.D., Mueller, E.M., 2023. Dissociable feedback valence effects on frontal midline theta during reward gain versus threat avoidance learning. Psychophysiology 60(5). https://doi.org/10.1111/psyp.14235.
Strobach, T., Liepelt, R., Schubert, T., Kiesel, A., 2012. Task switching: effects of practice on switch and mixing costs. Psychological Research 76(1), 74-83. https://doi.org/10.1007/s00426-011-0323-x.
The MathWorks Inc., 2021. MATLAB Version 9.11.0.1809720 (R2021b). https://www.mathworks.com. https://www.mathworks.com.
Tsujimoto, T., Shimazu, H., Isomura, Y., 2006. Direct Recording of Theta Oscillations in Primate Prefrontal and Anterior Cingulate Cortices. Journal of Neurophysiology 95(5), 2987-3000. https://doi.org/10.1152/jn.00730.2005.

van de Vijver, I., Cohen, M.X., Ridderinkhof, K.R., 2014. Aging affects medial but not anterior frontal learning-related theta oscillations. Neurobiology of Aging 35(3), 692-704. https://doi.org/10.1016/j.neurobiolaging.2013.09.006.
van de Vijver, I., Ridderinkhof, K.R., Cohen, M.X., 2011. Frontal Oscillatory Dynamics Predict Feedback Learning and Action Adjustment. Journal of Cognitive Neuroscience 23(12), 4106-4121. https://doi.org/10.1162/jocn_a_00110.
Varela, F., Lachaux, J.-P., Rodriguez, E., Martinerie, J., 2001. The brainweb: Phase synchronization and large-scale integration. Nature Reviews Neuroscience 2(4), 229-239. https://doi.org/10.1038/35067550.
Velanova, K., Lustig, C., Jacoby, L.L., Buckner, R.L., 2006. Evidence for Frontally Mediated Controlled Processing Differences in Older Adults. Cerebral Cortex 17(5), 1033-1046. 10.1093/cercor/bhl013.
Watson, T.D., Azizian, A., Squires, N.K., 2006. Event-related potential correlates of extradimensional and intradimensional set-shifts in a modified Wisconsin Card Sorting Test. Brain Research 1092(1), 138-151. https://doi.org/10.1016/j.brainres.2006.03.098.
Wecker, N.S., Kramer, J.H., Hallam, B.J., Delis, D.C., 2005. Mental Flexibility: Age Effects on Switching. Neuropsychology 19(3), 345-352. https://doi.org/10.1037/0894-4105.19.3.345.
Whitson, L.R., Karayanidis, F., Fulham, R., Provost, A., Michie, P.T., Heathcote, A., Hsieh, S., 2014. Reactive control processes contributing to residual switch cost and mixing cost across the adult lifespan. Frontiers in Psychology 5. https://doi.org/10.3389/fpsyg.2014.00383.
Winkler, I., Debener, S., Müller, K.R., Tangermann, M., 2015. On the influence of high-pass filtering on ICA-based artifact reduction in EEG-ERP, 2015 37th Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC). pp. 4101-4105. https://doi.org/10.1109/EMBC.2015.7319296.
Wylie, G., Allport, A., 2000. Task switching and the measurement of “switch costs”. Psychological Research 63(3), 212-233. https://doi.org/10.1007/s004269900003.
Yao, Z.F., Hsieh, S., 2022. Age Differences of the Hierarchical Cognitive Control and the Frontal Rostro-Caudal Functional Brain Activation. Cereb Cortex 32(13), 2797-2815. https://doi.org/10.1093/cercor/bhab382.
Yener, G., Hünerli-Gündüz, D., Yıldırım, E., Aktürk, T., Başar-Eroğlu, C., Bonanni, L., Del Percio, C., Farina, F., Ferri, R., Güntekin, B., Hajós, M., Ibáñez, A., Jiang, Y., Lizio, R., Lopez, S., Noce, G., Parra, M.A., Randall, F., Stocchi, F., Babiloni, C., 2022. Treatment effects on event-related EEG potentials and oscillations in Alzheimer's disease. International Journal of Psychophysiology 177, 179-201. https://doi.org/10.1016/j.ijpsycho.2022.05.008.
Yener, G.G., Başar, E., 2013. Chapter 16 - Biomarkers in Alzheimer's disease with a special emphasis on event-related oscillatory responses, in: Başar, E., Başar-Eroĝlu, C., Özerdem, A., Rossini, P.M., Yener, G.G. (Eds.), Supplements to Clinical Neurophysiology. Elsevier, pp. 237-273. https://doi.org/10.1016/B978-0-7020-5307-8.00020-X.
Yeung, M.K., Han, Y.M.Y., Sze, S.L., Chan, A.S., 2016. Abnormal frontal theta oscillations underlie the cognitive flexibility deficits in children with high-functioning autism spectrum disorders. Neuropsychology 30(3), 281–295. https://doi.org/10.1037/neu0000231.
Yordanova, J., Falkenstein, M., Kolev, V., 2020. Aging-related changes in motor response-related theta activity. International Journal of Psychophysiology 153, 95-106. https://doi.org/10.1016/j.ijpsycho.2020.03.005.
Zanto, T.P., Gazzaley, A., 2019. Chapter 20 - Aging of the frontal lobe, in: D'Esposito, M., Grafman, J.H. (Eds.), Handbook of Clinical Neurology. Elsevier, pp. 369-389. https://doi.org/10.1016/B978-0-12-804281-6.00020-3.
Zelazo, P.D., Craik, F.I.M., Booth, L., 2004. Executive function across the life span. Acta Psychologica 115(2-3), 167-183. https://doi.org/10.1016/j.actpsy.2003.12.005.
Zhang, N., Wang, J., 2022. Age Differences in the Tradeoff between Proactive and Reactive Cognitive Control in Emotional Information Processing. Brain Sci 12(8). https://doi.org/10.3390/brainsci12081043.
Zhu, Z., Johnson, N.F., Kim, C., Gold, B.T., 2015. Reduced frontal cortex efficiency is associated with lower white matter integrity in aging. Cereb Cortex 25(1), 138-146. https://doi.org/10.1093/cercor/bht212.

Ziegler, D.A., Piguet, O., Salat, D.H., Prince, K., Connally, E., Corkin, S., 2010. Cognition in healthy aging is related to regional white matter integrity, but not cortical thickness. Neurobiol Aging 31(11), 1912-1926. https://doi.org/10.1016/j.neurobiolaging.2008.10.015.

Figures

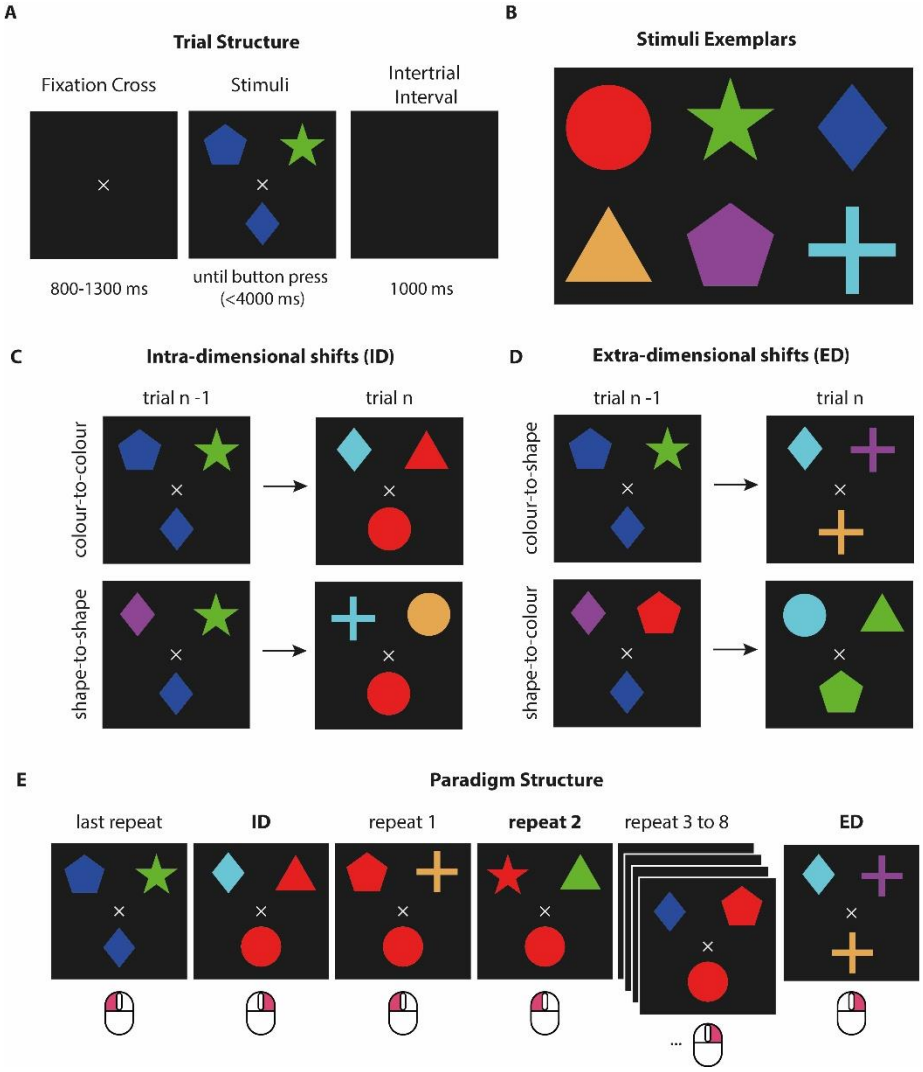

Figure 1: The IDED Task. **A:** Trial structure. After the presentation of the fixation cross for 800 to 1300 ms the stimuli appear at the top and targets at the bottom. The participants are asked to signal with a righthand mouse click which stimulus matches the target either by colour or shape. In this example the left stimulus matches the target by colour; a left mouse button press is therefore required. After button press or after a time of 4000 ms without response the stimuli and target disappear. An empty screen is visible for 1000 ms followed by the start of a new trial. **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; **E:** Paradigm structure. Here, an example of possible consequent trials is presented. In each trial the target matches one of the stimuli by colour or by shape. In ID or ED trials the target changes its form and colour eliciting a shift. Following that, a pseudorandomized number of repeat trials occurs (minimum: 3 trials, maximum: 8 trials), in which both the target and matching rule remain the same. Below each panel the correct mouse response (left or right) can be found. Trials in bold represent the conditions of interest.

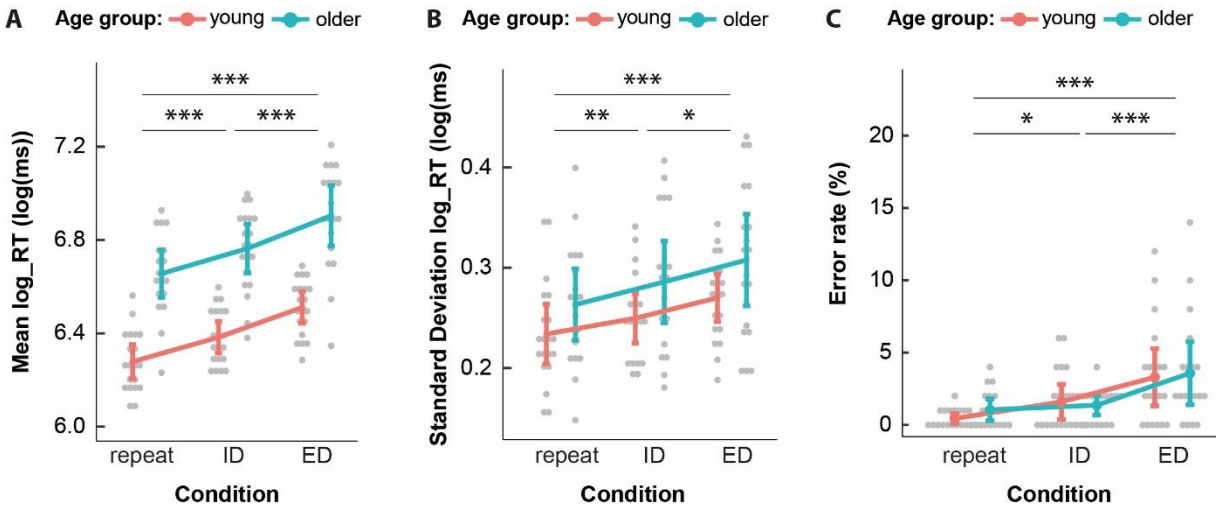

Figure 2: Behavioural results of the IDED task. A: Mean log transformed reaction times (log_RT) of each participant depending on condition. There is a significant difference in reaction time between all conditions in both age groups with ED trials reaching the longest log_RTs followed by ID and repeat (F (1.3, 47.94) = 163.57, p < .001, η_p^2= 0.82). Across conditions, older participants have longer log_RTs than younger participants (F (1, 37) = 62.00, p < .001, η_p^2= 0.63) (significance not depicted). **B:** Standard deviation of log_RTs grouped by age group and condition. There was a significant effect of condition (F (2, 74) = 11.49, p < .001, η_p^2= 0.237) and a significant effect of age group (F (1, 37) = 4.61, p = .038, η_p^2= 0.111) (significance not depicted). **C:** 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).

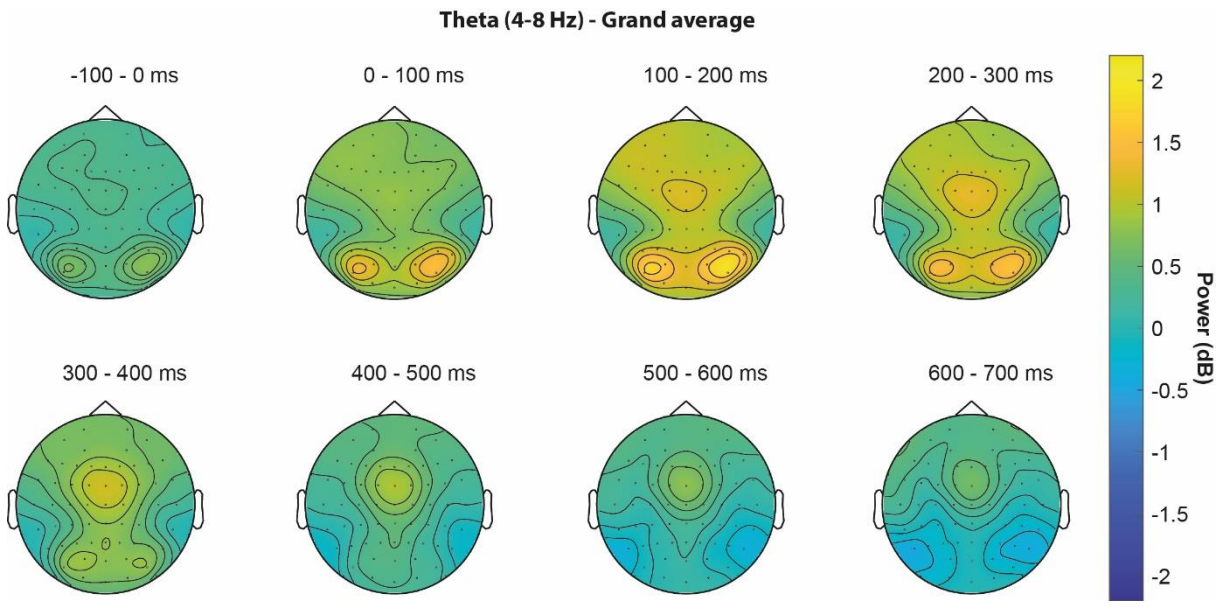

Figure 3: Mean theta power (dB) across all conditions and all participants. Occipital theta activations after stimulus presentation (0 to 200 ms) are followed by frontocentral theta activations in the time window between 200 to 500 ms after target presentation. Based on the topographical distribution and temporal progression of the grand average the average power of electrodes F1, F2, Fz, FC1, FC2 and FCz in the time window from 250 to 500 ms was used for further analysis.

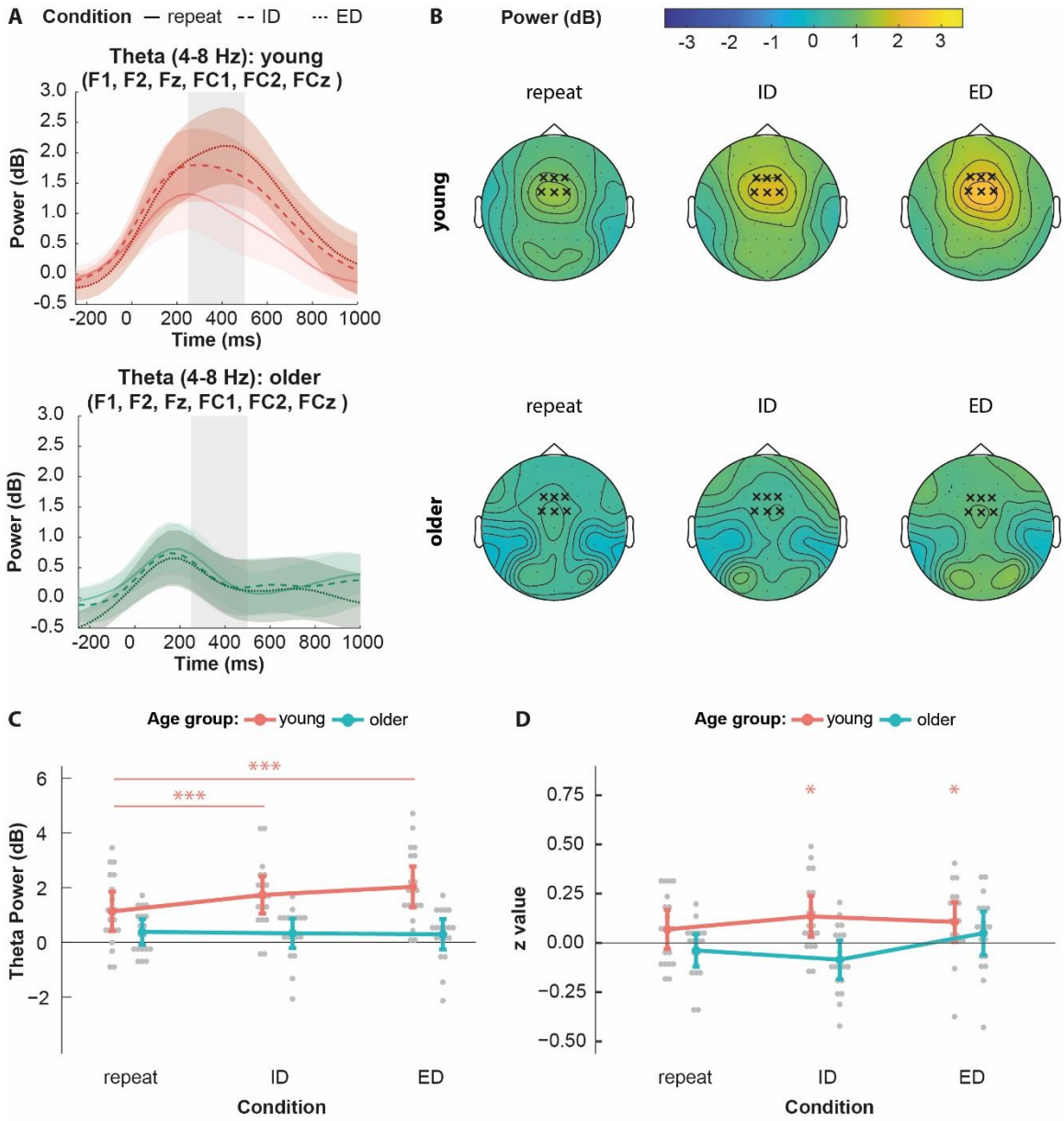

Figure 4: Condition-dependent modulation of midfrontal theta power within the two age groups. A: Average midfrontal theta power after target presentation in the young (top) and older (bottom) age groups, depending on condition. The grey shaded area indicates the time period used to calculate mean theta power (250 to 500 ms). The early peak theta activity in older individuals only appears to be earlier compared to young participants as the initial maximum that exists in both groups fails to grow to a later maximum in the older group.; **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. The frontocentral electrodes F1, F2, Fz, FC1, FC2 and FCz used for analysis are marked with X; **C:** Average theta power at the midfrontal electrodes for each individual, depending on condition. Here, only young individuals show a significant increase in theta power upon set-shifting 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).