

## Altered theta distribution and coherence during set-shifting in older age

Margarita Darna<sup>a,1,\*</sup>, Anni Richter<sup>a,b,c,1</sup>, Jens-Max Hopf<sup>a,h</sup>, Constanze I. Seidenbecher<sup>a,c,d</sup>, Björn H. Schott<sup>a,d,e,f,g</sup>

<sup>a</sup> Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

<sup>b</sup> German Center for Mental Health (DZPG), partner site Halle-Jena-Magdeburg, Germany

<sup>c</sup> Center for Intervention and Research on adaptive and maladaptive brain Circuits underlying mental health (C-I-R-C), Halle-Jena-Magdeburg, Germany

<sup>d</sup> Center for Behavioral Brain Sciences (CBBS), Magdeburg, Germany

<sup>e</sup> Department of Psychiatry and Psychotherapy, Medical Faculty, Otto-von-Guericke University Magdeburg, Germany

<sup>f</sup> German Center for Neurodegenerative Diseases (DZNE), Göttingen, Germany

<sup>g</sup> Department of Psychiatry and Psychotherapy, University Medical Center Göttingen, Göttingen, Germany

<sup>h</sup> University Clinic for Neurology, Otto-von-Guericke University Magdeburg, Germany

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### ABSTRACT

Cognitive flexibility is an executive function that enables adapting behaviour to a changing environment and is thus critical for daily life. The degree of its preservation upon healthy aging and the neural mechanisms underlying it are still a matter of debate. To investigate the electrophysiological correlates of cognitive flexibility in older age, we measured cognitive flexibility in 99 young (24.75 ± 4.45 years) and 83 older adults (69.19 ± 6.25) using electroencephalography (EEG). Compared to young adults, older adults showed a more conservative response pattern with longer reaction times, but lower error rates (speed-accuracy tradeoff). In the EEG, both age groups exhibited increased theta-power during set-shifting, with a fronto-central peak in the young, but a more fronto-lateral topography in older adults. Importantly, both groups displayed increases in theta coherence and global efficiency during set-shifting. Coherence modulations were restricted in frontocentral areas in the young but were diminished and distributed across the scalp in the older. Better set-shifting performance was most strongly associated with higher coherence in older adults and with global efficiency in both age groups. These results point to age-related differences in cortical processing underlying cognitive flexibility, which involve the employment of more distributed neural resources for successful task completion.

### 1. Introduction

Cognitive flexibility is an executive function that enables individuals to adapt their behaviour to a changing environment (Diamond, 2013). Its importance becomes evident in its associations with salutogenetic factors, such as trait resilience (Genet and Siemer, 2011), mindfulness (Moore and Malinowski, 2009) and social adjustment (Chen et al., 2024). In older age, in particular, cognitive flexibility has been linked to overall quality of life (Davis et al., 2010) and to planning and fluid intelligence in the presence of mild cognitive impairment (MCI) (Corbo et al., 2024). Despite its importance, age-related changes in cognitive flexibility at both the behavioural and the neural level are thus far insufficiently understood. The present study was conducted with the goal to evaluate age-related changes of set-shifting performance and

their association with electrophysiological measures of brain activity.

In laboratory settings, cognitive flexibility is often operationalized as task-switching and set-shifting performance using paradigms that require participants to shift their attention between different tasks, rules or dimensions. Performance is then assessed by comparing trials with and without shifts. Shift trials can include intra-dimensional (ID) or extra-dimensional (ED) shifts (Watson et al., 2006). In ID shifts, the new correct feature belongs to the previously correct dimension, whereas in ED shifts, the correct feature belongs to a different dimension. Deficits in cognitive flexibility usually appear as switch costs, most notably increased reaction times or error rates compared to trials without shifts (Wylie and Allport, 2000), and with perseverative errors, that is, when a previously correct response pattern is kept on being employed after the shift required a change (Heaton et al., 1993).

\* Corresponding author.

E-mail address: [margarita.darna@med.ovgu.de](mailto:margarita.darna@med.ovgu.de) (M. Darna).

<sup>1</sup> Present Address: Institute of Medical Psychology, Medical Faculty, Otto-von-Guericke University Magdeburg, Germany

Studies on behavioural manifestations of age-related changes in cognitive flexibility have thus far yielded inconsistent results. While several studies report deficits reflected by increased switch costs (Cepeda et al., 2001; Kray et al., 2002; Meiran et al., 2001) and more perseverative errors (Haaland et al., 1987; Zelazo et al., 2004), others describe an unaltered (Falkenstein et al., 2001; Karayanidis et al., 2011; Kolev et al., 2005; Kray and Lindenberger, 2000) or even improved performance compared to younger adults (Kray, 2006). Only few studies in older age have assessed the impact of different set-shifting demands, most notably ID versus ED shifts, with the latter engaging more neural resources (Watson et al., 2006). Again, some studies reported older adults to show increased difficulties during ED shifts (De Luca et al., 2003; Owen et al., 1991; Zelazo et al., 2004) but in our previous study (Darna et al., 2025), we found no evidence of higher ED switch costs in older adults.

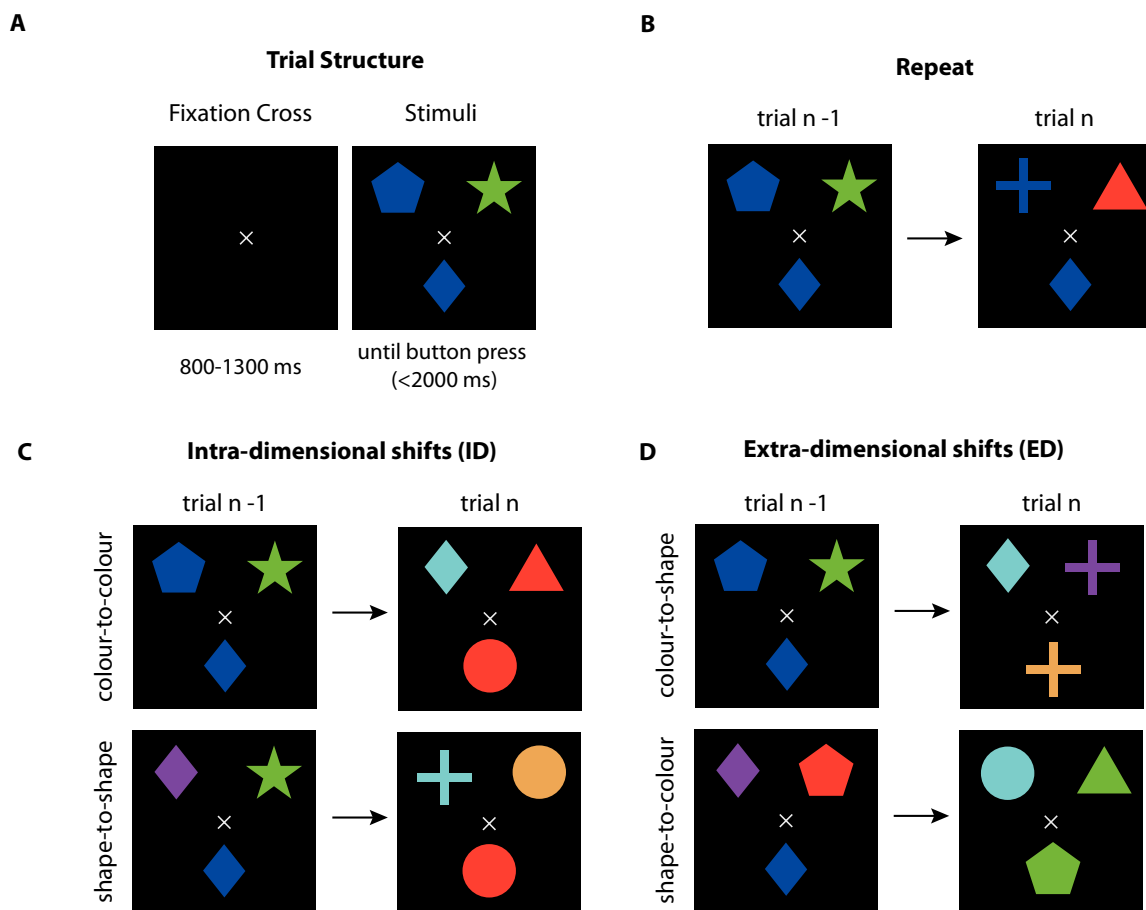
At the neural level, studies on error processing (Kolev et al., 2024) and motor coordination (Yordanova et al., 2020) point to a functional reorganization of frontal networks in older age. In the context of cognitive flexibility, evidence for such reorganization has been found, in the form of an age-related topographical shift of theta (4–8 Hz) amplitude modulations from parietal to fronto-temporal sensors (Huizeling et al., 2021). Other studies have reported attenuated frontal theta amplitude modulations in older adults during reversal learning (Küçük et al., 2023a) and during both ID and ED shifts (Darna et al., 2025).

At the network level, lower theta coherence across brain regions has

been observed in older adults during task-switching (Dias et al., 2015). Finally, increased global efficiency a network-based measure reflecting the efficiency of information transmission across a network (Latora and Marchiori, 2001) has been linked to higher cognitive demands (e.g. Cohen and D'Esposito, 2016) and is hypothesized to act as a mediator for executive functions in older age (Li et al., 2020), despite its age-related decrease (Ajilore et al., 2014; Li et al., 2020).

Taken together, these theta-band neural signatures refer to potential mechanisms underlying set-shifting performance in older age. To investigate their role, we applied the ID/ED set-shifting task (IDED, Figure 1; Darna et al., 2025; Oh et al., 2014) and recorded electroencephalographic brain activity (EEG). We chose the IDED, as it enabled us to isolate the different types of shifts (i.e., ID and ED), an aspect that is usually absent in other studies of cognitive flexibility.

We hypothesized that ED shifts would elicit higher theta power, coherence and global efficiency compared to ID shifts in both age groups. With respect to aging, we hypothesized that older participants would exhibit a) lower theta power and reduced theta power modulation in both ID and ED set-shifts, b) overall lower theta coherence between channel pairs c) lower global efficiency and reduced modulation of global efficiency. We also investigated the relationship between performance measures and theta measures using a linear mixed effect model approach and particularly explored age-related changes.



**Fig. 1. The IDED task (adapted from Darna et al., 2025).** **A:** Trial structure. After the presentation of the fixation cross for a pseudorandomized interval between 800 ms and 1300 ms, the stimuli (top) and target (bottom) appear. These are visible until a button press occurs or until 2000 ms have elapsed; **B:** Example of a repeat trial. Here, the target (here blue diamond) and the matching rule (match blue colour) remain the same from trial to trial; **C:** Example of intra-dimensional shifts (ID). Here, the matching rule changes from colour to colour (top row, e.g. blue-to-red) or from shape to shape (bottom row, e.g. diamond-to-circle); **D:** Example of extra-dimensional shifts (ED). Here, the matching rule changes from colour to shape (top row, e.g. blue-to-cross) or from shape to colour (bottom row, e.g. diamond-to-green).

## 2. Materials and methods

### 2.1. Participants

Participants were recruited via advertisements, and through the local university and institutional participant pools. Recruited participants were between the age of 18–35 to be included in the young age group and at least 60 years old to be recruited in the older age group. The Mini-International Neuropsychiatric Interview (M.I.N.I.; Sheehan et al., 1998; German Version by Ackenheil et al., 1999) and a standardized health questionnaire (Richter et al., 2011) were administered to exclude past or present manifest neurological or psychiatric disorders, substance abuse, use of neurological or psychiatric medication or serious medical conditions (e.g., heart failure NYHA stage III or IV, metastatic cancer, or diabetes mellitus with complications). Additionally, only right-handed individuals with fluent German language skills participated. The study was approved by the Ethics Committee of the Faculty of Medicine at the Otto von Guericke University of Magdeburg. All individuals gave written informed consent in accordance with the Declaration of Helsinki (World Medical Association Declaration of Helsinki: Ethical Principles for Medical Research Involving Human Subjects, 2013) and participation was compensated financially or with course credit, depending on participants' preference (Table 1).

Additional questionnaires to evaluate cognitive status were the German version of the crystallized intelligence test "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).

In total, 188 participants completed the study, out of which three older adults were excluded due to the self-reported inability to understand the task and three additional participants (2 young, 1 older) were excluded as they were identified as extreme outliers in the IDED task, as indicated by mean reaction time or error rates (criterion: 3rd quantile + 3\*interquartile range) (see Table S2). The final sample comprised 182 participants, including 99 young (age: 24.76 ± 4.44 years) and 83 older (age: 67.53 ± 12.36 years). Participant groups did not differ with respect to sex distribution and education years and old participants displayed a significantly higher MWT-B score as seen in our previous study (Darna et al., 2025).

A subset of the participants took part in an extended neuropsychological testing battery to investigate further psychological constructs such as attention, short- and long-term memory, working memory and executive functions (as described in Richter et al., 2023; for results see Table S1 in supplementary material). One task of interest for this study is the flexibility subtest of the Test Battery for Attention (TAP; Zimmermann and Fimm, 1992). In short, participants in this task were shown a letter and a number and they had to press the left or right arrow button according to the position of the target stimulus. The target stimulus was,

**Table 1**  
Participant summary statistics.

	Young M ± SD [N]	Older M ± SD [N]	Statistics
N	99	83	
Age	24.76 ± 4.44 [99]	67.53 ± 12.36 [83]	<b>W = 8217, p &lt; 0.001</b>
Sex	35 M, 64 F	39 M, 44 F	$X^2 = 2.07, p = 0.150$
Education (years)	15.82 ± 2.81 [97]	15.30 ± 2.23 [81]	<b>W = 3576, p = 0.301</b>
MWT-B	26.01 ± 3.69 [98]	31.68 ± 2.69 [82]	<b>W = 7165, p &lt; 0.001</b>
MMSE	-	28.51 ± 1.12 [83]	-

M: mean; SD: standard deviation; N: sample size; F: female; M: male; t: Welch two-sample t-test;  $X^2$ : Pearson's Chi-squared test; W: Wilcoxon rank sum test; MWT-B: Mehrfachwahl-Wortschatz-Intelligenztest B; MMSE: Mini Mental State Examination.

however, alternating from trial to trial between the two modalities (e.g. letter – number – letter – number – etc.). All participants also completed the attentional set-shifting task (ASST; Sahakian and Owen, 1992). Briefly, the ASST involved stages of increasing set-shifting demands, in which the correct stimulus had to be discerned through trial-and-error. Importantly, this task included three set-shifting trial types: reversal, ID and ED (for more information see Darna et al., 2025). The results of these two set-shifting tasks are presented in Table 2 and supplementary Figure 1.

### 2.2. Cognitive flexibility task

All participants completed the IDED, which has previously been described in detail (Darna et al., 2025; Oh et al., 2014) and is only briefly presented here (including some minor modifications from the previous version; Figure 1). The paradigm was executed using the Psychtoolbox (Brainard and Vision, 1997; Pelli, 1997) running on MATLAB R2021b (The MathWorks Inc., 2021, Natick, MA). Each trial began with a fixation cross presented for 800–1300 ms (jitter generated with uniformly distributed pseudorandom numbers in MATLAB), followed by the presentation of the target below the fixation cross and the stimuli above. Participants were asked to indicate which stimulus matched the target via a mouse click (left or right click for the left or right stimulus respectively). The matching features could be the colour or the shape of the target. After the button press or a maximum response time of 2000 ms, the stimuli disappeared and a new trial began. Participants received no feedback on the correctness of their response.

The task consisted of 100 ID and 100 ED trials each, in which the matching criterion was changed within a dimension or across dimensions respectively. After each shift trial, randomly 2–7 trials with no set-shift followed, in which the target and matching criterion remained the same (hence termed repeat trials). We only evaluated the second repeat trials after each set-shift resulting in 200 repeat trials (as done in:

**Table 2**  
Behavioural flexibility tasks – summary results in young and old.

	Young M ± SD	Older M ± SD	Statistics
<b>Flexibility subtest from TAP</b>			
N	53	63	
Error rate (%)	3.97 ± 4.13	11.06 ± 13.78	<b>W = 2220.5, p = 0.002</b>
RT (ms)	1071.42 ± 199.98	1918.74 ± 590.94	<b>W = 3208, p &lt; 0.001</b>
<b>ASST</b>			
N	100	80	
Overall survival probability [N-failed]	80.00 % [20]	43.80 % [45]	<b>X<sup>2</sup> = 26.40, p &lt; 0.001</b>
<b>First Reversal Stage (CDR)</b>			
N	99	77	
RT (ms)	886.73 ± 395.32	1108.83 ± 406.49	<b>W = 5327, p &lt; 0.001</b>
Trials-to-criterion	10.91 ± 3.55	13.62 ± 8.89	<b>W = 4542, p = 0.023</b>
<b>First ID Stage (IDS1)</b>			
N	99	76	
RT (ms)	895.24 ± 390.02	1152.50 ± 355.68	<b>W = 5617, p &lt; 0.001</b>
Trials-to-criterion	9.23 ± 2.27	10.55 ± 5.47	<b>W = 4279, p = 0.095</b>
<b>ED stage (ED)</b>			
N	80	45	
RT (ms)	1033.84 ± 327.83	1391.79 ± 385.72	<b>W = 2146, p &lt; 0.001</b>
Trials-to-criterion	17.55 ± 8.14	25.29 ± 11.21	<b>W = 2020, p &lt; 0.001</b>

M: mean; SD: standard deviation; TAP: Test Battery for Attention; ASST: attentional set-shifting task; N: sample size;  $X^2$ : Kaplan–Meier survival comparison using the log-rank test; W: Wilcoxon rank sum test; CDR: Compound Discrimination Reversal; IDS1: Intra-dimensional shift 1.

Darna et al., 2025).

Participants were explicitly instructed to respond as fast as possible, and a practice run of 20 trials was performed before the experiment, during which participants received feedback on the correctness of their responses. Here, we also ensured that the participants could differentiate the colours of the stimuli.

The session consisted of 6 blocks with self-paced breaks in between and lasted approximately 50–60 min. The practice trials and repeat trials before the first shift after a break were excluded from analysis. The recording took place in a dimmed, electrically shielded room. Participants were sitting at a distance of 110 cm away from the 32" presentation monitor with a resolution of 1920x1280 pixels and a refresh rate of 120 Hz. Mouse button responses were performed with the right hand.

### 2.3. Statistical analysis of behavioural measures

We evaluated performance in the IDED in RStudio R 4.5.1 (R Core Team, 2022; R Studio Team, 2020) using three distinct measures:

- (1) Reaction time (RT) was defined as the time taken to correctly respond after stimulus presentation. For RT analysis we excluded short RTs due to anticipatory responses (< 150 ms) and evaluated the median RT for each condition as RTs displayed a right-skewed distribution (mean skewness for all trials:  $0.91 \pm 0.26$ ).
- (2) Interquartile range of RTs (IQR) was evaluated to represent intertrial variability in performance.
- (3) Error rates were computed as the percentage of trials with incorrect, early (<150 ms) or no responses in each condition.

To evaluate switch costs in set-shifting performance we calculated them as the difference between ID and repeat and ED and repeat for RTs, IQRs and error rates as follows:

$$cost_{ID} = ID - repeat$$

$$cost_{ED} = ED - repeat$$

This resulted in two switch cost estimates per behavioural measure used as dependent variables for six separate robust analyses of variance (ANOVA) with the package WRS2 (Mair and Wilcox, 2014) with the factors age group (young vs. older; between group) and condition (ID vs ED; within group). Here, the highest and lowest 20% of the scores was trimmed using Wilcox's trimming procedure. Whenever an interaction effect was significant post-hoc *t*-tests on the trimmed means were conducted and a robust Cohen's *d* on 20% trimmed means was calculated as effect size.

To evaluate global switch costs, we calculated a composite performance *z*-score as the negative sum of the standardized switch scores for each performance measure according to:

$$z_{perf} = -(z_{error} + z_{RT} + z_{IQR})$$

$$with z_v = \frac{cost - \mu_{cost}}{\sigma_{cost}}$$

where *cost* represents the individual switch cost of an individual performance measure (Darna et al., 2025; Dias et al., 2015; Liesefeld and Janczyk, 2019) and  $\mu$  and  $\sigma$  represent the average and standard deviation, respectively, collapsed across conditions and age groups. Here, the negative sum was chosen, so that high *z*-scores indicate lower global switch costs, in other words, a better performance in the respective condition. Importantly,  $\mu$  and  $\sigma$  were calculated separately for each age group and then averaged to account for the different sample sizes of the two age groups. Here, we again performed a robust ANOVA and post-hoc *t*-tests as described above to evaluate the effect of age group and condition on the *z*-score.

### 2.4. EEG acquisition and pre-processing

We recorded the EEG at 1000 Hz sampling rate using 64 active electrodes (Brain Products GmbH, Gilching, Germany) of the actiCAP layout (EASYCAP) and an additional ground electrode at AFz. Online reference was the FCz. Four EOG electrodes were recorded for detection of (micro)saccades and blinks. These were: a horizontal EOG of the left eye (HEOGL), horizontal EOG of the right eye (HEOGR), superior vertical EOG of the left eye (VEOGS) and inferior vertical EOG of the left eye (VEOGI). The EEG was recorded with BrainRecorder from Brain Products and port event signalling was conducted the Mex-File Plug-in IO74 (<https://apps.usd.edu/coglab/psyc770/IO64.html>). Electrode impedances were kept below 10k $\Omega$  with electrolyte gel.

The first pre-processing steps were conducted using Brain Vision Analyzer 2.2 (Brain Products GmbH, Gilching, Germany). First, data were re-referenced to the average of all EEG channels and the old online reference was reused as a channel (FCz). Next, new EOG channels were calculated as followed: horizontal EOG: HEOG = HEOGR – HEOGL, vertical EOG: VEOG = VEOGI – VEOGS and radial EOG: REOG = ((HEOGR + HEOGL + VEOGI + VEOGS)/4) – Pz. The data were then filtered with a zero-phase shift Butterworth low-pass filter at 250 Hz with the order of 2. Artifacts were marked using a semi-automatic raw data inspection with a maximum allowed voltage step of 70  $\mu$ V/ms (Gradient; marked 400 ms before and after the event) and lowest allowed activity in intervals of 0.5  $\mu$ V for 100 ms (Low Activity; marked 200 ms before and after the event). Here, channels with more than 20% marked datapoints were visually inspected by a trained observer (author MD) for future channel interpolation. Next, eye blinks were detected via automatic raw data inspection on the VEOG channel. Here, all intervals were marked where the allowed difference of values in an interval length of 200 ms exceeded a value of 100  $\mu$ V (Max-Min; marked 100 ms before and after the event). The continuous data sets were then exported for further processing in MATLAB.

Within the MATLAB environment (R2024b), we used EEGLAB to import the data (Delorme and Makeig, 2004; Version 2024.0). Bad segments that were marked before, were now removed from the data and blinks were added as events in the structure. The EOG channels of individual participants (*n* = 8) with line noise in EOG were filtered with a Butterworth 2nd order notch filter from 48 to 52 Hz. Then, we extracted stimulus-locked trial epochs from –1500–3000 ms for the trials of interest (repeat, ID and ED) that were followed by a correct response. Here, incorrect responses also included trials without responses and trials with premature responses (< 150 ms), representing anticipatory responses. Participants with fewer than 30% trials remaining within each condition were excluded from analysis (*n* young = 7; *n* older = 24), resulting in 92 young and 59 older participants included (76.12 %  $\pm$  18.16 % trials remaining). Importantly, the performance of the excluded participants across all behavioural measures did not significantly differ from the final included sample (Wilcoxon rank sum tests, all *p*  $\geq$  0.112). The epochs were baseline corrected with the average obtained from the time window between –250–0 ms. Saccades, microsaccades and muscle artifacts were detected and corrected with the EEGLAB plug-in microDetect (Craddock et al., 2016) and an Independent Component Analysis (ICA; FASTICA; <http://research.ics.aalto.fi/ica/fastica/>; for details see [supplementary material](#)).

After ICA, individual noisy channels of the previously inspected datasets (10 participants; see [table S3](#)) were interpolated in EEGLAB with spherical spline interpolation ( $\lambda = 0$ , *m* = 4, *n* = 7).

The datasets obtained from this step were processed separately in each one of the following three sections.

### 2.5. Theta power analysis

For time-frequency analysis, data were first converted to Fieldtrip format using the “eeglab2fieldtrip” function in MATLAB. In Fieldtrip (Oostenveld et al., 2011; Version 20220104), frequency power from 1 to

100 Hz was calculated using Morlet wavelets with a width of 7 cycles and length equal to 3 standard deviations of the implicit Gaussian kernel, using a sliding time window in steps of 10 ms. Oscillation power was then baseline-corrected and normalized to dB (baseline range: –300 to –100 ms before stimulus presentation) as follows:

$$power_{dB} = 10 * \log_{10} \left( \frac{activity}{baseline} \right)$$

We then extracted the mean normalized power of the theta frequency band (4–8 Hz) across all channels in the time window between –300 ms and 1000 ms for each participant and condition and conducted a factor analysis (FA) in the temporal domain on the individual age groups. FA was performed as described by Scharf et al. (2022). Briefly, the Empirical Kaiser Criterion was employed to determine the number of factors to retain (eigenvalue > 1) and the unrotated factor loadings of the exploratory factor analysis were first estimated using custom R code (Braeken and Van Assen, 2017). Next, the Geomin rotation (Yates, 1987) was applied, an oblique rotation technique that minimizes the complexity of the loading matrix at the cost of allowing some degree of correlation between factors. The factor-specific explained variance was calculated by dividing the diagonal elements of  $\Phi L^T L$  (where  $L$  denotes the unstandardized rotated loadings and  $\Phi$  the factor correlation matrix) by the total observed variance. The resulting components were then evaluated based on their maximum peak latencies and overall topography. One component was chosen for further analysis, as it explained the highest proportion of variance, displayed the highest unstandardized loadings, and its peak was around the post-stimulus time-range of interest based on our previous study (Darna et al., 2025) at 420 ms in the young group and 490 ms in the older age group. To estimate factor scores, we extracted factor-wise reconstructed theta power time series across all electrodes. The peak-latency amplitudes of the respective reconstructed data were used in the statistical analyses.

## 2.6. Coherence and global efficiency

To circumvent the common reference problem (Bastos and Schoffelen, 2016), we computed Current Source Density estimations (CSD) from the raw EEG data using the CSD Toolbox (Kayser and Tenke, 2006; <https://psychophysiology.cpmc.columbia.edu/software/csdttoolbox/>). Coherence was calculated using a bootstrap procedure with 100 runs to account for the sample size bias resulting from different numbers of trials across conditions (Bastos and Schoffelen, 2016). In each bootstrap run, we randomly sampled 30 trials from each condition and calculated coherence values as follows. Spectral decomposition was performed using Morlet wavelets as described above, with the frequencies of interest now ranging from 1 to 10 Hz. We used the resulting Fourier spectra in the subsequent connectivity estimation with Fieldtrip's *ft\_connectivityanalysis*. Here, we computed the imaginary coherence between all pairs of channels over the time window from –300–1000 ms. The raw coherence values of the theta frequency band (4–8 Hz) across all electrode pairs ( $n_{pair} = 2080$ ) was input in a factor analysis to identify components of interest as described in the section above. The Geomin rotation of the obtained components with all conditions did not converge, we thus calculated the factor analysis with the relative change from repeat for ID and ED:  $ID_{rel} = \frac{(ID-repeat)}{repeat}$  and  $ED_{rel} = \frac{(ED-repeat)}{repeat}$ . Here, we identified two components of interest as they displayed a peak latency around the same time window as the component obtained from theta power. The peak-latency amplitudes of the respective reconstructed components were used in the statistical analyses.

Additionally, we extracted the global efficiency of the theta frequency band (4–8 Hz) for each participant and condition as a network-based measure reflecting the efficiency of information transmission across the entire network (Latora and Marchiori, 2001) using the Brain Connectivity Toolbox (Rubinov and Sporns, 2010). Global efficiency

was estimated within two time-windows reflecting the average peak latency of the components obtained from the previous sections (mean  $\pm$  50 ms):

- early global efficiency was estimated as the mean within the time window of 425–525 ms and
- late global efficiency was measured between 595 and 695 ms.

## 2.7. Linear mixed effects model

To evaluate whether the theta measures could predict behaviour in the IDEED we first standardized the theta measures by subtracting the mean and dividing by the standard deviation across all participants (measures were balanced across groups as done in 2.3). We then fitted a linear mixed-effects model on the data with z-score as dependent variables and the amplitude of the theta component (theta\_Early), early coherence (coh\_Early), early global efficiency (gl\_Early), late global efficiency (gl\_Late) as independent variables. Late coherence was not included as a parameter as it displayed no significant modulation during set-shifting (see results 3.3). The model also included the interaction of these variables with age group and condition and a random intercept for each participant to account for repeated measures as such:

$$z \sim (\text{theta}_{\text{Early}} + \text{coh}_{\text{Early}} + \text{gl}_{\text{Early}} + \text{gl}_{\text{Late}}) * \text{age group} + \text{condition} + (1|\text{subj})$$

where 'subj' refers to the individual participant pseudonym.

To identify the best fitting model, we performed an all-subsets model selection using the 'dredge()' function from the MuMIn package in R and ranked models by their Akaike Information Criterion (AIC). The three best-fitting models were extracted and are being described in the results.

## 2.8. Statistics

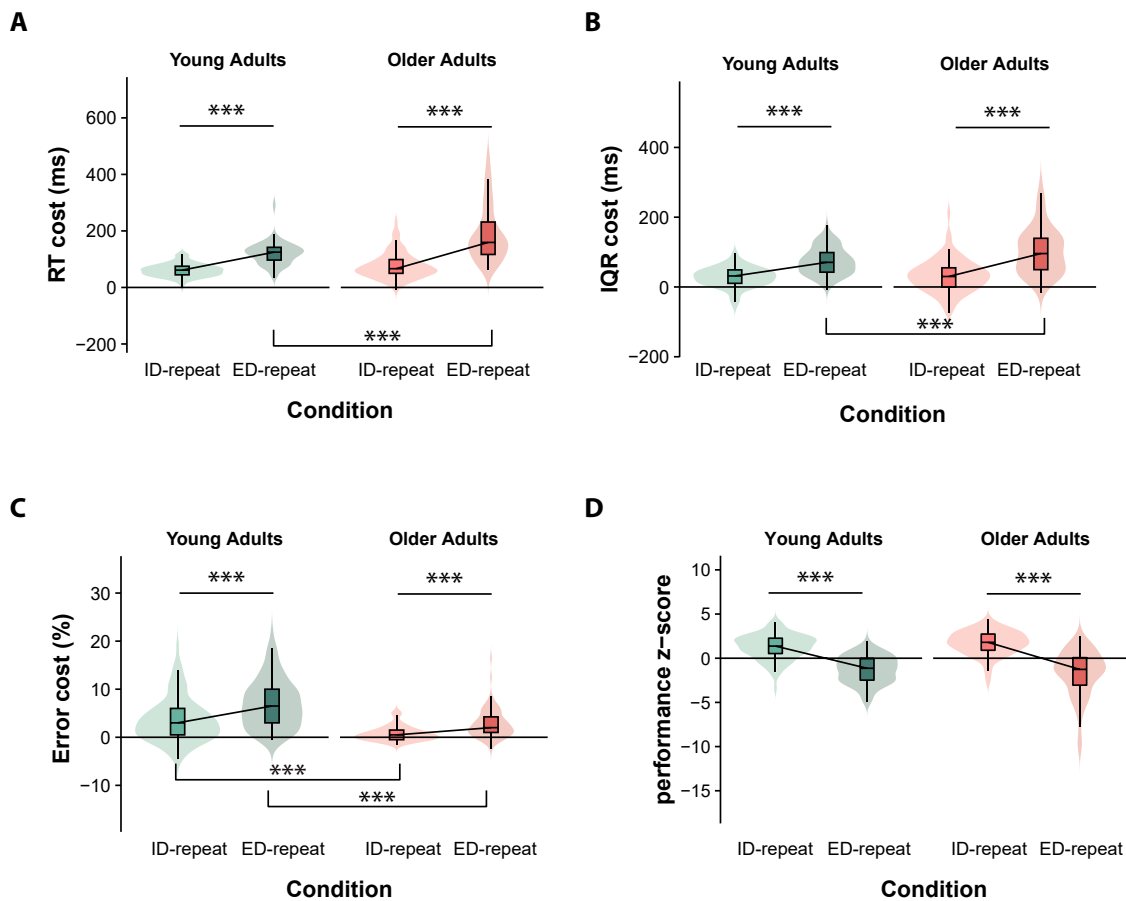
For all statistical tests reported, the alpha significance level was set to  $p = 0.05$ . Robust ANOVA results are reported with the obtained  $F$  value,  $p$  value and partial eta squared ( $\eta_p^2$ ) as measure of effect size. Robust  $t$ -tests on 20% trimmed means are reported with the obtained  $t$  value and Cohen's  $d$  as effect size. Statistical significance is reported in the graphs as follows: \* for  $p \leq 0.05$ , \*\* for  $p \leq 0.005$  and \*\*\* for  $p \leq 0.001$ . All average values are reported as mean  $\pm$  standard deviation.

## 3. Results

### 3.1. Behavioural results of the IDEED task

Overall, the average median RT was 533 ms  $\pm$  133 ms (mean  $\pm$  standard deviation), with older participants reacting more slowly than the young (young: 469 ms  $\pm$  42 ms; older: 706 ms  $\pm$  109 ms;  $t_{102} = -18.77$ ,  $p < 0.001$ ,  $d = -2.88$ ). A robust ANOVA of the switch costs (difference in RT between ID or ED from repeat) revealed a significant interaction between age group (young, old) and condition (ID, ED) ( $F_{1, 78.05} = 18.26$ ,  $p < 0.001$ ). Both age groups showed increased RT switch costs in ED compared to ID trials (young, ED-ID:  $t_{60} = 18.23$ ,  $p < 0.001$ ,  $d = 0.89$ ; older, ED-ID:  $t_{50} = 11.74$ ,  $p < 0.001$ ,  $d = 0.90$ ), but older participants showed significantly higher RT switch costs than the young in the ED condition (ID, old-young:  $t_{76.63} = 1.89$ ,  $p = 0.062$ ,  $d = 0.23$ ; ED, old-young:  $t_{64.03} = 4.18$ ,  $p < 0.001$ ,  $d = 0.67$ ; Figure 2A). A main effect of condition was also found ( $F_{1, 78.05} = 309.43$ ,  $p < 0.001$ ), where switch costs were significantly higher in the ED condition compared to the ID (ED-ID:  $t_{109} = 25.44$ ,  $p < 0.001$ ,  $d = 0.85$ ). Finally, there was also a significant main effect of age group ( $F_{1, 79.13} = 14.18$ ,  $p < 0.001$ ), with older adults displaying higher RT switch costs compared to young (old-young:  $t_{158.76} = 3.58$ ,  $p < 0.001$ ,  $d = 0.31$ ).

Overall, participants showed an IQR of RTs of 197 ms  $\pm$  61 ms, with younger participants exhibiting lower mean IQRs compared to older



**Fig. 2. Behaviour in set-shifting.** **A:** Mean reaction time (RT) costs relative to repeat. Costs are increased in the ED condition (young:  $t_{60} = 18.23$ ,  $p < 0.001$ ,  $d = 0.89$ ; older:  $t_{50} = 11.74$ ,  $p < 0.001$ ,  $d = 0.90$ ), with higher RT costs in older compared to young adults (ED:  $t_{64.03} = 4.18$ ,  $p < 0.001$ ,  $d = 0.67$ ); **B:** Mean cost of interquartile range (IQR) of RTs in the shift relative to the repeat condition, showing effects of ED vs. ID (young:  $t_{60} = 9.06$ ,  $p < 0.001$ ,  $d = 0.75$ ; older:  $t_{50} = 8.61$ ,  $p < 0.001$ ,  $d = 0.68$ ) and the higher ED costs in older vs. young adults ( $t_{81.67} = 2.76$ ,  $p = 0.007$ ,  $d = 0.31$ ); **C:** Mean error cost compared to the repeat condition, showing increased error costs in ED (young:  $t_{60} = -7.72$ ,  $p < 0.001$ ,  $d = -0.48$ ; older:  $t_{50} = -6.00$ ,  $p < 0.001$ ,  $d = -0.63$ ). Here, older adults had lower error costs than young adults (ID:  $t_{74.15} = -5.50$ ,  $p < 0.001$ ,  $d = -0.59$ ; ED:  $t_{98.03} = -6.44$ ,  $p < 0.001$ ,  $d = -0.63$ ); **D:** Global performance as indicated by composite z-scores of all behavioural measures. Both age groups display lower z-scores in ED compared to ID trials (young:  $t_{60} = -14.86$ ,  $p < 0.001$ ,  $d = 0.85$ ; older:  $t_{50} = -13.27$ ,  $p < 0.001$ ,  $d = -0.94$ ), with no significant z-score difference between the two age groups ( $F_{1, 111} = 0.49$ ,  $p = 0.486$ ).

participants (young:  $156 \text{ ms} \pm 29 \text{ ms}$ ; older:  $245 \text{ ms} \pm 54 \text{ ms}$ ;  $t_{121} = -13.54$ ,  $p < 0.001$ ,  $d = -2.06$ ). A significant interaction between condition and age group was present again ( $F_{1, 98.03} = 7.51$ ,  $p = 0.007$ ). IQR costs in the ID condition did not differentiate between young and older participants (old-young:  $t_{82.41} = 0.16$ ,  $p = 0.973$ ,  $d = 0.02$ ) but older participants exhibited higher IQR costs in the ED condition compared to the young (old-young:  $t_{81.67} = 2.76$ ,  $p = 0.007$ ,  $d = 0.31$ ). Both age groups showed an increase of IQR switch costs from the ID to the ED condition (young, ED-ID:  $t_{60} = 9.06$ ,  $p < 0.001$ ,  $d = 0.75$ ; older, ED-ID:  $t_{50} = 8.61$ ,  $p < 0.001$ ,  $d = 0.68$ ; Figure 2B). The robust ANOVA here again revealed a significant main effect of condition ( $F_{1, 79.13} = 14.18$ ,  $p < 0.001$ ), where the ED condition displayed higher switch costs compared to the ID (ED-ID:  $t_{109} = 11.61$ ,  $p < 0.001$ ,  $d = 0.76$ ). Additionally, a significant main effect of age group was found ( $F_{1, 95.77} = 4.54$ ,  $p = 0.036$ ). Here, older adults displayed a trend for marginally higher IQR switch costs compared to the younger adults (old-young:  $t_{150.43} = 1.83$ ,  $p = 0.069$ ,  $d = 0.17$ ).

On average, participants had very low error rates of  $4.54\% \pm 3.65\%$ , with error rates being lower in older compared to young participants (young:  $6.28\% \pm 3.88\%$ ; older:  $2.46\% \pm 1.84\%$ ;  $t_{145} = -8.70$ ,  $p < 0.001$ ,  $d = -1.26$ ). The robust ANOVA revealed a significant interaction ( $F_{1, 105.16} = 9.30$ ,  $p = 0.003$ ), with older participants displaying lower error switch costs in both set-shifting conditions compared to the young (ID:  $t_{74.15} = 5.50$ ,  $p < 0.001$ ,  $d = 0.59$ ; ED:  $t_{98.03} = 6.44$ ,

$p < 0.001$ ,  $d = 0.63$ ). Additionally, young participants showed a smaller effect size regarding switch cost differences between ID and ED ( $t_{60} = -7.72$ ,  $p < 0.001$ ,  $d = -0.48$ ) compared to older participants ( $t_{50} = -6.00$ ,  $p < 0.001$ ,  $d = -0.63$ ; Figure 2C). A significant main effect of condition was also revealed ( $F_{1, 105.16} = 95.07$ ,  $p < 0.001$ ), where significant higher switch costs were found in the ED condition compared to the ID (ED-ID:  $t_{109} = 8.67$ ,  $p < 0.001$ ,  $d = 0.50$ ). Additionally, we found a significant main effect of age group ( $F_{1, 87.42} = 48.18$ ,  $p < 0.001$ ), with older adults displaying lower error switch costs compared to young (old-young:  $t_{161.41} = -3.35$ ,  $p < 0.001$ ,  $d = -0.61$ ).

Finally, we created a composite z-score reflecting global switch costs in the IDED, that was based on all aforementioned behavioural measures (see Methods 2.3). A robust ANOVA revealed no significant interaction effect between condition and age group ( $F_{1, 111} = 3.08$ ,  $p = 0.082$ ) but a significant condition effect ( $F_{1, 111} = 380.76$ ,  $p < 0.001$ ). Here, both age groups showed a decrease in z-values from the ID to the ED condition (young, ED-ID:  $t_{60} = -14.85$ ,  $p < 0.001$ ,  $d = -0.85$ ; older, ED-ID:  $t_{50} = -13.27$ ,  $p < 0.001$ ,  $d = -0.94$ ), showing increased global switch costs (worse global performance) in the ED condition compared to ID. No significant between group effect was found ( $F_{1, 110.93} = 0.49$ ,  $p = 0.486$ ; Figure 2D).

### 3.2. Theta band power

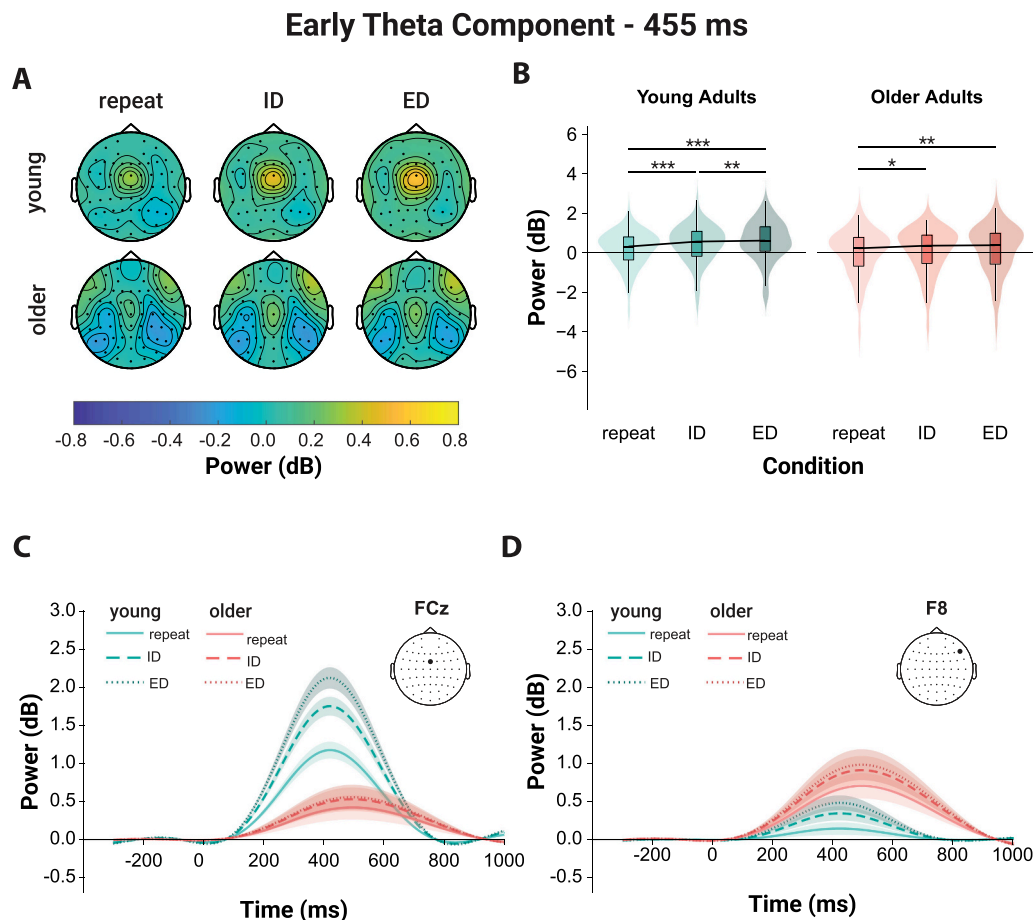
Separate temporal FAs on the two age groups revealed one component of interest. The theta component in the young group peaked over FCz around 420 ms post stimulus and explained 36.46% of the variance, whereas that of the older group reached a maximum over the F8 channel around 490 ms and explained 46.53% of the variance (Figure 3). A robust mixed ANOVA with the factors condition (repeat, ID, ED) and age group (young, old) revealed a significant two-way interaction ( $F_{2, 93.40} = 4.23, p = 0.017, \eta_p^2 = 0.06$ ). Here, the young age group displayed increased component power between all conditions (ID-repeat,  $t_{55} = 6.26, p < 0.001, d = 0.20$ ; ED-repeat,  $t_{55} = 8.52, p < 0.001, d = 0.29$ ; ED-ID,  $t_{55} = 2.83, p = 0.007, d = 0.09$ ), whereas the old age group showed increased component power in ID compared to repeat (ID-repeat:  $t_{36} = 2.23, p = 0.031, d = 0.07$ ) and in ED compared to repeat (ED-repeat:  $t_{36} = 3.32, p = 0.002, d = 0.11$ ) but not in ID compared to ED trials ( $p = 0.256$ ). Additionally, older adults exhibited no significant theta power differences compared to the young adults in none of the conditions ( $p \geq 0.108$ ; Figure 3B).

### 3.3. Theta coherence

Theta coherence across time was decomposed into factors with the condition contrasts ID-repeat and ED-repeat (see Methods 2.6). Here, we identified two components of interest with latency peaks within the time window of interest.

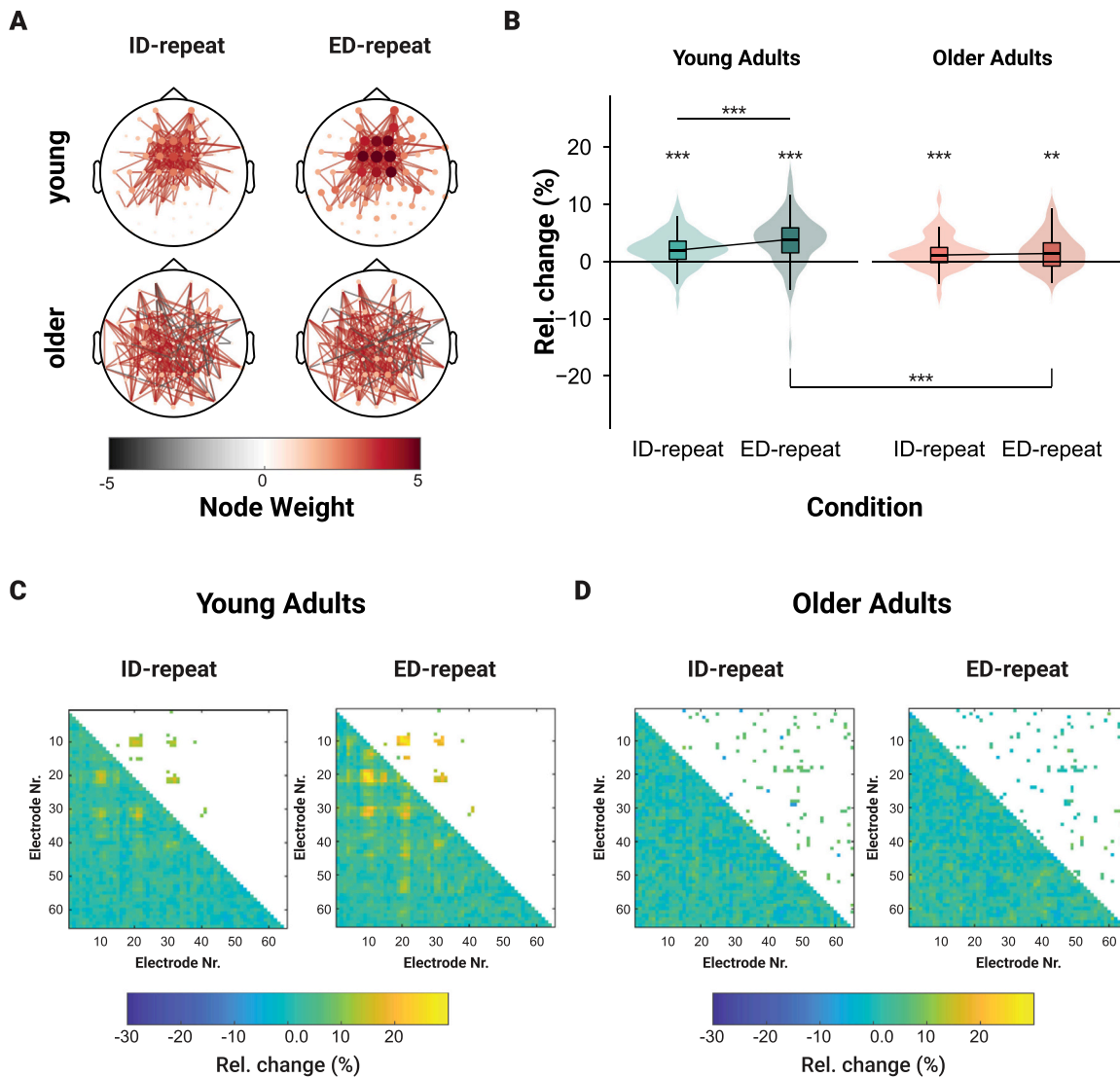
The early coherence component reached a peak amplitude at 500 ms in the young age group and explained 12.84% of the variance. The corresponding component in the older age group peaked at 490 ms and explained 11.29% of the variance (Figure 4). The robust ANOVA on the reconstructed components averaged across all channels revealed significant effects of condition ( $F_{1, 109.56} = 8.38, p = 0.005, \eta_p^2 = 0.04$ ) and age group ( $F_{1, 109.08} = 17.36, p < 0.001, \eta_p^2 = 0.05$ ) and a significant condition by age group interaction ( $F_{1, 109.56} = 7.22, p = 0.008, \eta_p^2 = 0.03$ ). Robust post-hoc tests revealed that theta coherence was higher in the ED-repeat contrast compared to the ID-repeat contrast in the young (ED-repeat:  $t_{55} = 4.08, p < 0.001, d = 0.38$ ), but not in the older adults (ED-repeat:  $t_{36} = 0.14, p = 0.888, d = 0.02$ ). Younger adults displayed higher coherence values compared to older adults in the ED condition (young-old:  $t_{85.96} = 4.38, p < 0.001, d = 0.47$ ) but not in the ID condition (young-old:  $t_{78.95} = 1.82, p = 0.065, d = 0.20$ ). Robust one-sample *t*-tests revealed a significant positive difference from zero (i.e., from the repeat condition) in both young (ID:  $t_{55} = 7.08, p < 0.001, d = 0.81$ ; ED:  $t_{55} = 9.35, p < 0.001, d = 0.84$ ) and older adults (ID:  $t_{36} = 3.50, p = 0.001, d = 0.88$ ; ED:  $t_{36} = 2.99, p = 0.005, d = 0.68$ ). Importantly, in the group of young adults, frontocentral electrodes were strongly represented in the electrode pairs belonging in the 95th percentile of the component peak, mirroring the theta-power component peak location (Figure 4). This was not the case in the older age group, as here no specific focal location was apparent in the topography.

The late coherence component reached a peak amplitude at 650 ms in the young age group and explained 11.85% of the variance. The



**Fig. 3. Early theta power component.** **A:** Average topographical distribution of the early theta power component at the average peak latency of 455 ms. The maximum amplitude of theta at peak latency was at the FCz in the young group and at the F8 in the older age group; **B:** Average component power at peak latency across all electrodes. Both age groups displayed a significant increase in theta power from repeat to ID and ED condition (maximum *t*-value, young ED-repeat,  $t_{55} = 8.52, p < 0.001, d = 0.29$ ). Young adults additionally displayed increased theta power in ED compared to ID trials ( $t_{55} = 2.83, p = 0.007, d = 0.09$ ); **C&D:** Theta power timeline of the early theta component at the FCz and F8 channels, respectively.

## Early Theta Coherence Component - 495 ms



**Fig. 4. Early theta coherence component.** **A:** Connectivity graph of the electrode pairs with absolute score values higher than the 95th percentile; **B:** Average relative change in coherence from repeat at peak latency across all electrode pairs. All conditions in both age groups are significantly higher than zero (i.e. the repeat condition) (maximum  $t$ -value, young ED,  $t_{55} = 9.35$ ,  $p < 0.001$ ,  $d = 0.84$ ). Young adults additionally displayed increased coherence in ED-repeat compared to ID-repeat ( $t_{55} = 4.08$ ,  $p < 0.001$ ,  $d = 0.38$ ) and increased coherence in ED-repeat compared to the same condition in the older adults ( $t_{85.96} = 4.38$ ,  $p < 0.001$ ,  $d = 0.47$ ); **C&D:** Representation of relative change from repeat in the individual conditions in young and old adults, respectively.

equivalent component in the older age group reached a peak at 640 ms and explained a variance of 12.11%. Here, we found no significant effect of age group, condition or their interaction ( $p \geq 0.202$ ).

### 3.4. Global efficiency

We investigated global efficiency in two separate time windows, reflecting the timing of the theta power and coherence peaks described in the previous sections. In the early window from 425 ms to 525 ms, we found a significant interaction between age group and condition ( $F_{2, 94.78} = 7.19$ ,  $p = 0.001$ ,  $\eta_p^2 = 0.04$ ; **Figure 5A**). Young adults exhibited increased global efficiency in both ID (ID-repeat:  $t_{55} = 4.66$ ,  $p < 0.001$ ,  $d = 0.30$ ) and ED compared to repeat trials (ED-repeat:  $t_{55} = 7.03$ ,  $p < 0.001$ ,  $d = 0.49$ ) and during ED compared to ID trials (ED-ID:  $t_{55} = 3.74$ ,  $p < 0.001$ ,  $d = 0.23$ ). On the other hand, older adults did not display higher global efficiency in any of the condition contrasts ( $p > 0.069$ ). Pair-wise comparisons between age groups did not show

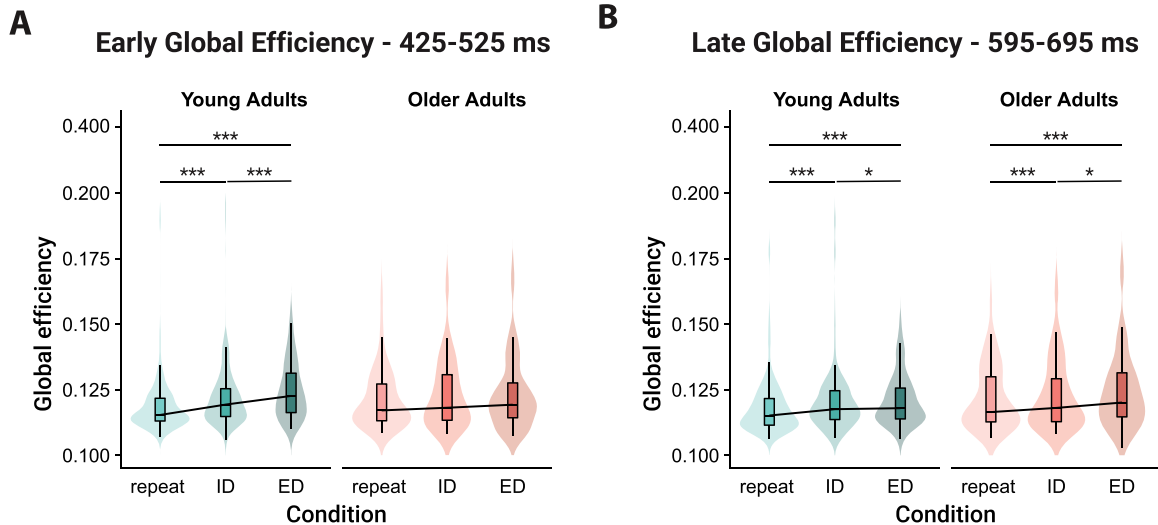
any significant difference in global efficiency in any of the three conditions ( $p > 0.122$ ).

In the second time window (595–695 ms), we found a significant effect of condition ( $F_{2, 85.18} = 8.45$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.06$ ), with higher global efficiency in both set-shifting conditions compared to the repeat condition (ID-repeat:  $t_{90} = 3.68$ ,  $p < 0.001$ ,  $d = 0.13$ ; ED-repeat:  $t_{90} = 5.27$ ,  $p < 0.001$ ,  $d = 0.22$ ; **Figure 5B**) and in ED compared to ID ( $t_{90} = 2.52$ ,  $p = 0.013$ ,  $d = 0.11$ ). No significant effect of age group ( $F_{1, 79.54} = 1.61$ ,  $p = 0.208$ ,  $\eta_p^2 = 0.02$ ) and no significant interaction between condition and age group were found ( $F_{2, 85.18} = 2.33$ ,  $p = 0.104$ ,  $\eta_p^2 = 0.00$ ).

### 3.5. Relationship between behaviour and theta measures

The best fitting models describing the relationship between behaviour and theta measures are given in **Table 3**.

The best fitting model (marginal  $R^2 = 0.75$ ) included both early



**Fig. 5. Global efficiency.** A: Average global efficiency in the early time window between 425 and 525 ms. Young individuals displayed significantly increasing global efficiency from repeat to ID and ED (highest  $t$ -value in ED-repeat:  $t_{55} = 7.03, p < 0.001, d = 0.49$ ), whereas older adults did not ( $p > 0.069$ ); B: Average global efficiency in the late time window between 595 and 695 ms. There was a significant condition effect, in which both set-shifting conditions displayed increased global efficiency compared to repeat (highest  $t$ -value in ED-repeat:  $t_{90} = 5.27, p < 0.001, d = 0.22$ ). ED also displayed higher global efficiency than ID trials ( $t_{90} = 2.52, p = 0.013, d = 0.11$ ).

**Table 3**  
Best fitting linear mixed-effect models.

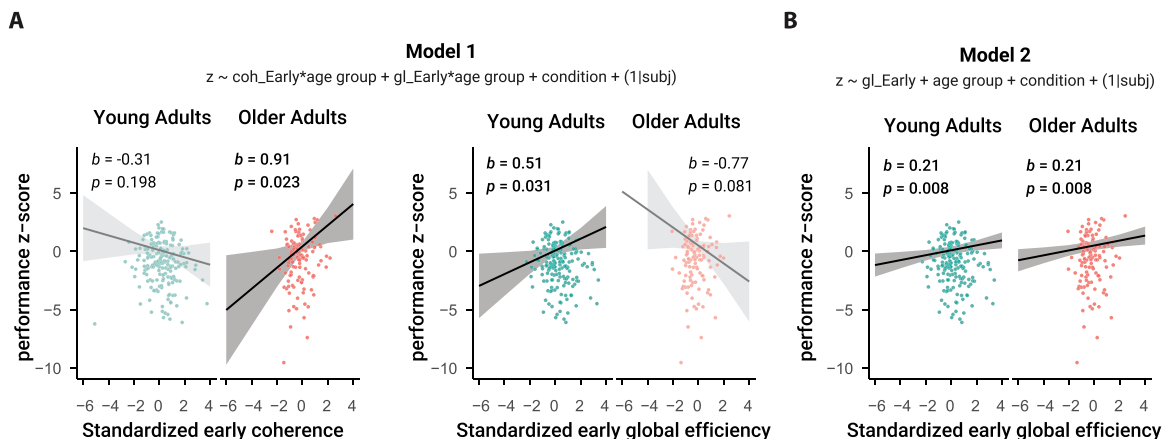
Model	logLik	AIC	weight
$z \sim \text{coh\_Early} * \text{age group} + \text{gl\_Early} * \text{age group} + \text{condition} + (1 \text{subj})$	-531.44	1081.50	0.46
$z \sim \text{gl\_Early} + \text{age group} + \text{condition} + (1 \text{subj})$	-535.02	1082.30	0.30
$z \sim \text{coh\_Early} * \text{age group} + \text{gl\_Early} * \text{age group} + \text{gl\_Late} + \text{condition} + (1 \text{subj})$	-531.05	1082.90	0.24

$z$ : performance z-score; coh\_Early: Amplitude of early coherence component at peak time.; gl\_Early; Amplitude of global efficiency in the early time window; logLik: Log Likelihood; AIC: Akaike information criterion.

coherence and early global efficiency as terms. An ANOVA of the resulting model revealed a significant effect of condition ( $F_{1, 152} = 425.98, p < 0.001$ ), a significant interaction of early coherence with age group ( $F_{1, 257.49} = 6.51, p = 0.011$ ) and a significant interaction between early global efficiency and age group ( $F_{1, 253.80} = 6.81, p = 0.010$ ).

Simple slopes analyses of the interactions revealed a significant positive association of early coherence and performance z-scores in the older ( $t_{260} = 2.28, p = 0.023, b = 0.91$ ), but not in the younger age group ( $t_{267} = -1.29, p = 0.198, b = -0.31$ ; Figure 6A). Here, pairwise contrasts revealed a significant difference between the simple slopes obtained from the two age groups ( $t_{262} = 2.62, p = 0.009, \Delta b = 1.21$ ). Conversely, a significant positive association of early global efficiency and performance z-scores was found in the young ( $t_{276} = 2.17, p = 0.031, b = 0.51$ ), but not in the older age group ( $t_{275} = -1.75, p = 0.081, b = -0.77$ ; Figure 6A). Here, a significant difference between the slopes of the two age groups was again found ( $t_{275} = 2.52, p = 0.011, \Delta b = 1.28$ ).

The second-ranking model (marginal  $R^2 = 0.75$ ) included early global efficiency and age group. Here, global efficiency displayed a significant main effect in the ANOVA ( $F_{1, 274.56} = 7.26, p = 0.007$ ). There was a significant effect of condition ( $F_{1, 153.95} = 434.92, p < 0.001$ ) but no significant effect of age group ( $F_{1, 154.94} = 3.00, p = 0.085$ ). Simple slope analyses revealed a positive association between early global efficiency and performance z-scores ( $t_{278} = 2.66,$



**Fig. 6. Models to predict performance.** A: Estimated regression from the best fitting model. Left: standardized early coherence and performance z-score; right: standardized early global efficiency and performance z-score. Older adults displayed a positive association between early coherence and performance ( $t_{260} = 2.28, p = 0.023, b = 0.91$ ), whereas the performance of young adults was positively associated with early global efficiency ( $t_{276} = 2.17, p = 0.031, b = 0.51$ ); B: Estimated regression between standardized early global efficiency and performance z-score obtained from the second ranked model fitting the data ( $t_{278} = 2.66, p = 0.008, b = 0.21$ ).

$p = 0.008$ ,  $b = 0.21$ ; Figure 6B).

The third-ranking model (marginal  $R^2 = 0.74$ ) included early global efficiency, early coherence and late global efficiency as terms. The ANOVA revealed a significant interaction between early coherence and age group ( $F_{1, 255} = 7.47$ ,  $p = 0.007$ ) and a significant interaction between early global efficiency and age group ( $F_{1, 268.17} = 7.24$ ,  $p = 0.008$ ). Additionally, a main effect of condition was found ( $F_{1, 151.97} = 422.42$ ,  $p < 0.001$ ). Simple slope analyses revealed a positive association between early coherence and performance z-scores in the older adults ( $t_{263} = 2.33$ ,  $p = 0.020$ ,  $b = 0.93$ ) but not in the young ( $t_{269} = -1.31$ ,  $p = 0.190$ ,  $b = -0.32$ ). Here, pairwise contrasts revealed that the age-specific slopes were significantly different from each other ( $t_{264} = 2.68$ ,  $p = 0.008$ ,  $\Delta b = 1.25$ ). None of the two age groups displayed a significant association between early global efficiency and performance z-scores (young:  $t_{285} = 1.88$ ,  $p = 0.062$ ,  $b = 0.45$ ; older:  $t_{280} = -1.92$ ,  $p = 0.056$ ,  $b = -0.87$ ). However, pairwise contrasts revealed that the age-specific slopes were significantly different from each other ( $t_{264} = 1.32$ ,  $p = 0.009$ ,  $\Delta b = 1.32$ ).

#### 4. Discussion

In this study we aimed to identify whether EEG measures of theta activity and synchrony during set-shifting are modulated differently in older compared to young adults. Our results overall indicated that behaviourally, older adults show a more conservative response pattern with lower error rates and longer reaction times during set-shifting, accompanied by pronounced age differences in the underlying electrophysiological processes. Older adults displayed a fronto-lateral topography of theta power modulation and distributed coherence modulations, whereas young adults exhibited a fronto-central peak in both measures. Global efficiency was modulated at different time points in both age groups.

##### 4.1. Speed-accuracy trade-off in set-shifting

As summarized in the introduction, it has thus far been unclear if and how set-shifting performance declines with age. In the present study, using the IDED task, we observed increased RT and IQR costs in older adults, particularly in the ED condition, the most cognitively demanding condition, compatible with the frequently observed age-related slowing of cognitive processes (Salthouse, 1996). From reaction times alone, one might therefore conclude that older adults exhibit behavioural costs in set-shifting mirroring the results of several previous studies (e.g. Cepeda et al., 2001; Kray et al., 2002; Meiran et al., 2001). Conversely, when solely relying on error rates as performance measure, one might conclude that older adults exhibited reduced error switch costs compared to young adults in both set-shifting conditions. However, when we computed z-scores reflecting the composite of all behavioural measures, we found that the global set-shifting ability of older adults was not significantly different from that of younger participants, suggesting an age-related shift in response dynamics. This shift can be summarised as the speed-accuracy trade-off, a phenomenon observed in older age already over four decades ago (e.g. Rabbitt, 1979; Salthouse, 1979). Such a speed-accuracy trade-off aligns with previous research demonstrating similar phenomena in relation to other cognitive tasks, where increased deliberation in older adults may offset declines in processing efficiency (Ratcliff et al., 2003; Starns and Ratcliff, 2010), thus reflecting a compensatory mechanism. As highlighted by Starns and Ratcliff (2010), older adults show a tendency to primarily focus on error minimization, even when speed costs are substantial. This more cautious approach to task-solving is most probably involuntary and may help attenuate adverse effects of a slower processing system (Eckert, 2011; Preprint: Heathcote et al., 2022) or may reflect age-related changes in brain connectivity (Forstmann et al., 2011; also see below).

It cannot be excluded that, in more difficult tasks, older adults may actually show lower performance rather than the speed-accuracy trade-

off observed in the IDED task. For example, when participants of our study performed the Flexibility subtask of the Test Battery for Attention (TAP), older adults showed both higher error rates and longer reaction times (Table 2). A majority of older adults also failed to complete the ED stage of the Attentional Set-shifting Task (ASST), another cognitive flexibility task. Those that successfully completed it, required on average more trials than young participants to reach the completion criterion (Table 2).

More generally, our results underscore the importance of considering multiple performance metrics when evaluating age-related cognitive changes, as, for example, relying on reaction time alone may obscure the adaptive strategies employed by older adults to maintain – or, as in our study, even improve – performance accuracy.

##### 4.2. Brain connectivity in older age

At the neural level, we observed marked age-related differences in both theta power and connectivity measures, which were differentially modulated during set-shifting in older compared to young adults.

First, we showed that theta modulations do take place during set-shifting in older age, opposing our previous results with a smaller cohort (Darna et al., 2025). This modulation was visible in both set-shifting conditions and had its maximum over frontal channels, contrasting that of young adults, which was most pronounced over frontocentral channels. As the EEG is only a projection of cortical activity, the precise source of this modulation cannot be conclusively determined by our present data, but the overall topography is nevertheless in line with the previously described posterior-anterior shift in aging (Davis et al., 2008; Festini et al., 2018), which refers to the phenomenon that increased frontal activity accompanies a reduction of posterior activity in aging, possibly reflecting functional compensation. We cannot exclude, however, that other types of switch paradigms, such as multistable perception, may elicit different topographic shifts, as for example, diminished frontal and increased reliance on parietal theta activity (Küçük et al., 2023a) or compensatory increase of activity in other frequency bands, such as the alpha band (Küçük et al., 2023b).

Second, we showed increased coherence during set-shifting in older adults compared to the repeat condition. However, the distribution of this modulation was widespread across the scalp, contrasting that of young adults, where increased coherence was most prominent over frontocentral electrodes, in line with previous results (Myers et al., 2021; Sauseng et al., 2006). Additionally, in contrast to the young adults, we saw no further increases in coherence in the ED condition compared to ID in the older adults. We suggest that this global decrease of coherence modulation may reflect a previously proposed age-related network dedifferentiation (Fjell et al., 2016; Koen et al., 2020) and the reduced specificity of functional connectivity in the aging brain (Geerligs et al., 2014), resulting in decreased within-network connectivity. Increased age-related network dedifferentiation is also supported by our global efficiency analysis, which was modulated in older adults during set-shifting in the late time window across all conditions. This supports the interpretation that processes associated with focused activity in younger age, shift to a more global response in older adults, where we observe an increase in global activity due to the decreased functionality of the region originally responsible for a specific function, prompting the need for compensatory, more widespread activity. Alternatively, or likely additionally, more global activity in aging may result from reduced inhibition of brain activity not required for the task at hand (Legon et al., 2016; Morcom and Henson, 2018; Schott et al., 2023).

Hence, our results point to an altered theta distribution and coherence as a neural manifestation of cognitive flexibility in older age. These alterations might explain the speed-accuracy trade-off in older adults and may, at least in part, reflect a compensatory mechanism by which additional cognitive resources are engaged to enable successful set-shifting in older age.

### 4.3. Relationship between EEG measures and behaviour

In a model comparison we found that theta coherence and global efficiency were the EEG measures most robustly associated with performance in our cohort in an age-dependent manner. In particular the first model demonstrated that early coherence was associated with better overall performance in older adults, whereas younger adults displayed a positive relationship of performance with early global efficiency. This is in line with previous studies, in which theta coherence was associated with more favourable indices of cognitive flexibility in older adults (Ferreira et al., 2013). According to the second model, on the other hand, global efficiency primarily predicted better performance in both age groups.

Overall, these results therefore provide further evidence for the possibility that theta coherence and global efficiency may be markers of neural processes underlying set-shifting performance or, more broadly, cognitive flexibility and potentially other executive functions. In line with this interpretation, increased theta-coherence in particular has previously been associated with better performance in tests of executive function (Basharpoor et al., 2021; Dias et al., 2015) and working memory (Smit et al., 2023). Thus, if these connectivity measures can indeed be regarded as mediators of executive functioning (Li et al., 2020), this opens the possibility of developing targeted tools and interventions aimed specifically at these mechanisms. Such interventions would focus on modulating the neural dynamics reflected in these metrics, for example by increasing theta-band coherence among regions implicated in cognitive control or by enhancing the overall efficiency of large-scale brain networks that support flexible, goal-directed behaviour. Early work in this direction has already yielded promising results, demonstrating enhanced adaptive behaviour following non-invasive brain stimulation (Reinhart, 2017) as well as after neurofeedback training (Enriquez-Geppert et al., 2014).

### 4.4. Conclusion and future perspectives

In summary, our study reveals that set-shifting in older age exhibits a speed-accuracy trade-off, that is, older adults focus on reducing errors at the expense of response speed. This strategy shift may reflect a compensatory mechanism in the presence of age-related functional alterations in the connectivity within and between brain networks. This observation reveals the ability of the aging brain to employ alternative neural resources to compensate for the decline of task-specific neural resources in the form of cognitive reserve, as it is mediated by theta coherence and global efficiency. Prospectively, targeted training protocols and interventions such as non-invasive brain stimulation may help to counteract cognitive decline with or without the presence of a neurodegenerative disease.

### CRediT authorship contribution statement

**Margarita Darna:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anni Richter:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Jens-Max Hopf:** Writing – review & editing, Methodology. **Constanze I. Seidenbecher:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Björn H. Schott:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

### Verification

We affirm that this manuscript has not been published elsewhere and is not under consideration by any other journal. All authors have approved the manuscript and agree with its submission to *Neurobiology of Aging*.

### Funding conflict of interest declaration

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neurobiolaging.2026.04.001](https://doi.org/10.1016/j.neurobiolaging.2026.04.001).

### Data availability

Experimental Code, MATLAB Scripts, RStudio Scripts can be provided upon request.

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