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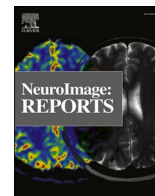
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Midfrontal theta is associated with errors, but no evidence for a link with error-related memory

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ABSTRACT

Midfrontal theta is widely observed in situations with increased demand for cognitive control, such as monitoring response errors. It also plays an important role in the cognitive control involved in memory, supporting processes like the binding of single items into a memory representation or encoding contextual information. In the current study, we explored the link between midfrontal theta and error-related memory. To this end, we recorded EEG from 31 participants while they performed a modified flanker task. Their memory for the errors made during the task was assessed after each experimental block, and its relationship with error-related midfrontal theta effects was investigated. We have replicated the error-related increase in midfrontal theta power, reported in previous literature. However, this error-related theta effect could not predict subsequent memory of the committed errors. Our findings add to a growing literature on the prefrontal cortex-guided control process in error monitoring and memory.

1. Introduction

When we make a mistake, our brain sets in motion processes to prevent us from making additional mistakes. To learn from our errors, we need to monitor them and adjust our behavior accordingly. This happens on different timescales, in the milliseconds following an error, the brain needs to identify the event as an error to adjust immediate behavior accordingly. For instance, when accidentally hitting the gas pedal instead of the brake, our brain needs to quickly send a signal to our feet to initiate a motor response to correct this. In addition, we need to be able to remember the errors we made in the past to prevent them from happening again. The next time you step in a car you will remember the error you made hours, days, or weeks ago and you will be mindful of not making the same mistake again. Therefore, our brain needs the joint efforts of error-related and memory-related processes for us to learn from our mistakes in daily life.

The detection of an error is reflected by midfrontal theta oscillations (4–7 Hz), recorded from electroencephalography (EEG) channels over the medial prefrontal cortex (PFC; Cavanagh and Frank, 2014; Cohen, 2011a; Fusco et al., 2018; Kalfaoğlu et al., 2018). Neural oscillations are thought to be important for transient brain computations needed for

cognitive functions, and theta appears to coordinate processes needed for post-error cognitive control (Bonfond et al., 2017; Duprez et al., 2020; Fries, 2005; Jensen et al., 2014; Kalfaoğlu et al., 2018). During various tasks, midfrontal theta power is increased around –100 to 500 ms relative to error commission (Kalfaoğlu et al., 2018; Novikov et al., 2015; Trujillo and Allen, 2007; Yordanova et al., 2004). Moreover, when participants are given the opportunity to correct committed errors, midfrontal theta can predict subsequent error corrections (Kalfaoğlu et al., 2018). This suggests that midfrontal theta reflects processes involved in error awareness and the subsequent post-error cognitive control. In addition, when applied externally through transcranial alternating current stimulation (tACS), midfrontal theta modulated behavioral adjustments following errors in a flanker task (Fusco et al., 2018). It is thought that midfrontal theta originates from the anterior cingulate cortex (ACC) and is cognitively associated with the monitoring of the errors (Botvinick et al., 2004; Cavanagh et al., 2009; Chevalier et al., 2021; Cohen, 2011a). The increase in midfrontal theta may signal an increased need for top-down control to adjust behavior, recruiting the PFC to prevent subsequent errors (Cavanagh et al., 2012; Cohen, 2011a; Kerns, 2006). Given this involvement of midfrontal theta in real-time error adjustments, it would be of interest to know if theta encodes

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error-related information that can predict error memory at a later point in time. If this is the case, it suggests that midfrontal theta can influence behavioral adjustments on a timescale of minutes or even longer.

We know that theta oscillations play a role in various stages of memory processes, including the encoding of new information. Intracranial and scalp EEG studies have shown that encoding-related theta power is greater for items that are later remembered, as compared to those that are later forgotten (Hanslmayr, Spitzer, & Bäuml, 2009; Nyhus and Curran, 2010b; Osipova et al., 2006; Sederberg et al., 2003; Sederberg et al., 2007; White et al., 2013; Wynn et al., 2019). These effects are the most pronounced 300–1000 ms after stimulus onset over frontocentral regions. Additionally, Cohen (2011b) utilized a combined EEG-MRI design to show a close interplay between hippocampal-PFC connectivity, midfrontal theta and long-term memory performance. This is in line with other studies proposing that memory-related theta mediates PFC-guided control processes needed for task-relevant encoding (Cavanagh and Frank, 2014; Nyhus and Badre, 2015; Nyhus and Curran, 2010a). This supports the idea that midfrontal theta mediates processes that are needed for memory, like the binding of single items into a memory representation or encoding contextual information (Hsieh and Ranganath, 2014). Therefore, midfrontal theta appears to play a supporting role in both error monitoring and memory encoding.

In the current study, we aimed to bridge the error- and memory-related literature by exploring the link between midfrontal theta and error-related memory. If midfrontal theta during error commission can predict subsequent error memory, this would suggest that midfrontal theta plays an important role in the encoding of errors into memory. This could provide an initial indication that midfrontal theta is not only involved in momentary error awareness right after an erroneous response, but also in learning from errors on a longer time scale (e.g., to prevent new errors in the future). Our participants performed a modified flanker task (Eriksen and Eriksen, 1974), while we assessed their error memory after each experimental block. This enabled us to explore if midfrontal theta reflects the online detection of the errors and will predict participants' memory of the errors they have made. We predict that midfrontal theta is involved in both error detection and the encoding of the error. Therefore, we hypothesized that (1) we would replicate the increase in midfrontal theta after error commission, and (2) this error-related theta effect would be a significant predictor of the ability to recall the number of errors made.

2. Methods

2.1. Participants

A total of 31 healthy right-handed adults participated in this study, recruited through the Radboud Research Participation System. All had normal or corrected-to-normal vision, were native Dutch speakers, and were free from any self-reported neurological or psychiatric conditions. All participants received course credit or monetary compensation. Of these 31 participants, four participants were excluded from the analyses reported here, due to limited number of trials left after artifact rejection ($N = 1$), chance-level performance during the flanker task ($N = 1$), or data acquisition issues ($N = 2$) that rendered the data unusable for data analyses reported here. This results in a total 27 participants (15 females, 12 male, $M_{\text{age}} = 22.52$, $SD_{\text{age}} = 3.91$) reported in the current analyses. One additional participant without working memory (WM) measures was excluded from the correspondent analysis. The study was approved by the local ethics committee of the Faculty of Social Sciences of the Radboud University.

2.2. Procedure

All participants received written information prior to participation but remained naive regarding the aim of the study. Upon arrival at the laboratory, all participants were screened for eligibility to participate in

EEG studies and provided written informed consent.

2.2.1. Working memory task

Prior to the flanker task, a computerized version of the digit span task from the Wechsler Adult Intelligence Scale fourth edition (WAIS-IV; Kreutzer et al., 2011) was used as a measurement of WM. The digit span task consisted of three conditions (forward, backward, and sequencing) and the order of these was kept consistent across participants. During all conditions, a single digit (1–9) was presented centrally on the screen for 1000 ms, followed by a 300 ms inter-stimulus interval. Digit presentation and recording of responses were attained using PsychoPy (v1.80; Peirce et al., 2019) on a Windows PC. For each condition, every trial consisted of two series of digits, which increased by one digit on every trial (e.g., first trial: 3–5 and 8–4; second trial: 9-5-2 and 1-7-6). In the forward condition, participants were asked to reproduce the digits in the same order as previously presented after each series (e.g., first trial: 3–5 and 8–4; second trial: 9-5-2 and 1-7-6). In the backward condition, they were asked to reproduce the series in the reversed order (e.g., first trial: 5–3 and 4–8; second trial: 2-5-9 and 6-7-1). In the sequencing condition, participants had to recall the digits in ascending order (e.g., first trial: 3–5 and 4–8; second trial: 2-5-9 and 1-6-7). Participants responded by typing the digit sequence on a keyboard. Participants were able to alter their response up to the moment of confirmation, which was operationalized by pressing the return key. The task was aborted when a participant was not able to respond correctly in both two series in a single trial. The total number of correct responses was used as their WM score. The maximal score that could possibly be obtained was 16 for all three conditions.

2.2.2. Flanker task

Thereafter, participants performed a modified flanker task (Eriksen and Eriksen, 1974), where they were required to give a speeded response to a central target arrow, while ignoring congruent (">>>>") or "<<<<<") or incongruent (">><<>>" or ">>>>>") flanker arrows (see Fig. 1). Half of the trials were congruent, and half were incongruent. Participants responded to the target arrows by pressing the "D" key (left arrows) and the "H" key (right arrows) on a keyboard, with their left and right index fingers, respectively. Stimuli were presented on a grey background for 200 ms, with stimulus onset asynchronies randomly selected from a uniform distribution with a mean of 1550 ms and varying between 1400 and 1700 ms with 50 ms increments. During the intertrial interval, a white cross was centrally presented, and participants were instructed to keep fixation on the cross.

To elicit enough errors, we trained the participants to respond within a time limit prior to the main task. The time limit (range 336–640 ms, $mean = 438$ ms, $SD = 74$ ms) was computed dynamically across the training and calibrated individually for each participant (based on the 70 percentile of previous ten trials). If participants failed to respond within a given time limit, the fixation cross became red as a warning. The speed training consisted of 100 trials.

The main task that followed, was divided into six blocks of 100 trials. Participants were not given feedback on their performance during the main task, they were also allowed to respond after exceeding the time limit for each trial (i.e., slow trials). At the end of each block, participants were instructed to recall their task performance. Specifically, after each block, participants were asked to recall the number of errors made in the preceding block and rate their confidence in this judgment. To minimize any influence on task strategy, we also asked them to recall the number of times they felt their response was too slow in the preceding block. The numerical responses were given with the numbers on the keyboard, and the confidence ratings were submitted by clicking with a mouse on a visual analog scale, ranging from "completely not sure" to "completely sure". The scale ranged from 0 to 100, although these values were not presented to the participants.

the left-skewed distribution of the error memory scores, we used a generalized linear mixed model with a zero-inflated gamma distribution (glmmTMB package, (Brooks et al., 2017)). We modeled error memory as a function of the error-related midfrontal theta effect, error rate, WM score, and block number. Error rates were included as a random slope for participants.

```
glmmTMB(error_memory_abs ~ theta_effect + error_rate + WM_sum +
ordered(block) + (1 + error_rate | participant), data = data_by_block., family
= ziGamma(link = "log"), ziformula = ~1)
```

In addition, we modeled whether the error-related theta effect could predict the sign of the error memory scores (i.e., under-vs. over-estimation) using a generalized mixed effect model. To exclude the potential confound that participants using counting strategy to enhance error memory performance (i.e., when they were very confident about their guesses), we also included an interaction model using the confidence score reported after each block. All models used in these analyses are provided in Supplementary Material A. We centered all the continuous predictors for all the models.

3. Results

3.1. Flanker task performance and working memory

Participants' performance on the flanker task is shown in Fig. 2. In line with the literature, participants showed a congruency effect; they were slower ($\beta = 0.16$, $SE = 0.01$, $t = 10.91$, $p < .001$) and made more errors ($\beta = 2.48$, $SE = 0.18$, $z = 13.92$, $p < .001$) in the incongruent than the congruent condition. In addition, they were faster when making an erroneous response as compared to a correct one ($\beta = -0.20$, $SE = 0.02$, $t = -12.46$, $p < .001$). We observed post-error slowing ($\beta = 0.02$, $SE = 0.01$, $t = 2.89$, $p = .008$), but no post-error accuracy change ($\beta = 0.07$, $SE = 0.06$, $z = 1.08$, $p = .28$). Over time, participants got faster ($\beta = -0.02$, $SE = 0.003$, $t = -4.85$, $p < .001$), but their accuracy remained the same ($\beta = -0.04$, $SE = 0.06$, $z = -0.65$, $p = .51$).

Participants' working memory performance was quantified as the

total number of correct responses on the digit span task. Participant had an average total WM score of 32 ($M = 31.85$, $SD = 5.50$) over the three subtasks ($M_{\text{forward}} = 9.93$, $SD_{\text{forward}} = 2.09$; $M_{\text{backward}} = 10.81$, $SD_{\text{backward}} = 2.40$; $M_{\text{sequencing}} = 11.11$, $SD_{\text{sequencing}} = 2.50$). Their WM score could not predict their performance on the flanker task (RT: $\beta < 0.001$, $SE = 0.002$, $t = 0.36$, $p = .73$; accuracy: $\beta = 0.02$, $SE = 0.02$, $z = 0.73$, $p = .47$).

3.2. Midfrontal theta is modulated by flanker errors

We explored whether theta power was modulated by flanker performance, as suggested by the literature (e.g., Nigbur et al., 2011), and inspect the temporal nature of this effect. When we look at Fig. 3, comparing error and correct trials, there appears to be an increase in theta power over midfrontal channels in the first 250 ms after an error is made. This observation was tested by a cluster-based permutation analysis on the TFRs, which revealed a significant positive cluster ($p < .001$). This indicates that midfrontal theta power increased significantly following an erroneous, compared to a correct response. This effect was most pronounced between -31 ms and 545 ms relative to response onset, based on inspection of this cluster, further analyses in the manuscript were restricted to 0-500 ms.

3.3. Error-related midfrontal theta cannot predict error memory performance

Participant' ability to remember their errors across blocks is visualized in Fig. 4 (top panel). As can be seen in this figure, error memory performance increased over time ($\beta = 0.34$, $SE = 0.14$, $z = 2.35$, $p = .019$). Participants' confidence of their error memory (Fig. 4, bottom panel) showed a wide range across participants and blocks, suggesting that they were unlikely to use strategies such as counting the errors.

Fig. 5 (left panel) shows the relationship between participants' error-related theta effect during each flanker block and their error memory performance after each block. In general, it appears that there is no clear relationship between this neural theta effect and the memory

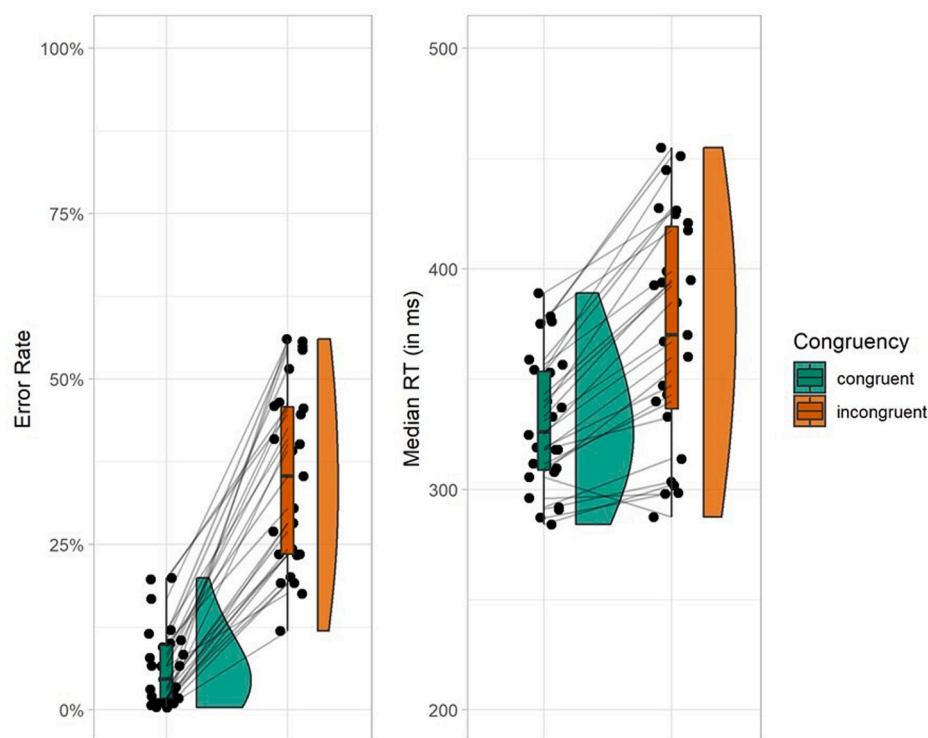


Fig. 2. Raincloud plots of error rate (left panel) and median reaction time (RT, in ms, right panel) as a function of trial congruency. The outer shapes represent the distribution of the data over participants, the thick horizontal line inside the box indicates the group median, and the bottom and top of the box indicate the group-level first and third quartiles of each condition. Each dot represents one participant, the thin lines in between connect the same participant's data for different conditions.

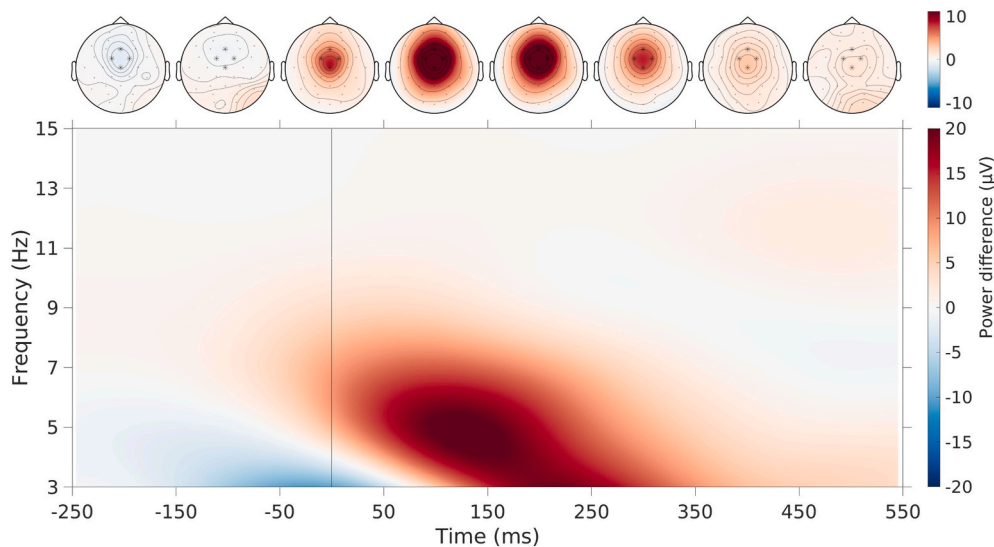


Fig. 3. The theta power difference between error and correct trials over time. All time windows are relative to response onset. On the top row the topographical distribution of the effect is plotted, with the midfrontal channels marked (FC1, FC2, Fz, Cz). The time-frequency representation for these midfrontal channels is plotted on the bottom row.

performance. In addition, there also seems to be very little consistency between participants as can be seen in three example participants in the right panel of Fig. 5. This observation was tested by utilizing a generalized linear mixed effects model. The model showed that error memory performance could not be predicted by the error-related midfrontal theta effect ($\beta = -0.03$, $SE = 0.22$, $z = -0.15$, $p = .88$). This indicated that contrary to our prediction, online modulation of error-related midfrontal theta was not predictive of later error memory. We also accounted for participants' WM score and their performance accuracy in the same model. Neither error rates ($\beta = -1.14$, $SE = 1.46$, $z = -0.78$, $p = .43$), nor participants' WM score ($\beta = -0.01$, $SE = 0.03$, $z = -0.46$, $p = .65$) affected their error memory performance. We further included the confidence measure to account for the situations where participants used a different strategy (e.g., counting, although unlikely). Neither does confidence predict error memory ($\beta = -0.004$, $SE = 0.003$, $z = -1.24$, $p = .22$), nor does confidence interact with theta effect in predicting error memory ($\beta = -0.01$, $SE = 0.01$, $z = -1.35$, $p = .18$). To explore whether potentially any sub-components of midfrontal theta (Beldzik et al., 2022; Zuure et al., 2020) could better predict the error memory performance, we ran additional post-hoc analyses on the phase-locked power, non-phase locked power (Cohen and Donner, 2013), and utilized a multivariate source separation approach (generalized eigendecomposition; GED) to separate out midfrontal theta from additional theta sources (Cohen, 2022; Zuure et al., 2020). All these additional post-hoc analyses yielded comparable results to the ones reported above (i.e., midfrontal theta effect cannot predict error memory). Details on these analyses and the results can be found in the [Supplementary Material B](#).

4. Discussion

Midfrontal theta is enhanced in situations that call for more cognitive control (Cavanagh and Frank, 2014; Cavanagh et al., 2012). One of these instances is the occurrence of an error, where cognitive control is needed for subsequent behavioral adjustments (Cavanagh et al., 2012; Cohen, 2011a; Fusco et al., 2018; Luu et al., 2004). On the other hand, midfrontal theta also plays a crucial role in memory-related processes (Hsieh and Ranganath, 2014). For example, theta is higher during memory encoding for items that are subsequently recollected (Hanslmayr et al., 2009; Summerfield and Mangels, 2005; White et al., 2013). In the current study, we examined the link between the error-related midfrontal

theta effect and participants' memory of the errors they have made.

While participants were performing a modified flanker task, we recorded their EEG activity and compared response-related theta power after erroneous and correct responses. Our results are in line with previous literature on the involvement of midfrontal theta in error processing (Cavanagh et al., 2012; Cohen, 2011a; Luu et al., 2004; Nigbur et al., 2011). Like previous studies, we observed enhanced theta power following an error commission as compared to a correct response. This error-related theta effect was present mainly in the medial frontal scalp region and in the first 500 ms after a response was made. This theta effect likely reflects error detection and the signaling of post-error cognitive control (Bonnefond et al., 2017; Cavanagh and Frank, 2014; Duprez et al., 2020; Fries, 2005).

Does the detection of response errors also affect the memory of these errors? We asked participants to indicate how many errors they remembered making in each experimental block and explored the relationship between their memory performance and the trial-by-trial brain oscillation. Our results provide no evidence that error memory can be predicted by the error-related theta effect, which seems to suggest a discrepancy between the error-related and memory-related control processes. In line with the idea that the same neural implementations can be driven by distinct neuronal computation principles (Buzsaki et al., 2012), it is plausible that error-related and memory-related midfrontal theta have different underlying mechanisms. For instance, midfrontal theta has long been viewed as the EEG signature of the unitary process of response conflict detection. However, it has been recently proposed that midfrontal theta reflects multiple uncorrelated processes, which give rise to comparable EEG compositions (Beldzik et al., 2022; Zuure et al., 2020). Therefore, it is plausible that even though error-related and memory-related control processes are both associated with "midfrontal theta", the underlying neural mechanisms differ and are uncoupled. We further attempted to separate multiple theta sources and explore whether sub-component of error-related theta effect could predict error memory (Supplementary Material B). However, without high-resolution Magnetoencephalography (MEG) or EEG recordings, we acknowledge that the current exploration is not sufficient to fully investigate this.

An influential hypothesis is that theta oscillations may coordinate the timing of cognitive processes due to large-scale cross-frequency coupling (Duprez et al., 2020; Lisman and Jensen, 2013). Processes specific to post-error control may be linked to a specific midfrontal theta

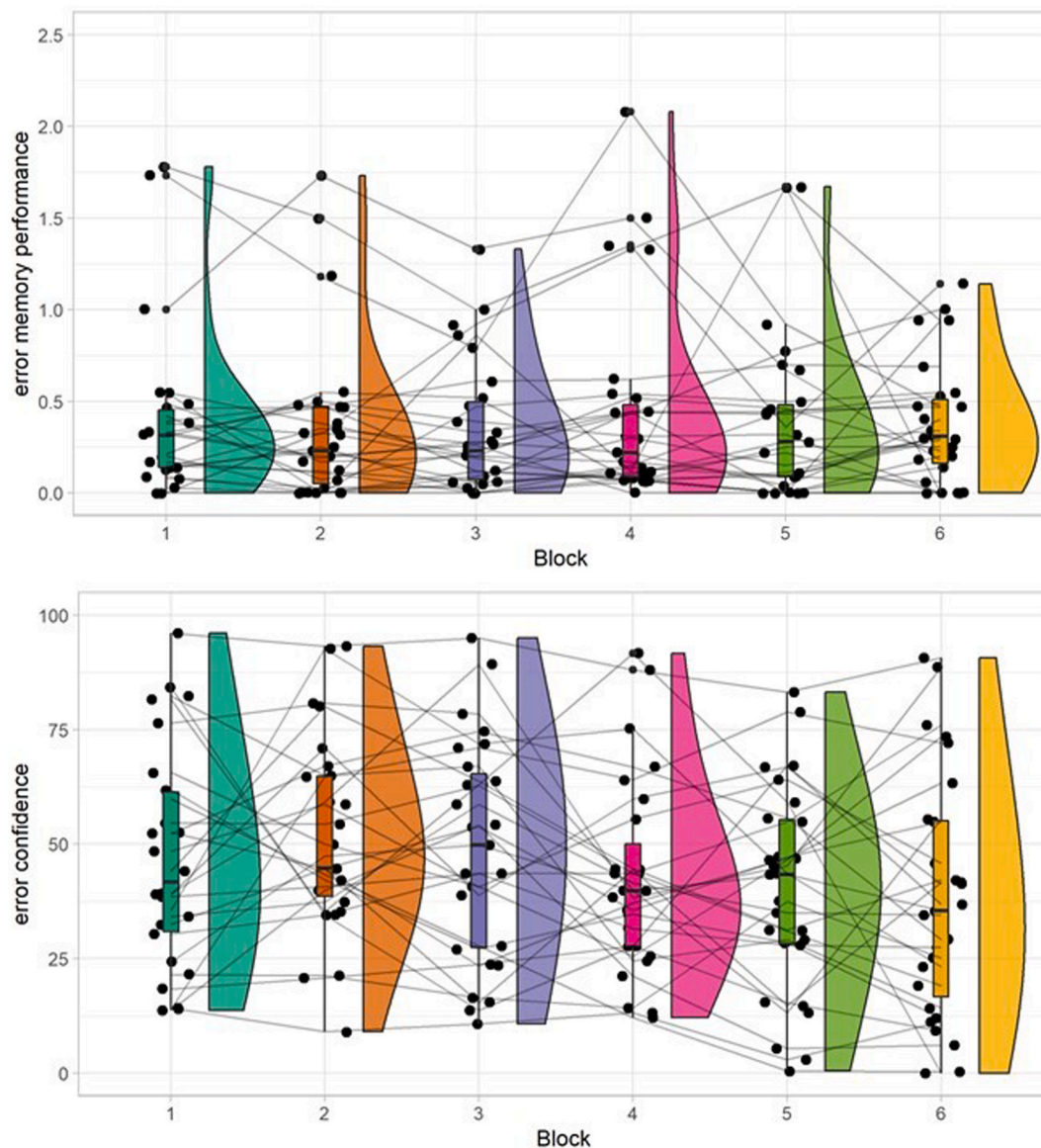


Fig. 4. Top panel: Raincloud plots of participants' error memory performance as a function of block numbers. The smaller the value, the more accuracy participants were in recalling their errors. Bottom panel: Raincloud plots of participants' confidence rating for their error memory, as a function of block numbers. 0 means "completely not sure", 100 means "completely sure". For both panels, the outer shapes represent the distribution of the data over participants, the thick horizontal line inside the box indicates the group median, and the bottom and top of the box indicate the group-level first and third quartiles of each condition. Each dot represents one participant, the thin lines in between connect the same participant's data for different blocks.

phase, while another cognitive process, like memory encoding could have a different preferential theta phase. Information arriving at specific phases would initiate multiple parallel processes in various brain regions. For instance, after error detection, communication in an extended neural network comprising of the PFC, medial temporal lobe and posterior parietal cortex might be required for subsequent memory and decision-making processes (Cohen, 2011a; Thakral et al., 2017). In concordance, it has been proposed that theta oscillations mediate top-down control from the PFC to the hippocampus for selective encoding and retrieval of episodic memories (Nyhus and Curran, 2010a). It is therefore a possibility that the initial increase in theta power after an error is made, is not predictive of subsequent error memory due to additional processing that occurs afterwards.

It could be a concern that participants during the task counted the number of errors and the error memory we tried to predict merely reflects their working memory. We consider this to be very unlikely given that (1) we asked the participants not only to report the number of errors

made, but also the number of times they were too slow. Performing well on the flanker task and actively counting both the number of errors made and the times the response was too slow would be very demanding on the attentional resources and unlikely to be achieved. This is also what participants indicated when asked about strategy use at the end of the experimental session. Only two participants indicated to have used counting as a strategy, when we removed these two participants and performed the same analyses, all conclusions remain the same (Supplementary Material C). (2) The participants showed a wide range of confidence ratings, suggesting they were uncertain about the guesses rather than counting. This is again supported by the fact that participants error memory performance cannot be predicted by their working memory capacity.

Several limitations of the study should be mentioned. First, contrary to most memory studies, our measure of error-related theta does not reflect a contrast between successful and unsuccessful encoding. It would be ideal if we could dissociate errors that have been successfully

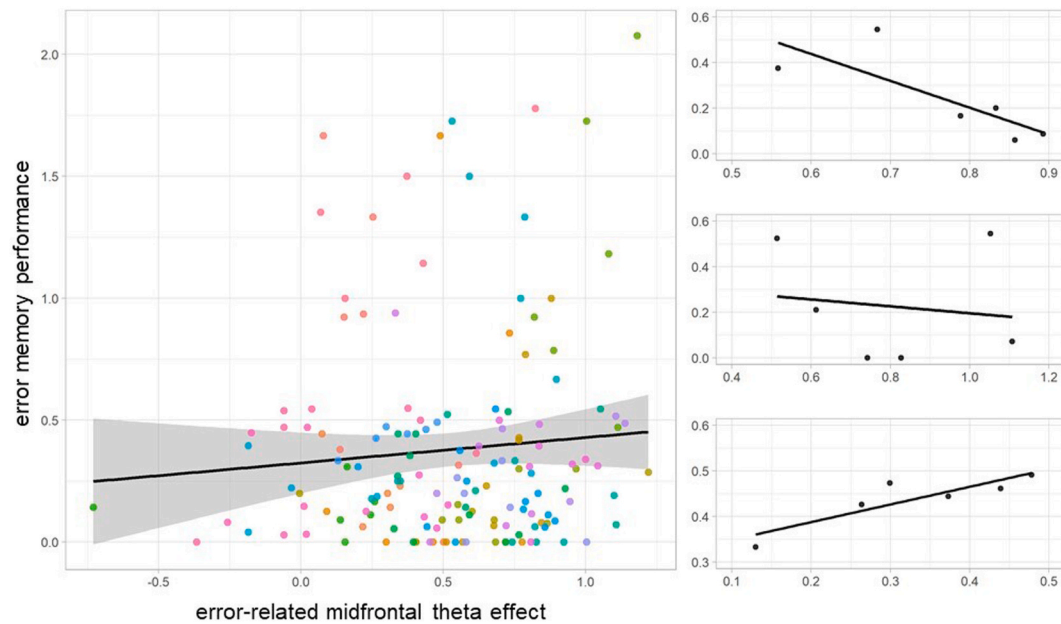


Fig. 5. The relationship between the error-related midfrontal theta effect and error memory performance. Left panel: Each color codes for an individual participant and the corresponding regression line. The black regression line fits all the data points, and the grey area depicts the confidence interval. Right panel: three example participants. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and unsuccessfully encoded during the task, which however was not possible in the current design. With state-of-art pattern analysis and decoding techniques of the neural data, future studies might be able to examine this further. Second, we quantified memory accuracy as the absolute difference between recalled errors and truly committed errors. This quantification does not differentiate between errors that were forgotten (misses) and correct trials misremembered as errors (false alarms). It could be that we found no evidence for a link between error-related theta and error memory due to the pooling of these errors. Since we could not directly differentiate between misses and false alarms, we used the error under- or overestimation as a proxy and explored its link with error-related theta. Nevertheless, our exploratory analysis (Supplementary Material D) shows no evidence that midfrontal theta can predict misses and false alarms.

To summarize, we have replicated the error-related midfrontal theta using a modified flanker task. However, the error-related theta power increase cannot predict subsequent memory performance of committed errors. These findings add to a growing literature on the PFC function in cognitive control and memory process. Still, much remains to be explored on whether midfrontal theta, a seemingly distinctive neural signature of cognitive control, reflects multiple cognitive processes.

Data availability

Data and codes are available at the Donders Repository (<https://doi.org/10.34973/pc1w-ee63>).

Conflict of Interest

We declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yinrp.2022.100129>.

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