Oscillatory Correlates of Control over Working Memory Gating and Updating: An EEG Study Using the Reference-back Paradigm

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Abstract

■ Optimal working memory (WM) functioning depends on a control mechanism that balances between maintenance and updating by closing or opening the gate to WM, respectively. Here, we examined the neural oscillation correlates of WM updating and of the control processes involved in gating. The reference-back paradigm was employed to manipulate gate opening, gate closing, and updating independently and examine how the control functions involved in these processes are mapped to oscillatory EEG activity. The results established that different oscillatory patterns were associated with the control process related to gate opening than in gate closing. During the time of gate closing, a relative increase in theta power was observed over midfrontal electrodes. This theta response is a known EEG signature of cognitive control that is proposed here to reflect reactive conflict resolution, achieved by closing the gate when facing irrelevant information. On the other hand, proactive gate opening in preparation for relevant information was associated with an increase in relative delta power over parietal-occipital electrodes. Finally, WM updating was associated with relative increase in delta power over midfrontal electrodes, suggesting a functional role of delta oscillations in WM updating. ■

INTRODUCTION

Working memory (WM) is the mental workspace that maintains information for short periods of time. At the same time, as the environment is constantly changing, WM must also adaptively accommodate these changes by updating the stored representations with newer ones. Hence, WM updating is essential for keeping the correspondence between the internal representations and the external world. A fine balance is therefore required between these two functions of WM—maintenance on the one hand and updating on the other (Hommel, 2015). This is because excessive updating would lead to distractibility, whereas extreme maintenance could lead to maladaptive perseveration (Müller et al., 2007; Dreisbach & Goschke, 2004; Hinson, Jameson, & Whitney, 2003). The coordination between the maintenance and updating demands of WM is carried out by controlled selection of information. The control over the input to WM also serves to make an efficient use of WM limited capacity (e.g., Cowan, 2001) in the service of the present goal.

Computational models and neurophysiological data propose that control over WM content is achieved by a gate over WM, which can either be opened or closed (D'Esposito, 2007). The decision of when to open the gate to WM is attained by a frontostriatal mechanism (Cools, 2011; Murty et al., 2011; McNab & Klingberg, 2008; O'Reilly & Frank, 2006) that learns the utility of information through trial and error, thereby improving the efficiency of selecting only goal-relevant information (Chatham & Badre, 2015; D'Ardenne et al., 2012; Braver & Cohen, 2000). When relevant and useful information is detected, the gate opens and facilitates flexible updating of WM (Cools, 2008; Frank, Loughry, & O'Reilly, 2001). However, when a distracting information is detected, robust maintenance is enabled by closing the gate to WM, thereby preventing new perceptual information from entering WM and inappropriately using its scarce capacity (Broadway, Frank, & Cavanagh, 2018).

The Reference-back Paradigm

The reference-back paradigm (Kessler, 2017, in press; Rac-Lubashevsky, Slagter, & Kessler, 2017; Rac-Lubashevsky & Kessler, 2016a, 2016b) is used in this study. This paradigm enables us to distinguish empirically between the subprocesses related to WM updating and specifically between gate opening, gate closing, and updating. This task is composed of two types of trials: reference (denoted by red frames) and comparison (denoted by blue frames). In this task, participants are required to decide whether the current stimulus is the same as or different from the last stimulus presented within a red frame. Notably, both trial types (reference and comparison) require a same/different response; however, only reference trials involve

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WM updating. Previous studies using the reference-back task supported the notion of gate opening and gate closing by demonstrating that switching between reference and comparison trials leads to increased RT (Rac-Lubashevsky & Kessler, 2016a, 2016b) and eye blink rate (EBR; Rac-Lubashevsky et al., 2017)—the latter is associated with central dopaminergic activity (Jongkees & Colzato, 2016).

EEG Correlates of WM

The aim of this study was to investigate the neural oscillations that are associated with the control processes involved in controlling and updating the content of WM.

Converging evidence shows a relative theta power increase and a relative alpha power decrease when memory task demands increase (for a review, see Klimesch, 1999). Specifically, increase in relative theta power and decrease in relative alpha power are modulated by WM load (Pesonen, Hämäläinen, & Krause, 2007; Busch & Herrmann, 2003; Jensen & Tesche, 2002; Schack & Klimesch, 2002; Raghavachari et al., 2001; Krause et al., 2000; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; Gevins, Smith, McEvoy, & Yu, 1997). For example, in the *n*-back task, theta activity increases with memory load, from 1-back to 2-back (Deiber et al., 2007) and from 0-back to 3-back (Gevins et al., 1997). Furthermore, the phase coupling between theta and alpha oscillations is also modulated by WM load (Schack, Klimesch, & Sauseng, 2005). Moreover, mental manipulation in WM is supported by anterior decrease in alpha power and increase in frontoparietal phase coupling in the theta band (Sauseng, Klimesch, Schabus, & Doppelmayr, 2005).

These patterns of alpha and theta activity are commonly observed in memory tasks, both in WM (e.g., Deiber et al., 2007; Krause et al., 2000) and long-term memory (e.g., Jacobs, Hwang, Curran, & Kahana, 2006; Klimesch, Doppelmayr, Schwaiger, Winkler, & Gruber, 2000). However, most of these findings are predominantly explained by task difficulty, without offering a more specific interpretation of their role in memory functioning. This interpretation is consistent with the more general findings that cognitive effort is associated with increased power in the very low (delta, theta) and very high (gamma) frequencies and usually decreased power in the alpha and beta bands (Esposito, Mulert, & Goebel, 2009; Jensen & Tesche, 2002; Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Raghavachari et al., 2001; Gevins et al., 1997). However, it is still unclear what the mechanistic role of these frequencies in WM tasks is and how they relate to specific WM processes.

The inhibition timing hypothesis (Klimesch, Sauseng, & Hanslmayr, 2007) offers a mechanistic explanation for alpha oscillations in visual WM tasks with distractors. Under this hypothesis, relative increase in alpha power expresses the inhibition of task-irrelevant brain regions (Roux & Uhlhaas, 2014; Bonnefond & Jensen, 2012; Klimesch, 1999, 2012; Haegens, Osipova, Oostenveld, & Jensen, 2010; Sauseng et al., 2009; Klimesch et al., 2007). Specifically, increased alpha power at occipital areas reflects the inhibition of the dorsal visual stream that prevents visual input flow to WM (Tuladhar et al., 2007). Although this account is very similar to the notion of gate closing, it is not likely that increased alpha power will be observed in the reference-back task because all trials in the task are task relevant.

A framework explaining the functional role of rhythmic activity at theta, alpha, and gamma frequencies during WM maintenance in humans was offered by Roux and Uhlhaas (2014). They suggested that gamma-band oscillations reflect a basic mechanism for active maintenance in WM. This gamma activity is not specific to the presentation type (e.g., serial or simultaneous) or the modality. On the other hand, theta activity is specific to sequential presentation, and alpha activity is specific to simultaneous visual or spatial presentation of information.

A promising framework for understanding the relationship between WM processes and EEG oscillations modes is provided by a spiking network model that employed the DMS task with distractors (Dipoppa & Gutkin, 2013). This model ascribed each oscillatory band of gamma, theta, and alpha a specific functional role: input gating, selective gating, and output gating, respectively. However, this model does not distinguish between WM encoding (i.e., updating) and gate opening, which leads to (and perhaps precedes) encoding. The selective-gating mode in the model, which is very close to our notion of gate closing (Rac-Lubashevsky & Kessler, 2016b), was reflected by theta activity, arguably responsible for distractor-resistant maintenance. Also, the gate-out mode, which is responsible for clearing WM content, was associated with alpha activity. These results offer important insights on the specific role of gamma–beta, theta, and alpha oscillations in controlling WM content.

This Study

At present, very little in known on the oscillatory dynamics that support the updating of WM and the control mechanisms behind it. The aim of this study was to fill this gap by using a process-based approach that utilizes the reference-back task to test how each of these processes unfolds in time and which frequency band supports it. To this end, the control processes involved in gate opening and in gate closing is tested with scalp EEG. Although we are unlikely to capture at the scalp surface the dopaminergic gating signaling at the basal ganglia, which is anatomically composed of unaligned spiny cells (Nambu & Llinás, 1997), we aim to measure the cortical dynamics associated with, as well as resulting from, gating. Specifically, controlled gating also regulates the projection of dopamine to pFC (D'Ardenne et al., 2012; Hazy, Frank, & O'Reilly, 2007), which plays a key role in controlling WM (Curtis & D'Esposito, 2003; Miller, 2000). Furthermore, being a controlled process, WM gating likely depends

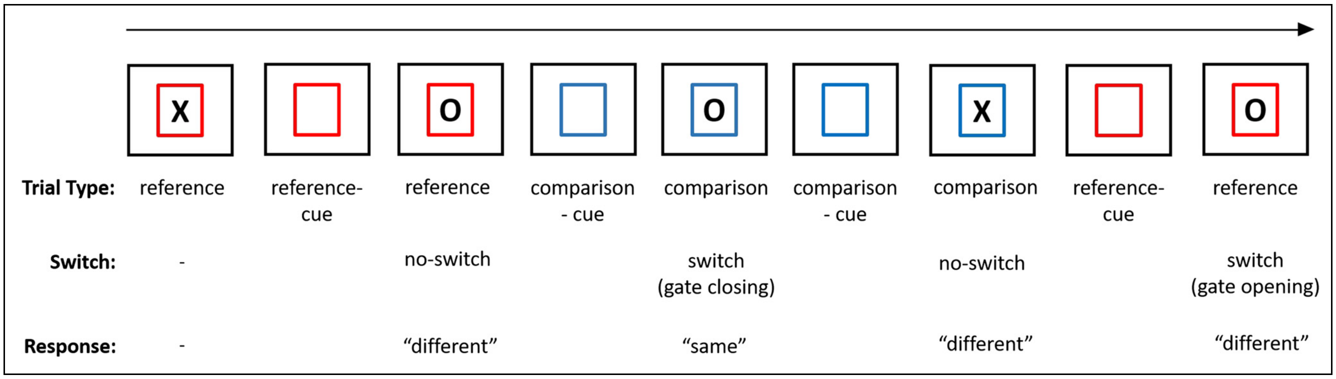


Figure 1. The reference-back task. Trials with a red frame are reference trials and trials with a blue frame are comparison trials (see text for details). The cue was presented before the stimulus as an empty colored frame for 1–1.3 sec. The probe was presented until response. A fixation screen was presented after response was completed for 2–2.3 sec.

on neural networks that support cognitive control initiation and, specifically, the frontoparietal control network (Cole, Yarkoni, Repovš, Anticevic, & Braver, 2012; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Braver & Barch, 2002). Therefore, we aim to tap into the cortical EEG correlates of the control processes involved in gate opening and closing.

Based on our previous work with a cued version of the reference-back task (Rac-Lubashevsky et al., 2017), the time–frequency analysis is performed on three planned contrasts (see Figure 1 and Table 1): (1) Switching effect in reference trials: This is the difference between switch reference trials (namely, reference trials that were preceded by comparison trials) and no-switch reference trials (reference trials that were preceded by reference trials). The logic is that switching from a comparison to a reference trial entails shifting from a "maintenance mode" of WM to an "updating mode" (see Kessler & Oberauer, 2014). Accordingly, this contrast is sensitive to the processes involved in gate opening. (2) Switching effect in comparison trials: This is the difference between switch-comparison trials (i.e., comparison trials that were preceded by reference trials) and no-switch comparison trials (i.e., comparison trials that were preceded by comparison trials). This contrast captures moving from an "updating mode" to a "maintenance mode" and thus is sensitive to processes involved in gate closing. (3) WM updating: This is the difference between no-switch reference trials and no-switch comparison trials and thus is sensitive to the processes involved in updating WM with the information presented by the probe. Notably, this contrast only involves no-switch trials and, therefore, does not involve processes associated with gating (that only takes place in switch trials). We restrict our analysis of this contrast to the probe phase only, because there is no reason to expect WM updating at the cue phase, where there is no information to update WM with. In contrast to updating, alternating between maintenance and updating might take place at the cue phase as part of a proactive control strategy that prepares for an upcoming relevant or irrelevant information (Braver, 2012). Indeed, in a previous study (Rac-Lubashevsky et al., 2017), reduced switch costs in RT were observed in both reference and comparison trials in the cued reference-back compared with the reference-back without the cue. This effect is analogous to preparatory effects in task switching (however, this cannot be fully explained by mere task switching; see Kessler, 2017).

Table 1. The Calculation of the Planned Contrast Derived from the Reference-back Task

	Comparison Trials		*Reference Trials*	
	Switch	*No Switch*	*Switch*	*No Switch*
WM updating		−		+
Switching effect in reference ("gate opening")			+	−
Switching effect in comparison ("gate closing")	+	−		

"Switch" and "no switch" refer to the alternation or repetition of the trial type (being reference or comparison). Note that switching might take place during the cue-locked interval and/or during the probe-locked interval, but WM updating can only take place in the probe-locked time window. See text for details.

METHODS

Participants

Forty-six participants were tested. Participants were students at Ben-Gurion University of the Negev who were paid for their participation. An informed consent was obtained from all participants. Eleven participants were removed from the analysis because of low accuracy on the reference-back task (1), using their fingers to remember the reference (3), or very noisy data (7).

Thirty-five participants (16 women, age: $M = 24.3$ years, $SD = 2.6$ years) were therefore included in the analysis.

Stimuli and Procedure

Stimuli presentation and behavioral data collection were done using E-Prime v2.0 (Psychology Software Tools). The reference-back task was composed of two trial types: reference and comparison (see Figure 1). Each trial started with a presentation of a cue, being a red or blue empty frame, which indicated whether it was a reference or a comparison trial. The colors (red/blue) used to indicate the trial types were counterbalanced between participants. The duration of the cue was jittered between 1000 and 1300 msec. The stimulus "X" or "O" was then presented in black inside the colored frame until response. The color of the frame and the stimulus in each trial were selected at random with 50% probability. Participants had to indicate whether the stimulus was the same as or different from the one presented in the most recent reference trial. In other words, they were required to compare each letter stimulus to the one that appeared in the most recent reference trial. "Same" and "different" responses were indicated using the right and left index fingers, respectively, using a serial response box. The response was followed by an intertrial interval of 2000–2300 msec. Participants were instructed to keep their eyes fixated on the center of the screen throughout the experimental blocks and not to blink during stimulus presentation (cue and probe) but only during the fixation screen. The first trial in a block was always a reference trial and did not require a response. The experiment comprised 13 blocks, including 62 trials each. Participants completed one practice block before they began the experiment.

EEG Recordings

EEG recordings were obtained using BioSemi Active Two 64-electrode system with linked mastoid as a reference. Additional electrodes were placed at the outer left and right canthus and below the left eye for measurement of eye movements (EOG). Data were acquired using a 0.01–100 Hz band-pass filter. The sampling rate was 512 Hz. The signal was digitized using a 24-bit A/D converter.

EEG Preprocessing

Preprocessing was done using the EEGLAB toolbox (Delorme & Makeig, 2004). The continuous EEG data were first high-pass filtered offline at 0.5 Hz and subsequently segmented twice into two epochs, cue-locked and probe-locked. Cue-locked epochs were segmented from −1.2 to +1.8 sec surrounding the cue onset (i.e., the presentation of the empty colored frame). To avoid edge artifacts resulted from the wavelet convolution (explained below), an 800 msec buffer zone was added to the window of interest within the segment. Namely, the buffer was added after the 1000-msec presentation time of the cue and before the baseline, which was set between −200 and −400 msec. The probe-locked analysis was segmented from −2.4 to +1.6 sec surrounding probe onset. Again, to avoid edge artifacts, an 800-msec buffer zone was added after the 800-msec window of interest and before the baseline, which was set between −1600 and −1400 msec (the baseline used for the probe analysis was taken from the time window before the cue presentation). Error trials, posterror trials, and two trials following errors were excluded from the analysis. The epoched data were visually inspected, and those containing large artifacts due to facial EMG activity or other artifacts (except for eye blinks) were manually removed. Independent components analysis was next conducted using EEGLAB's runica algorithm. Components containing blink, oculomotor artifacts, or other artifacts that could be clearly distinguished from genuine neural activity signals were subtracted from the data. Finally, the EEG was subjected to automatic bad electrodes and artifact detection, followed by manual verification. Bad electrodes were interpolated. Before the analysis, data were current source density transformed (Kayser & Tenke, 2006). The second spatial derivative of the field potential (Laplacian transformation) was computed to map the electrical activity of the brain (Tenke & Kayser, 2012).

EEG Power Analysis

Single-trial data were decomposed into their time–frequency representation using custom scripts written in MATLAB (The MathWorks). The power spectrum of the EEG was multiplied by the power spectrum of complex Morlet wavelets (Cohen, 2014b),

$$\left[e^{i2\pi tf}e^{-t^2}/\left(2\sigma^2\right)\right]$$

where t is time, f is frequency, and σ defines the width of the Gaussian tapper of each frequency band. Frequencies increased from 2 to 50 Hz in 15 logarithmically spaced steps, and σ was set to $n/(2\pi f)$, where n increases logarithmically from 3 to 12 in the same number of steps to maintain a fair balance between temporal and frequency resolution. Following convolution, the inverse fast Fourier transform was taken to reshape the data back into individual epochs. Edge artifacts were confined to 800-msec long buffer zones at both ends of each epoch.

From the resulting complex signal, trial-averaged power values were computed. Power was normalized using a decibel transform (dB power = 10 × log10[power/baseline]), where baseline activity was taken as the average power at each frequency band, averaged from −400 to −200 msec precue for the cue-locked analysis. For the probe-locked analysis, baseline activity was taken as the average power at each frequency band, averaged from −1600 to −1400 msec preprobe. Power was calculated for each electrode, separately for each condition (reference-switch, reference-repeat, comparison-switch, and comparison-repeat) and participant, relative to the subject condition baseline.

Statistics on time–frequency changes in power were performed by map-wise t tests followed by cluster-based test statistics. t Values were obtained via permutation testing (Nichols & Holmes, 2002) where the difference mapping between two conditions was randomly shuffled for each subject. Cluster-based test statistics was calculated by taking the sum of the t values within a cluster of significant pixels, $p < .05$ (Maris & Oostenveld, 2007). This was repeated 1000 times, generating a distribution of maximum cluster-level statistics under the null hypothesis. The cluster threshold was defined as the 97.5th quantile of a t distribution for positive and negative t values.

RESULTS

Behavioral Results

Trials containing error, trials following an error, fast trials (<200 msec), and RT outliers (3 *SD* above or below the participant's mean RT in each condition) were excluded from the RT analysis.

A two-way ANOVA was conducted on mean RT with Trial type (reference, comparison) and Switch (switch, repeat) as within-subject independent variables (see Figure 2). The main effect of Trial type was significant, 107 msec, $F(1, 34) = 27.04$, $MSe = 2156.80$, $p < .001$, $\eta_p^2 = .44$, reflecting slower responses for reference trials, which required WM updating, compared to comparison trials. The main effect of Switch was also significant, $F(1, 34) = 18.79$, $MSe = 2143.76$, $p < .001$, $\eta_p^2 = .36$, in the expected direction: Switch trials were 100 msec slower than repeat trials. The interaction between Trial type and Switch was not significant, $F(1, 34) = 1.70$, $MSe = 1120.33$, $p = .20$, $\eta_p^2 = .05$, reflecting a symmetrical switching cost in both directions.

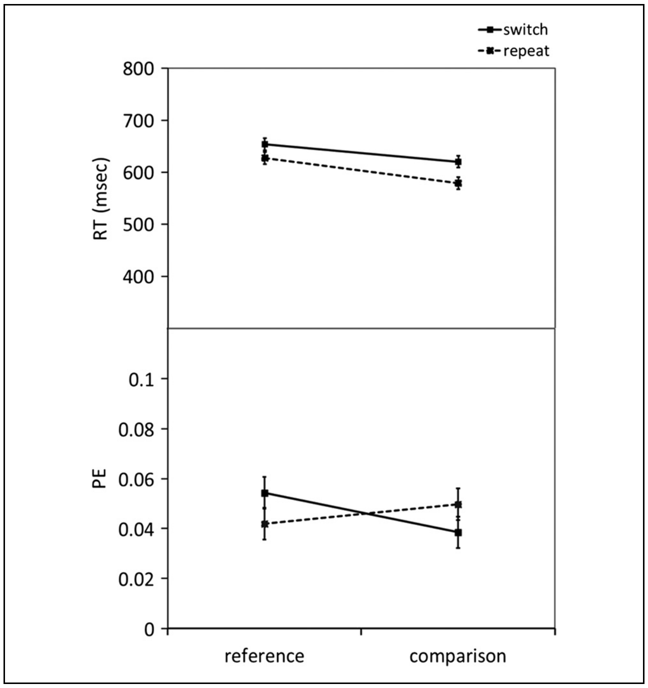


Figure 2. Behavioral results: RT (top) and PE (bottom). Error bars represent 95% confidence intervals.

A similar two-way ANOVA was conducted on error proportions (PE; see Figure 2). Only the two-way interaction was significant, $F(1, 34) = 14.40$, $MSe = 0.0003$, $p < .001$, $\eta_p^2 = .30$. In the reference trial type, more errors were observed in the switch condition compared with the repeat condition, $F(1, 34) = 8.03$, $MSe = 0.0003$, $p = .008$, $\eta_p^2 = .19$. However, a switch cost in the opposite direction was observed in comparison trials, $F(1, 34) = 12.24$, $MSe = 0.0002$, $p = .001$, $\eta_p^2 = .26$ (the effect in PE was 1.6% in reference trials and −0.8% in comparison trials). The unexpected reversed switch cost in comparison trials but not in reference trials might reflect an inefficient gate closing. Gate closing is required for robust maintenance of the reference stimulus. In the first comparison trial in a row (i.e., a comparison-switch trial), participants could rely on recency in comparing the presented stimulus to the one presented in the previous (reference) trial. However, if the gate over WM did not close on the first comparison trial, then it may have led to inappropriate updating of the reference stimulus and hence to errors in the matching decision in subsequent trials.

EEG Results

We calculated event-related changes in band power in the frequency range of delta (2–4 Hz), theta (4–7.5 Hz), and alpha (7.5–12.5 Hz) across conditions at the locations where condition average activity was maximal (see Figures 3, 4, and 6). The condition average activity at gamma (31–50 Hz) exhibited very weak activity over the scalp and, therefore, was not tested further. The analysis was calculated twice, once at the cue-locked time window and once at the probe-locked time window.

Delta activity was examined at the midfrontal area (FCz, FC1) where the average condition activity peaked both in the cue and in the probe time window (see Figure 3A). Delta exhibited relative power increase in reference trials, especially in reference-switch condition in both time windows (Figure 3B). Therefore, the switching effect in reference trials (the difference between reference-switch and reference-no switch trials) was subjected to time–frequency permutation testing. This analysis revealed no significant effect in none of the time windows. The WM updating contrast was also subjected to time–frequency permutation testing, which revealed a strong power increase in delta and theta in the probe time window (see Figure 9).

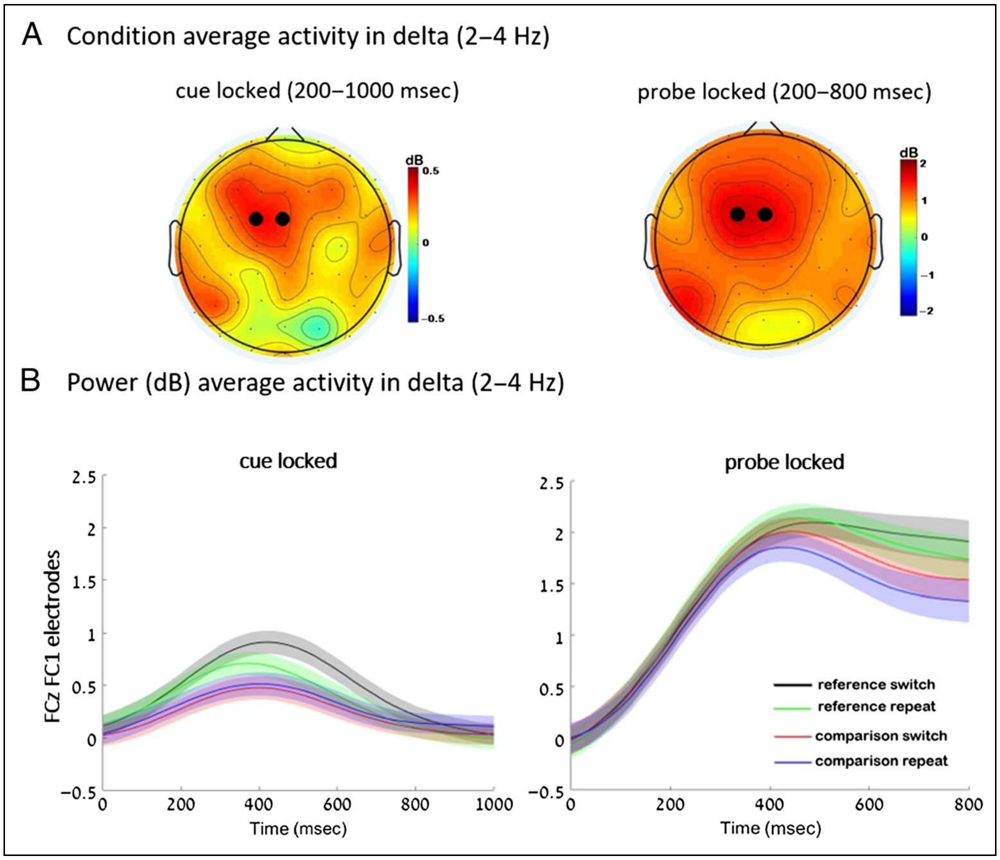


Figure 3. (A) Topographic maps show the spatial distribution of the condition average activity in delta (2–4 Hz) within the cue-locked time window (200–1000 msec; left) and within the probe-locked time window (200–800 msec; right). Black circles depict the electrode where the activity was largest. (B) The time course of condition average activity in delta (2–4 Hz) at the cue-locked time window (left) and the probe-locked time window (right) at the electrode group where delta activity was largest: midfrontal (electrodes FCz and FC1). The shade around the average represents confidence interval. Data in this figure were scalp Laplacian-transformed.

An exploratory approach was employed to search for the optimal site in which the switching effect in reference trials took place. The topographical distribution of the difference activity in delta between the reference-switch and reference-repeat conditions revealed increased activity in left temporal channels (C5, CP5, T7, TP7) and central parietal-occipital area (POz Oz; see Figure 4). Subsequent time–frequency permutation testing at the cue-locked time window confirmed that the switching effect in reference trials was modulated by increased delta power beginning around 400 msec post-cue presentation at both sites (see Figure 5). The time–frequency permutation testing at the probe-locked time window also revealed a significant switching effect in reference trials expressed by a relative increase in delta power through the entire probe time window, but only at the central parietal-occipital area (see Figure 5).

Theta activity was tested at a midfrontal site (Fz) where the average condition activity peaked at the probe-locked time window (see Figure 6A). Theta activity exhibited a strong power increase in the comparison-switch condition in the probe-locked time window (see Figure 6B). Therefore, the switching effect in comparison trials was subjected to time–frequency permutation testing which revealed a significant effect only in the theta frequency range, peaking between 300 and 500 msec post-probe presentation (see Figure 7). No switching effect in comparison trials was detected at the cue-locked time window at this site.

Alpha activity over bilateral parietal-occipital electrodes (mean of PO4, PO8, O2, PO3, PO7, O1) exhibited a strong power decrease in all the conditions; the weakest power decrease was observed in comparison-repeat condition (see Figure 8). Therefore, the switching effect in comparison trials was subjected to time–frequency permutation testing at the cue-locked time window. This analysis revealed no significant effects at the parietal-occipital sites (see Figure 7). The switching effect in comparison trials and the effect of WM updating were also tested in the probe-locked time window. The time–frequency permutation testing revealed a strong alpha power decrease for both contrasts throughout the entire probe-locked time window (see Figures 7 and 9).

DISCUSSION

In this study, the reference-back paradigm was used to study the oscillatory correlates of the control processes involved in WM gating and updating. The results demonstrated a distinct oscillatory activity for the two switching effects that are proposed to be related to gate closing and gate opening (see Table 2).

The switching effect in comparison trials was associated with an increased theta activity at midfrontal electrodes, possibly reflecting an increased need for cognitive control (for a review, see Cavanagh & Frank, 2014). Rhythmic frontal theta synchronization is a neural signature of cognitive control, typically evoked by a conflicting stimulus–response but also in response to negative feedback or error (Cavanagh & Frank, 2014; Cohen, 2014a; Cohen & Donner, 2013; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012). Moreover, this theta activity arguably reflects integration of relevant information around decision points (Womelsdorf, Vinck, Leung, & Everling, 2010). The novelty of our finding in the context of the reference-back is that that activity was not observed following a stimulus–response conflict but rather an updating conflict. Although all comparison trials require the robust maintenance of the last reference stimulus, only comparison-switch trials elicit an updating dilemma. This dilemma possibly arises because the dominant tendency is to update information that had changed (e.g., Rac-Lubashevsky & Kessler, 2016a; Jones, Curran, Mozer, & Wilder, 2013; Soetens, Boer, & Hueting, 1985). This dominant tendency to update needs to be suppressed to enable the more demanding (hence controlled) choice—"not to update." The inhibition of updating is conceivably stronger in comparison-switch trials than in comparison-repeat trials because the former is immediately preceded by reference trials where changes in the stimulus trigger WM updating. Thus, when the stimulus in a comparison-switch trial is different from the previous reference trial, the conflict monitoring system (Botvinick, Braver, Barch, Carter, & Cohen, 2001) is triggered to resolve the updating conflict. This interpretation is consistent with the idea of gate closing that is proposed to be triggered by

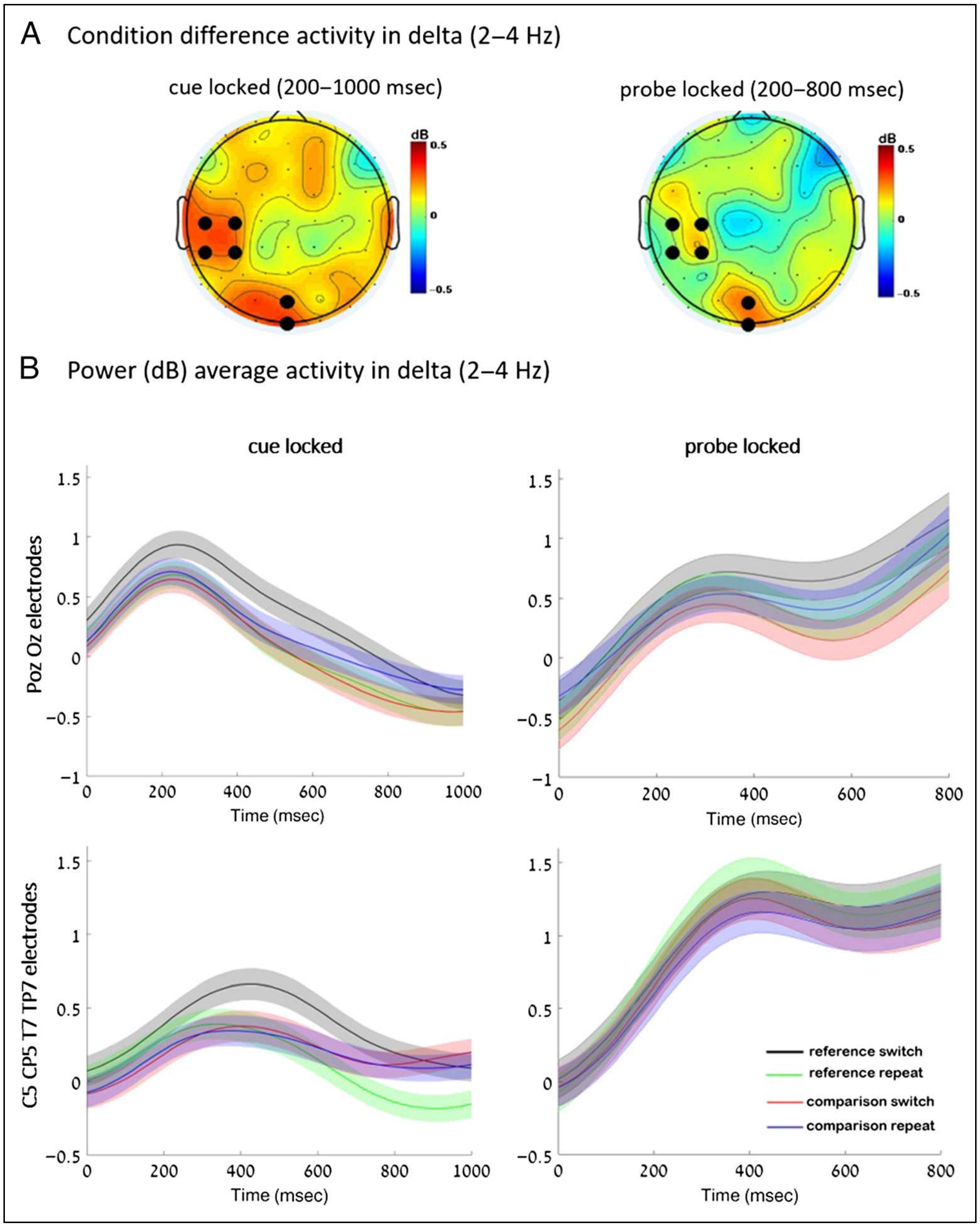
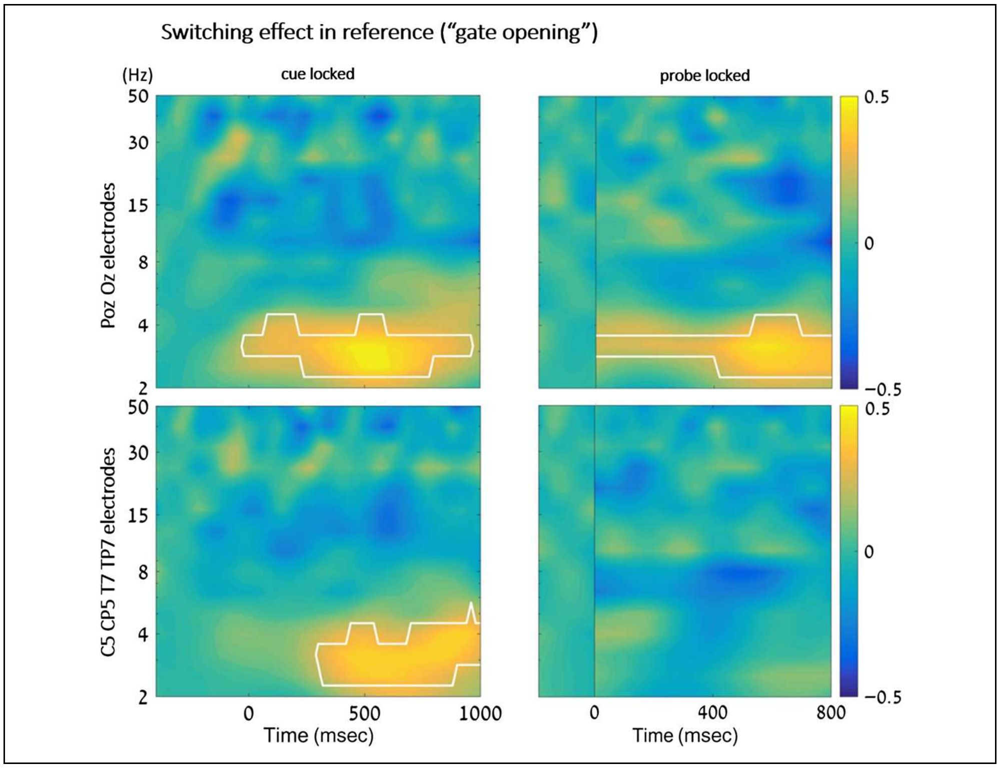


Figure 4. (A) Topographic maps show spatial distribution of the difference activity between switch and repeat reference trials in delta (2–4 Hz) within the cue-locked time window (200–1000 msec; left) and within the probe-locked time window (200–800 msec; right). Black circles depict the electrode where the difference activity was largest. (B) The time course of condition average activity in delta (2–4 Hz) at the cue-locked time window (left) and the probe-locked time window (right) at two electrode groupings where delta activity was largest: central parietal-occipital (electrodes POz and Oz; top) and left temporal (electrodes C5, CP5, T7, and TP; bottom). The shade around the average represents confidence interval. Data in this figure were scalp Laplacian-transformed.

Figure 5. Time–frequency power plots for the switching effect in reference (the difference between reference-switch and reference-no switch). The time–frequency plots show two electrode groups: left temporal (electrodes C5, CP5, T7, and TP7; top) and parietal-occipital (electrodes POz and Oz; bottom) within the cue-locked (left) and probe-locked (right) time windows. The area marked in white is the significant area revealed by time–frequency permutation testing.



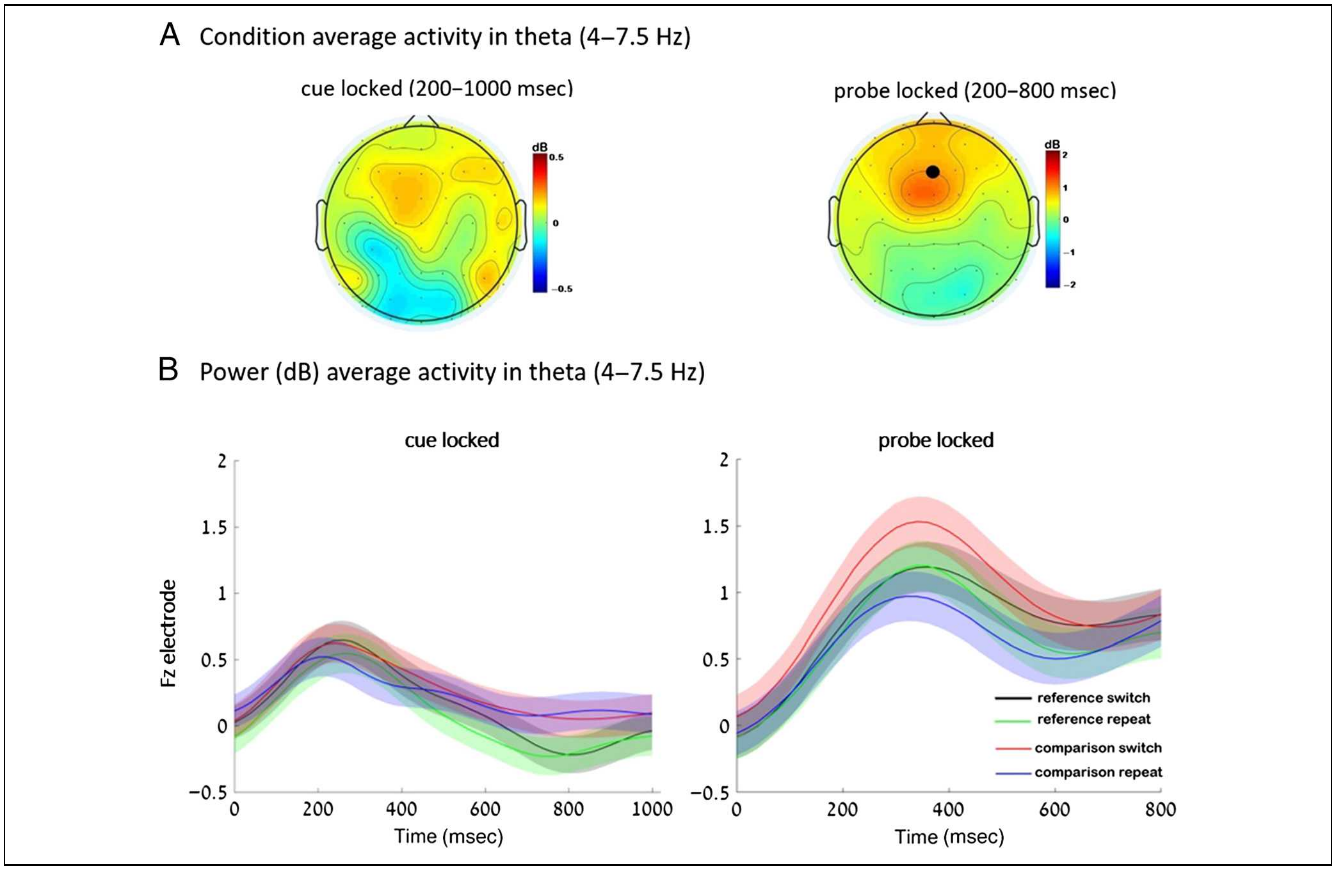


Figure 6. (A) Topographic maps show the spatial distribution of the condition average activity in theta (4–7.5 Hz) within the cue-locked time window (200–1000 msec; left) and within the probe-locked time window (200–800 msec; right). Black circles depict the electrode where the activity was largest. (B) The time course of condition average activity in theta (4–7.5 Hz) at the cue-locked time window (left) and the probe-locked time window (right) at the midfrontal electrode where theta activity was largest (Fz). The shade around the average represents confidence interval. Data in this figure were scalp Laplacian-transformed.

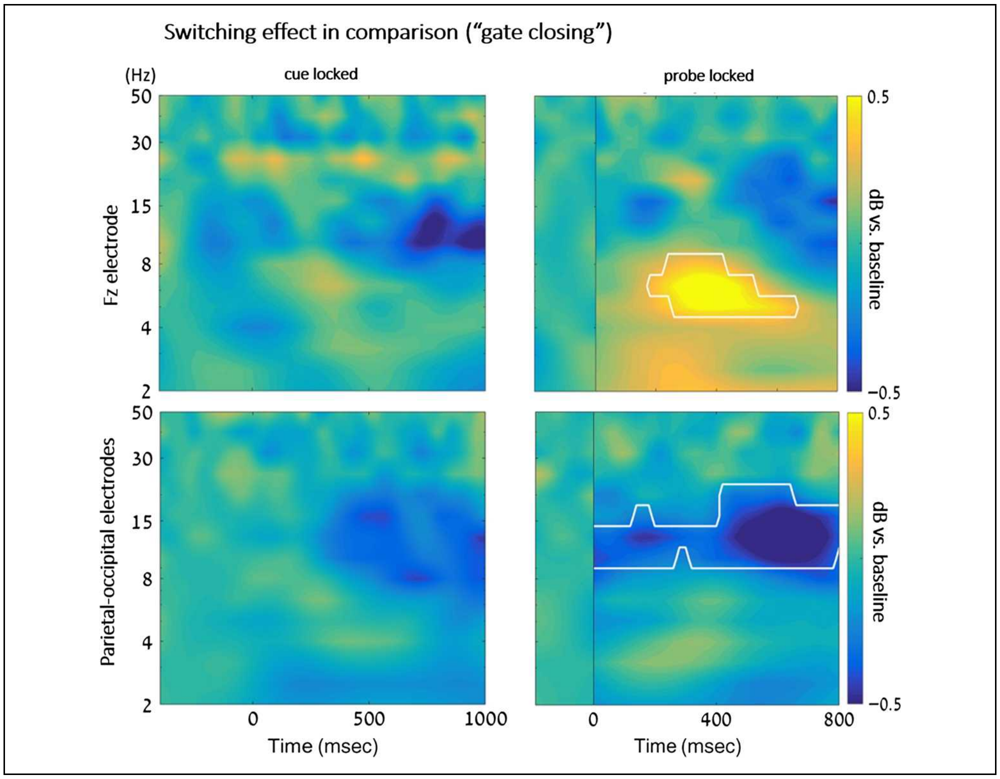


Figure 7. Time–frequency power plots for the switching effect in comparison (the difference between comparison-switch and comparison-no switch). The time–frequency plots show two electrode groups: midfrontal (Fz; top) and parietal-occipital (PO4, PO8, O2, PO3, PO7, O1; bottom) within the cue-locked (left) and probe-locked (right) time windows. The area marked in white is the significant area revealed by the time–frequency permutation testing.

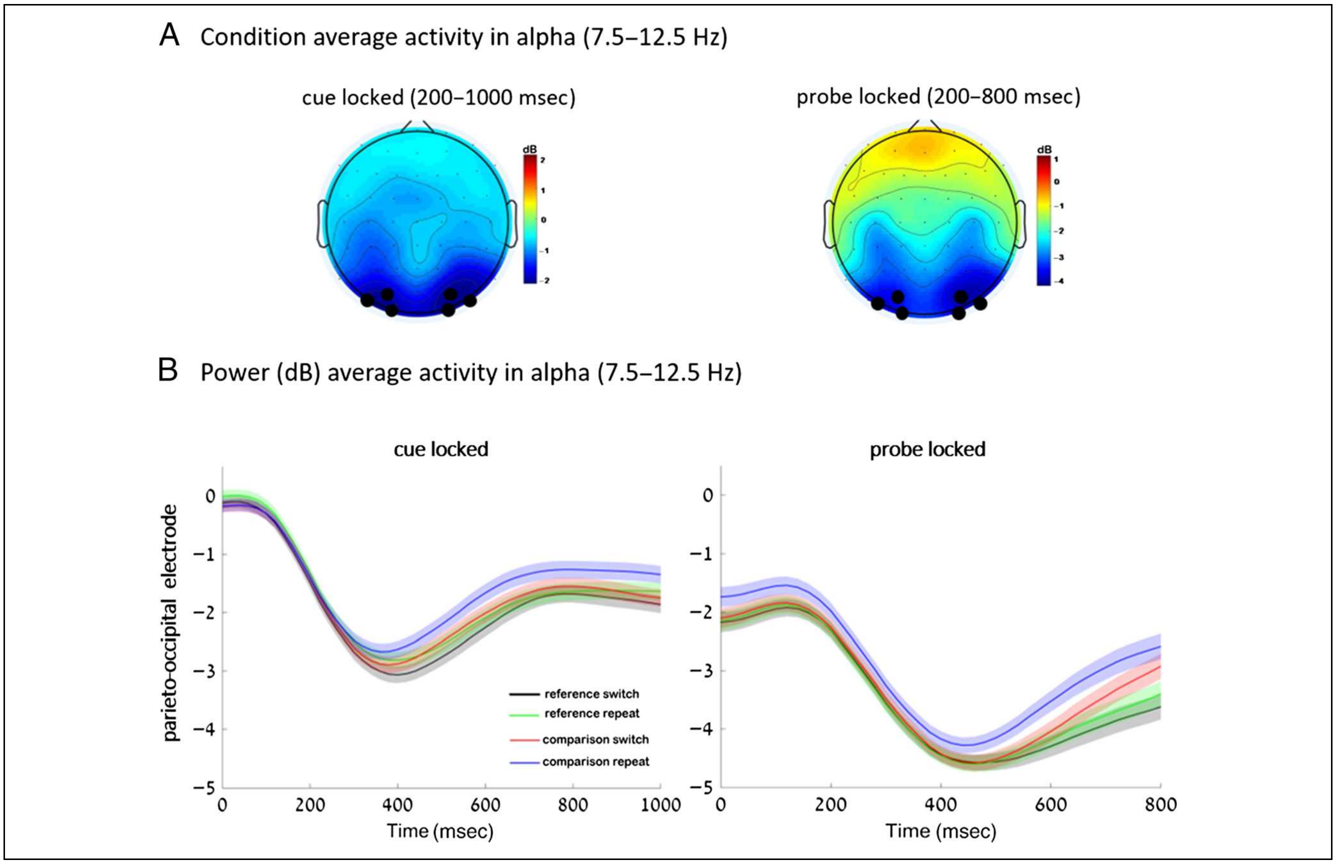


Figure 8. (A) Topographic maps show spatial distribution of the condition average activity in alpha (7.5–12.5 Hz) within the cue-locked time window (200–1000 msec; left) and within the probe-locked time window (200–800 msec; right). Black circles depict the electrode where the activity was largest. (B) The time course of condition average activity in alpha (7.5–12.5 Hz) at the cue-locked time window (left) and the probe-locked time window (right) at the electrode group where alpha activity was largest: central parietal-occipital (PO4, PO8, O2, PO3, PO7, O1). The shade around the average represents confidence interval. Data in this figure were scalp Laplacian-transformed.

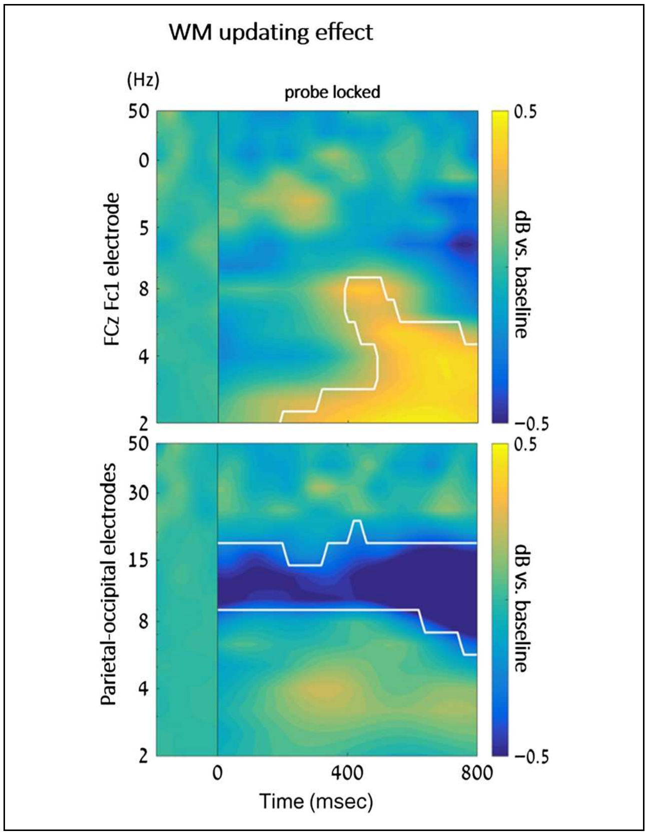


Figure 9. Time–frequency power plots for the effect of WM updating (the difference between reference-no switch and comparison-no switch). The time–frequency plots show two electrode groups: midfrontal (FCz and Fc1; top) and parietal-occipital (PO4, PO8, O2, PO3, PO7, O1; bottom) within the cue-locked (left) and probe-locked (right) time windows. The area marked in white is the significant area revealed by the time–frequency permutation testing.

switching to comparison (Rac-Lubashevsky et al., 2017; Rac-Lubashevsky & Kessler, 2016b). Gate closing is the control mechanism that deals with the updating dilemma by changing the state of WM to a "maintenance mode." The observed theta response during gate closing extends the functional role of the midfrontal theta marker by positing that this marker may reflect suppression of a dominant tendency, which does not need to be a motor response, but also—as in our case—an automatic tendency to update WM.

Increased delta activity was observed during switching to reference, a contrast proposed to trigger gate opening (Rac-Lubashevsky et al., 2017; Rac-Lubashevsky & Kessler, 2016b), and during updating itself. Although there is not much investigation of the role of delta in the context of WM and cognitive control, our results support previous studies demonstrating the involvement of delta in top–down control (Gulbinaite, van Rijn, & Cohen, 2014; see review by Harmony, 2013). Furthermore, central-posterior delta activity was suggested to have a mechanistic role in processing reward prediction errors and in action selection. According to this view, delta links state representations (i.e., representations of the environment) with actions and outcomes by influencing subcortical areas such as the midcingulate cortex and the striatum (Cavanagh, 2015). Therefore, the delta activity observed at parietal-occipital sites already at the cue time window may reflect top–down influence, which is perhaps guided by reward prediction error signaling, on brain areas responsible for initiating gate opening.

The novelty in the current findings is that central-parietal delta is suggested to be part of a proactive control process responsible for preparing for WM updating rather than for action. Proactive control refers to the preference or ability, in some cases, to keep task goals continuously active even before conflicting information is detected. This control mode optimizes preparation, although it minimizes and even prevents interference induced by the stimulus. In contrast, in a reactive control mode, conflict interference is resolved only after the stimulus is detected (Braver, 2012). Successful cognition depends upon an optimal combination of the gating policy with the control strategy of proactivity and reactivity that is learned during the task (Bhandari & Badre, 2018).

To conclude, current results highlight a dissociative role of theta and delta in terms of their role in conflict resolution (Cohen & Ridderinkhof, 2013; Agam et al., 2011) during WM gating. The midfrontal theta activity

Table 2. Summary of the Significant Effects in Delta, Theta, and Alpha Power in the Cue and Probe Time Windows for Gate Closing, Gate Opening, and WM Updating

	Cue-locked Time Window			*Probe-locked Time Window*		
	Switching Effect in Comparison (Gate Closing)	*Switching Effect in Reference (Gate Opening)*	*WM Updating*	*Switching Effect in Comparison (Gate Closing)*	*Switching Effect in Reference (Gate Opening)*	*WM Updating*
Delta (POz, Oz)		↑			↑	
Delta (FCz, FC1)						↑
Theta (Fz)				↑		
Alpha (occipital electrodes)				↓		↓

Upward arrows represent a relative power increase, whereas downward arrows represent a relative power decrease.

is interpreted as the marker of the monitoring system employed to trigger the reactive suppression of updating, whereas the delta activity is interpreted to mark the proactive preparation for updating as part of a top–down control processing that may be guided by reward prediction error. Notably, these results complement our previous findings using the reference-back paradigm, showing increased EBRs associated with gate closing but not gate opening during the cuing interval, before the stimulus was presented (Rac-Lubashevsky et al., 2017). It is therefore conceivable that EBR and the oscillatory activity observed here are sensitive to different but complementary processes: The former possibly marks the dopaminergic signaling in the striatum that closes and opens the gate, whereas the delta activity and theta activity respond to the control process (i.e., cue-induced top–down control and stimulus-induced conflict monitoring, respectively), which in turn triggers the dopamine signaling. Unfortunately, this study was not suitable to measure EBR. The short cue duration was not optimal for EBR measurement, and the participants were explicitly instructed not to blink throughout the trial. Future research should therefore investigate the interplay between oscillatory activity and EBR in the context of gate closing and gate opening, as well as the role of individual differences in the computational cost of proactivity (Westbrook & Braver, 2016) that might moderate these physiological markers.

Finally, strong alpha suppression over parietal-occipital area was also observed during switching to comparison, interpreted as gate closing. Previous studies showed that decrease in alpha power is usually detected in areas that are active during the task (Pfurtscheller & Da Silva, 1999) insofar that the magnitude of the decrease in alpha power reflected the degree of cortical activation or task difficulty elicited by the cognitive demands of the task (Klimesch, 2012; Klimesch et al., 2007; Keil, Mussweiler, & Epstude, 2006; Stipacek, Grabner, Neuper, Fink, & Neubauer, 2003; Pfurtscheller, 2001; Krause et al., 2000). Thus, the decrease in alpha power perhaps reflects a general increase in computational demands during visual processing (Klimesch et al., 2007; Medendorp et al., 2006; Mazaheri & Picton, 2005; Klimesch, Doppelmayr, Roehm, Pöllhuber, & Stadler, 2000; Pfurtscheller, Neuper, & Mohl, 1994). Once the probe was presented, it initiated a cascade of processes, in additional to perceptual processing, such as making the same/different decision, updating WM, and switching the state of a gate. These additional processes possibly lead to the observed effects in alpha (gate closing and WM updating), which were calculated as the difference from the least demanding condition, the comparison-repeat condition. We therefore suggest that the observed pattern of alpha suppression is the result of nonspecific processing difficulty.

To conclude, a process-based approach was employed to examine the functional role of neural oscillations during WM updating and gating. The results extend the role of midfrontal theta in not only managing response conflict but also in reactively suppressing updating in WM. Delta at central parietal-occipital areas is suggested to mark the top–down control of updating, whereas delta at midfrontal area is associated with the updating process per se.

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