

Published in final edited form as:

Neurosci Lett. 2010 January 14; 468(3): 339–343. doi:10.1016/j.neulet.2009.11.028.

Theta and Alpha oscillations during working-memory maintenance predict successful long-term memory encoding

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Abstract

To date, much is known about the neural mechanisms underlying working-memory (WM) maintenance and long-term-memory (LTM) encoding. However, these topics have typically been examined in isolation, and little is known about how these processes might interact. Here, we investigated whether EEG oscillations arising specifically during the delay of a delayed matching-to-sample task reflect successful LTM encoding. Given previous findings of increased alpha and theta power with increasing WM load, together with the assumption that successful memory encoding involves processes that are similar to those that are invoked by increasing WM load, alpha and theta power should be higher for subsequently remembered stimuli. Consistent with this assumption, we found stronger alpha power for subsequently remembered stimuli over occipital-to-parietal scalp sites. Furthermore, stronger theta power was found for subsequently remembered stimuli over parietal-to-central electrodes. These results support the idea that alpha and theta oscillations modulate successful LTM encoding.

To date, much is known about neural mechanisms underlying active maintenance of information in working memory (WM) and the encoding and retrieval processes that support long-term memory (LTM). However, these topics have typically been examined in isolation, and little is known about how these processes might interact. For example, it is presently unclear how WM maintenance affects LTM formation. According to Hebb [6], the transient maintenance of information serves to strengthen LTM traces in the brain. Thus, if WM maintenance supports LTM formation, neural activity during WM maintenance should be predictive of subsequent LTM performance. Consistent with this hypothesis, results from fMRI studies showed that activity in the dorsolateral prefrontal cortex, occipital cortex, and hippocampus during the initial stage of WM maintenance was predictive of subsequent LTM performance [1,3,31,35]. Furthermore, it has been found that negative event-related slow potentials of the EEG during a WM delay also reflect successful LTM encoding, i.e., they were stronger for subsequently remembered stimuli [16]. These results are consistent with the idea that WM maintenance contributes to LTM formation.

In the present study, we sought to further substantiate the claim that WM activity promotes LTM encoding by examining neural oscillations. EEG was recorded while participants performed a delayed matching-to-sample task with either line drawings of novel three-dimensional objects or letter strings as stimuli (Fig. 1). Next, they completed a surprise LTM recognition test consisting of items that were seen during the WM task and unstudied foil

items. We then examined oscillatory power during WM maintenance as a function of LTM performance. Based on research linking EEG oscillations in the alpha and theta bands to memory processes, we focused our analyses on these frequency bands [for reviews, see 17,18]. Prior research has shown that alpha power during WM retention intervals increase with WM load [11,21,33]. To the extent that WM maintenance promotes successful LTM encoding, we might expect to see increased power in the EEG alpha band during WM maintenance for subsequently remembered stimuli than for stimuli that were not subsequently remembered (i.e., a difference based on later memory, or “*Dm*” effect in the alpha band). In addition, several studies have shown that theta power increases with increasing WM load [4,12], and theta power during encoding tasks has been shown to predict later memory [19,20,36]. Based on these prior findings, we predicted that theta power during WM maintenance should be increased for subsequently remembered items relative to items that are not subsequently remembered.

Methods

Participants

The present study is a frequency-domain analysis of a previous ERP study [16]. Due to several selection criteria (see EEG-data acquisition and analysis), the final sample consisted of 17 participants (9 female, mean age = 22.12 years, SD = 1.90 years), which were all right-handed, healthy, and native speakers of German. The study was conducted in accordance with the Declaration of Helsinki (<http://www.wma.net>) and all procedures were carried out with the written consent of the participants.

Stimuli, Task, and Procedure

Participants performed 200 trials of a delayed matching-to-sample task (Fig. 1), in which a cue object or letter string was shown for 1 s, and subjects were instructed to internally rehearse the stimulus across a variable 5–7 s delay period. Following the delay, a probe stimulus was shown for 2 s, and participants indicated by a button press whether the probe was identical to or different from the cue. A variable inter-trial interval of 2–3 s preceded the start of the next trial. Object stimuli were 200 line drawings of novel “possible” objects drawn in part from previous studies [34,40]. Letter strings were 200 letter strings with six letters each, consisting of a three-letter syllable (consonant-vowel-consonant), followed by three random consonants (see Fig. 1). The same letter could appear more than once in a letter string. This combination of vowels and consonants was chosen through pilot studies which showed that subsequent memory for these stimuli was equivalent to that for the object stimuli. Participants were instructed to suppress blinks or eye movements throughout the trial. 150 objects and 150 letter strings were used in the WM task, with 50 stimuli for the “match” condition, 50 stimuli for the “non-match” condition, and 50 stimuli as non-matching targets. The remaining 50 objects and 50 letter strings were used as new foils in the subsequent memory test. After the WM phase, a surprise recognition test was applied, including all cue stimuli from the WM task, interspersed with the 100 new items. All stimuli had to be rated on a confidence scale with categories 1 (“definitely seen”), 2 (“probably seen”), 3 (“probably not seen”), and 4 (“definitely not seen”). The Oldfield Handedness Inventory [26] served as a distracter task after the WM task to reduce recency effects on memory retrieval. For a more detailed description of the stimuli and the experimental procedure, see the Methods in [16].

EEG-Data Acquisition and Analysis

The EEG was recorded from 61 Ag/AgCl electrodes (Easycap System, Falk Minow, Munich, Germany) by two 32-channel DC amplifiers (SYNAMPS, NeuroScan) and NeuroScan software Acquire (sampling rate = 500 Hz) referenced to one earlobe during the

recording and re-referenced offline to averaged earlobes. Additional electrodes were attached around the eyes for horizontal and vertical EOG recording. Impedances were kept below 5 k Ω . DC drift was corrected according to a regression-based algorithm [7]. Power spectra were calculated by conducting a Fast Fourier Transform (FFT) on EEG data from 5 non-overlapping Hanning-windowed 1000-ms epochs that spanned the WM delay period. Prior to FFT, epochs containing artifacts were identified and removed by applying the following criteria: (1) the maximal allowed absolute difference of two values in the segment was 150 μ V, (2) the minimal absolute difference of two values in any 200 ms interval was 0.50 μ V (“dead-channel criterion”), and (3) the maximal allowed voltage step between two adjacent sampling points was 20 μ V.

For the FFT analysis, we collapsed the data across material type, because the present analysis did not aim at material-specificity of possible subsequent-memory effects. Furthermore, our selection criterion that only those participants with more than 15 artifact-free EEG segments in either the “remembered” or “forgotten” condition entered the FFT analysis would not have provided a sufficient number of participants for the present study. Finally, a visual inspection of alpha and theta power during the maintenance delay showed that the topographies were comparable across material types with a parietal-occipital maximum of alpha power and a midfrontal maximum for theta power for both objects and letter strings (see Fig. 1).

Alpha (9–13 Hz) and theta power (5–8 Hz), obtained from the FFT spectra, was averaged over trials for each participant, electrode, experimental condition (later remembered vs. forgotten), material type (objects vs. letter strings), and time window. Only correct responses on the WM task were used for the average. EEG analysis was performed using the BrainVision-Analyzer software (www.brainproducts.com). As in our previous ERP study [16], we excluded the mid-range confidence ratings of “probably seen” from the analyses in order to minimize the influence of trials with guessing responses. Therefore, analyses of subsequent memory effects contrasted trials with confidently remembered items (i.e., trials with “definitely seen” responses) against items that were forgotten (i.e., trials associated with “probably not seen” and “definitely not seen” responses). A subset of 19 electrodes that were evenly distributed across the scalp corresponding to the international 10–20 system [10] entered the statistical analysis.

Focusing on theta and alpha does not fully capture the complete range of memory-related EEG frequencies. However, we think that a restriction to alpha and theta is appropriate for the present dataset: First, looking for effects in the delta range (1–4 Hz) is always problematic with DC-recorded EEG data, as slow drifts that are preserved in the EEG signal are hard to disentangle from “real” oscillations. A bandpass filter for delta captures parts of these slow drifts, producing a distorted signal with very low signal-to-noise ratio. Second, obtaining effects in the gamma range (>25 Hz) with scalp-recorded EEG is a generally difficult enterprise, as signal-to-noise ratios are usually very low and baseline correction is necessary for obtaining reliable signals. However, we refrained from baseline correction, because the prestimulus interval, which is typically used for baseline correction, is the period in which the participants prepared for the trial, i.e., for not blinking for an interval of at least 9 seconds (cf. Fig. 1). Therefore, the prestimulus interval is full of ocular artefacts and therefore not suited for EEG analysis. Furthermore, as we were interested in the difference between remembered and forgotten items, the baseline anyway would cancel out in this difference. To conclude, the situation is most unfavorable for detecting gamma effects. Nevertheless, we checked for effects in the gamma range, but found no reliable amplitude changes and topographies for remembered and forgotten items, and no significant *Dm* effect. This was also true for the beta frequency range (13–18 Hz). Here, the results were also inconsistent and not reliable in the statistical analysis.

Results

Behavioral Data

In order to assess recognition performance, we compared the mean percentages of “definitely seen” judgments for studied and unstudied items, i.e., the hit and false-alarm rates. The hit rates were significantly higher (31.44 %) than the false alarm rates (17.87 %), $F(1,16) = 35.48, p < .0001$, indicating that subsequent memory performance was well above chance.

EEG Oscillations

The topography of alpha power during the maintenance delay for remembered and forgotten stimuli, as well as the topography of the difference (alpha *Dm* effect), are shown in Figure 2A. The visual impression that both the individual power maxima and the maximum effect, i.e., stronger power for subsequently remembered stimuli, were found over the parietal-occipital cortex was substantiated by the statistical analysis: ANOVAs for each 1000-ms time epoch of the maintenance delay with factors of memory status (remembered vs. forgotten) and electrodes revealed a main effect of memory status and a Memory Status x Electrodes interaction between 3000 and 5000 ms after cue presentation, 3000–4000 ms: main effect: $F(1,16) = 7.23, p = .0161$; interaction: $F(18,288) = 4.32, p < .0001, \epsilon(H-F) = .0191$; 4000–5000 ms: main effect: $F(1,16) = 8.12, p = .0116$; interaction: $F(18,288) = 3.40, p < .0001, \epsilon(H-F) = .0114$. Electrode-wise *t* tests showed that the alpha *Dm* effect was significant at electrodes C3, Pz, P4, and O2 of the 10–20 System [9] with stronger power for subsequently remembered stimuli (all *p*'s < .05). Additional *t* tests computed specifically at the electrodes showing the maximum effect (i.e., electrodes PO3, POz, and PO4 that were not initially included in the standard analysis with the 19 electrodes of the 10–20-system) also proved to be significant (all *p*'s < .05).

The topography of theta power for subsequently remembered and forgotten items and the topography of the theta *Dm* effect are shown in Fig. 2B. Overall theta power for each trial type was maximal over the midfrontal sites (between electrodes Cz and Fz), but the difference between subsequently remembered and forgotten stimuli was located more posterior over central-parietal electrodes. Time-epoch-specific ANOVAs revealed a significant effect of memory status between 3000 and 5000 ms poststimulus by a Memory Status x Electrodes interaction between 3000 and 4000 ms, $F(18,288) = 2.82, p = .0002, \epsilon(H-F) = .0341$, and a main effect of memory status between 4000 and 5000 ms, $F(1,16) = 5.84, p = .0280$. Electrode-wise *t* tests showed stronger power for subsequently remembered stimuli at electrodes Cz, C4, and P4 of the 10–20-system. An additional *t* test computed specifically at the electrode of the maximum effect (CPz) also proved to be significant (all *p*'s < .05).

To examine whether the topography of the alpha and theta *Dm* effects differed, we conducted an ANOVA with frequency (alpha/theta) and electrode site as factors and the *Dm* effect, i.e., the difference between remembered and forgotten items, as dependent variable. This analysis revealed a significant interaction, $F(18,288) = 3.57, p < .0001, \epsilon(H-F) = .0119$, supporting the claim of different topographies and speaking against the notion that the alpha effect could be a methodological artifact of the frequency analysis arising from theta “harmonics” [14].

Discussion

The present study investigated the relationship between EEG alpha and theta oscillations during WM maintenance and successful LTM encoding. We found that both alpha and theta

power increased for stimuli that are later successfully remembered, showing that EEG oscillations reflect successful LTM encoding during WM maintenance.

Increased alpha power for later remembered stimuli was expected, given the finding that alpha power increased with WM load during WM retention intervals [11,21,33] and the assumption that successful memory encoding involves processes that are similar to those that are invoked by increasing WM load. Accordingly, successful LTM encoding could be related to increased WM activity. However, this notion apparently contradicts many findings that increased neural activation is generally associated to a decrease in alpha power (i.e., “alpha desynchronization”) and that synchronized alpha (i.e., high alpha power) thus reflects a resting state of the brain [29,30]. In addition, our finding of increased alpha for later remembered stimuli is at variance with several previous papers associating “reductions” in alpha power with successful LTM encoding [5,24,39].

Klimesch and colleagues [22,23, see also 28 for a similar approach] proposed a framework that might reconcile these findings. According to this view, alpha power might reflect the inhibition of sensory (bottom up) processing areas via attentional (top-down) control mechanisms. This idea is consistent with results showing that occipital alpha activity in cats was increased during top-down as compared to bottom-up processing [38], and that alpha power was increased in humans during performance of internal mental processing tasks (as compared to processing of external stimuli) [2]. A similar explanation has been provided by Jensen and colleagues [11,13] for the enhanced alpha synchronization over the parietal-occipital cortex they found with increasing WM load during a Sternberg-like task. They suggest that “the inhibition or disengagement of occipital-parietal areas could serve to suppress input from the visual stream”. Following Jensen and colleagues’ line of reasoning, external visual information might interfere with the information maintained in WM. Therefore, the inhibition of visual processing areas might be a top-down-driven control mechanism for shielding to-be-maintained information from possibly distracting visual input, leading to an increase of alpha synchronization over the parietal-occipital cortex.

Alternatively, it is possible that the alpha *Dm* effect reflects processes by which the participants elaborate on the memoranda during the delay. This might be related to findings showing that alpha power is increased during WM manipulation [32], and that active manipulation also supports LTM encoding [1].

In addition to effects in the alpha band, we found that theta power was enhanced for subsequently remembered stimuli relative to stimuli that were not remembered. This result fits well with the findings of increased theta power with increasing WM activity [4,12] and of increased theta power for successfully remembered compared to forgotten stimuli [19,20]. It is notable, however, that in the studies by Klimesch and colleagues words were encoded in the context of an animacy judgment task, and there was no requirement to actively maintain the items. Here, the theta *Dm* effect was visible during the delay of a delayed matching-to-sample task and thus supports the conclusion that it is linked to processes directly related to WM maintenance.

The parietal topography of the theta *Dm* effect is different from the midline anterior frontal topography of the individual theta maxima. Such a midline frontal topography has often been observed for effects in the theta range during tasks that generally demand attentional processing [9,25]. The finding that frontal theta power increases systematically with WM load [4,12] suggests that frontal theta is directly related to the active maintenance of memory representations. However, the parietal *Dm* effect found in the present study corresponds more to the findings of Osipova et al. [27], who found enhanced theta over the parietal-temporal cortex for successfully remembered stimuli. Together, these results suggest that

parietal theta-related processes that promote successful memory encoding could be separate from more frontal theta-related processes that mediate general attentional processing and active WM maintenance. The assumption that more parietally located processes mediate successful LTM encoding is also substantiated by a large amount of neuroimaging data showing *Dm* effects in the parietal cortex [for a recent review, see 37]. However, from where the posterior theta *Dm* effect originates remains an open question. Osipova et al. [27] reported that they attempted to identify the sources of this effect, but were not successful. They suggested that the signal might originate from the hippocampus, which could be an explanation for their unsuccessful source-localization attempt, because it is much more difficult to localize deep sources. However, as noted above, others have found the parietal cortex to be involved in successful LTM encoding. Therefore, the neural source of the posterior theta *Dm* effect remains to be determined in future studies.

To conclude, the present study showed that EEG alpha and theta power during an extended period of WM maintenance are stronger for later successfully recalled stimuli, substantiating the claim that alpha and theta oscillations modulate successful LTM encoding. Given the fact that alpha and theta oscillations support WM maintenance, and that the same pattern also supports LTM encoding, the present results suggest that more effort within the WM system (like with increasing WM load) supports successful LTM encoding. Thus, the same neural processes underlying WM maintenance can support LTM encoding.

Acknowledgments

This work was supported by Grant FOR254/2-1 of the German Research Foundation (DFG) assigned to FR. We thank Anna Seemüller for help in collecting the data and Ole Jensen, Esther Meeuwissen, Ali Mazaheri, and two anonymous reviewers for helpful comments.

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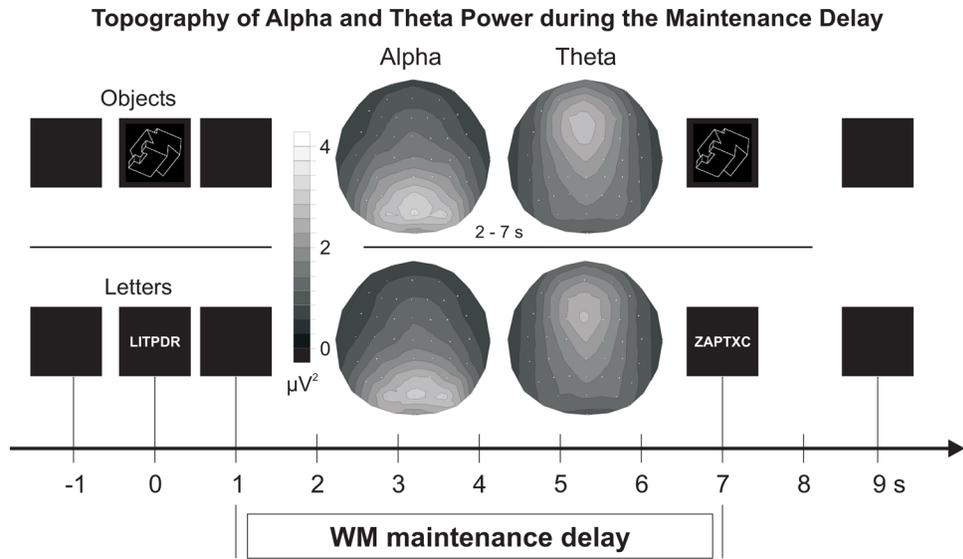


Figure 1.

Trial timing of the delayed matching-to-sample-task, in which either objects or letter strings had to be maintained throughout the delay period. The length of the delay was randomly varied between 5 and 7 seconds with an average of 6s. In addition, topographic maps of overall alpha and theta power during the WM-maintenance delay (2 – 7 s poststimulus) are shown separately for objects (upper maps) and letter strings (lower maps). The maps reveal comparable topographies for objects and letter strings across material types with a parietal-occipital maximum for alpha and a midfrontal maximum for theta. Therefore, the data were collapsed across material type in the subsequent analyses (see Methods for details).

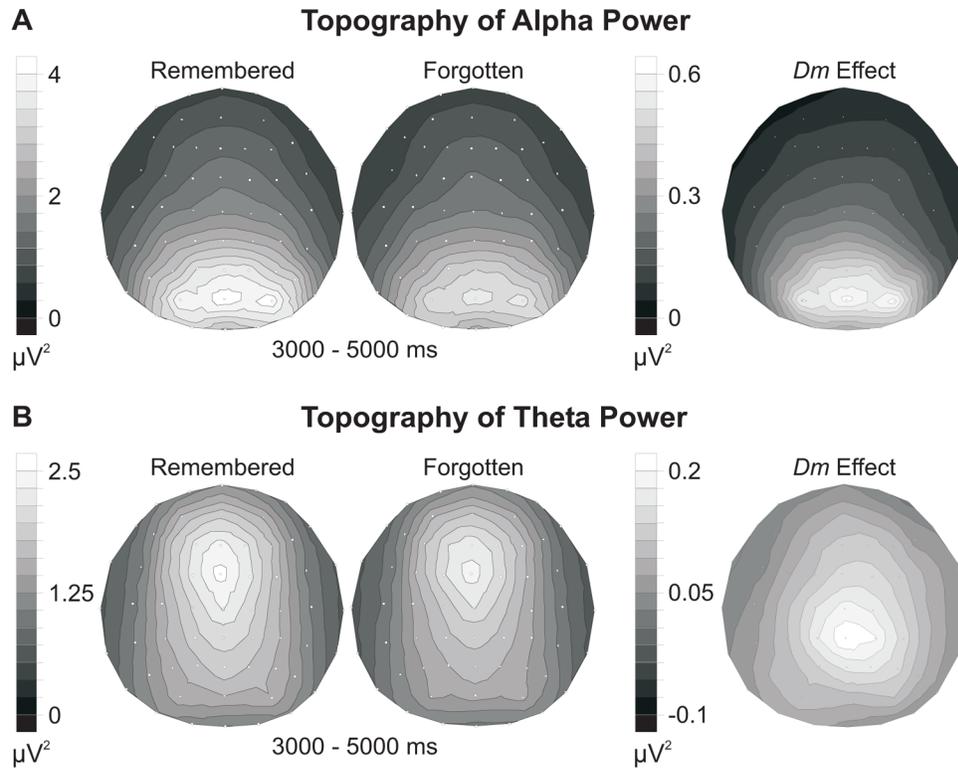


Figure 2.

Topographic maps of alpha (A) and theta (B) power for remembered and forgotten stimuli, as well as the “remembered-forgotten” difference maps (*Dm* effects). The individual alpha power maxima and the maximum effect were found over the parietal-occipital cortex. As usually found for theta, the individual theta power maxima were located over the midfrontal cortex between electrodes Cz and Fz. The maximum difference between later remembered vs. forgotten stimuli, however, was located more posterior over central-parietal electrodes (see Results for details).