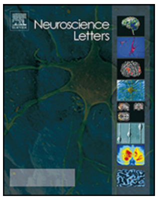
Neuroscience Letters 468 (2010) 339–343

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet



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

Patrick H. Khader[a,*], Kerstin Jost[b], Charan Ranganath[c], Frank Rösler[a]

[a] *Experimental and Biological Psychology, Philipps-University Marburg, Germany*
[b] *Institute of Psychology, RWTH Aachen University, Germany*
[c] *Center for Neuroscience and Dept. of Psychology, University of California at Davis, USA*

ARTICLE INFO

Article history:
Received 7 August 2009
Received in revised form 2 November 2009
Accepted 9 November 2009

Keywords:
EEG
Oscillations
Alpha
Theta
Dm effect

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.

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 parti-

---

* Corresponding author at: Department of Psychology, Philipps-University Marburg, Gutenbergstr. 18, 35032 Marburg, Germany. Tel.: +49 6421 2823838.
E-mail address: khader@staff.uni-marburg.de (P.H. Khader).
URL: http://www.uni-marburg.de/fb04/team-roesler/people/khader-en (P.H. Khader).

0304-3940/$ – see front matter © 2009 Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.neulet.2009.11.028

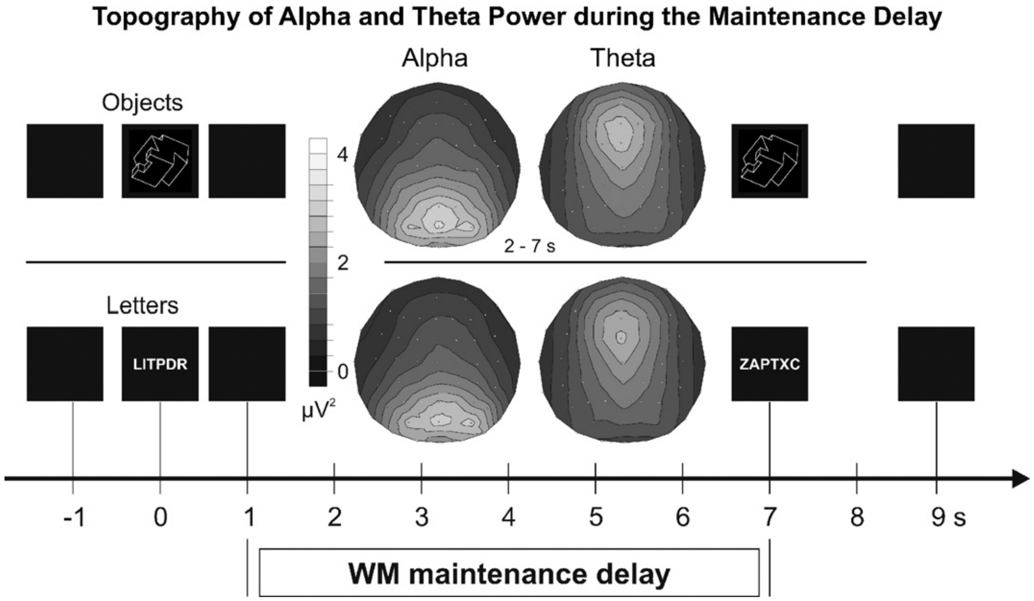


Fig. 1. Trial timing of the delayed matching-to-sample-task, in which either objects or letter strings had to be maintained throughout the delay period. The length of the delay was randomly varied between 5 and 7 s with an average of 6 s. In addition, topographic maps of overall alpha and theta power 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 text for details).

cipants (9 females, 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.

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].

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 kΩ. 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 μV, (2) the minimal absolute difference of two values in any 200 ms interval was 0.50 μV ("dead-channel criterion"), and (3) the maximal allowed voltage step between two adjacent sampling points was 20 μV.

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 midfontal 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