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Distinct slow and fast cortical theta dynamics in episodic memory retrieval

Bernhard Pastötter *, Karl-Heinz T. Bäuml

Department of Experimental Psychology, Regensburg University, Germany

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ABSTRACT

Brain oscillations in the theta frequency band (3–8 Hz) have been shown to be critically involved in human episodic memory retrieval. In prior work, both positive and negative relationships between cortical theta power and retrieval success have been reported. This study examined the hypothesis that slow and fast cortical theta oscillations at the edges of the traditional theta frequency band are differentially related to retrieval success. Scalp EEG was recorded in healthy human participants as they performed a cued-recall episodic memory task. Slow (~3 Hz) and fast (~7 Hz) theta oscillations at retrieval were examined as a function of whether an item was recalled or not and as a function of the items' output position at test. Recall success typically declines with output position, due to increases in interference level. The results showed that slow theta power was positively related but fast theta power was negatively related to retrieval success. Concurrent positive and negative episodic memory effects for slow and fast theta oscillations were dissociable in time and space, showing different time courses and different spatial locations on the scalp. Moreover, fast theta power increased from early to late output positions, whereas slow theta power was unaffected by items' output position. Together with prior work, the results suggest that slow and fast theta oscillations have distinct functional roles in episodic memory retrieval, with slow theta oscillations being related to processes of recollection and conscious awareness, and fast theta oscillations being linked to processes of interference and interference resolution.

Introduction

Human brain oscillations in the theta frequency range (3 to 8 Hz) have been shown to be crucially involved in episodic memory retrieval (Axmacher et al., 2006; Düzel et al., 2010; Hsieh and Ranganath, 2014; Klimesch, 1999; Nyhus and Curran, 2010). In prior work on the relationship between cortical theta activity at retrieval and retrieval success, both positive and negative episodic memory (EM) effects have been reported.[1]

On the one hand, theta oscillations have been shown to be positively related to retrieval success in item recognition studies (Addante et al., 2011; Burgess and Gruzelier, 1997; Guderian and Düzel, 2005; Gruber et al., 2008; Jacobs et al., 2006; Klimesch et al., 1997, 2001; Osipova et al., 2006; Spitzer et al., 2009; Zion-Golumbic et al., 2010). For instance, Osipova et al. (2006) demonstrated that theta power is larger for hits than for correct rejections over posterior cortical regions. Gruber et al. (2008) showed that theta power is larger for hits with correct source judgments than for hits with incorrect source judgments and correct rejections over the fronto-central cortex. On the other hand, cortical theta oscillations have been shown to be negatively related to retrieval success in interference and inhibition studies (Hanslmayr et al., 2010; Khader and Rösler, 2010; Staudigl et al., 2010). For instance, Staudigl et al. (2010) demonstrated that mid-frontal theta power increases with increasing interference from related non-target material during selective memory retrieval. Khader and Rösler (2010) showed that interference-induced increases in mid-frontal theta power are negatively related to recall success. Together, these findings suggest that, within the traditional theta frequency range, distinct networks of cortical theta oscillations may be differentially related to retrieval success and thus may have distinct functional roles in episodic memory retrieval.

Indeed, recent work on hippocampal brain oscillations revealed that distinct slow (~3 Hz) and fast (~7 Hz) theta oscillations – at the edges of the traditional theta frequency band – can play different roles for episodic memory retrieval, showing that slow hippocampal theta oscillations are positively related but fast hippocampal theta oscillations are negatively related to retrieval success (Lega et al., 2012). Following this recent work, here, we examined whether the distinction of positive and negative EM effects for slow and fast theta oscillations also applies

* Corresponding author at: Department of Experimental Psychology, Regensburg University, Universitätsstr. 31, 93053 Regensburg, Germany. Fax: +49 941 943 3872.
E-mail address: bernhard.pastoetter@psychologie.uni-regensburg.de (B. Pastötter).

[1] The present study is on retrieval-related episodic memory (EM) effects in theta power, that is, the relationship between theta power at retrieval and retrieval success. It is not on encoding-related subsequent memory (SM) effects in theta power, that is, the relationship between theta power at encoding and retrieval success (for reviews on SM effects in human brain oscillations in general and theta power in particular, see Axmacher et al., 2006; Düzel et al., 2010; Hanslmayr and Staudigl, 2014; Nyhus and Curran, 2010).

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to brain oscillations in the human cortex. Scalp EEG was recorded as participants retrieved previously studied word lists. A cued-recall procedure was employed and serial output position of a list's items was controlled by presenting the items' unique initial letters as retrieval probes. Slow and fast theta oscillations were examined as a function of retrieval success (recalled vs. not recalled items) and the items' output position at test (tested-first vs. tested-last items). Success rates typically decline as a function of the items' serial position in a testing sequence, a finding known as output interference (Kahana, 1996; Malmberg et al., 2012; Roediger, 1973; Smith, 1971). Output interference has been attributed to interference and interference resolution mechanisms, assuming that the testing of some first items increases the interference level for the still-to-be-remembered items and/or induces inhibition of these items (Bäuml and Samenieh, 2012; Roediger, 1978; Roediger and Schmidt, 1980; Verde, 2009). By varying items' output position we thus were able to vary items' interference and inhibition level at test.

We tested the hypothesis that cortical theta activities at retrieval underlie retrieval success and the effects of output position at test. In particular, we examined whether distinct slow and fast theta oscillations play different roles for retrieval success, with the one being positively and the other being negatively related to retrieval success. In addition, we examined the effects of output position on cortical theta oscillations. The results will show whether slow and fast theta oscillations are differentially susceptible to interference and inhibition and thus differentially related to the detrimental effect of output position at test. Such pattern of results might help in reconciling the results from prior work on the role of cortical theta oscillations at retrieval, in which quite different relations between retrieval success and theta oscillations have been observed.

Materials and methods

Participants

Twenty students (18 females) at Regensburg University, Germany, participated in the study. Mean age was 21.8 years ($SD = 2.0$) with a range of 19 to 27 years. All participants were right-handed, reported normal or corrected-to-normal vision, spoke German as native language, gave written informed consent, and were paid 15 Euros for participation. No participant reported a history of neurological disease or psychiatric disorder. The study was conducted in accordance with the Declaration of Helsinki.

Materials

Two hundred sixteen German nouns of medium frequency were drawn from CELEX database using WordGen v1.0 software (Duyck et al., 2004). Eighteen lists of 12 words each were prepared. Words in each list were chosen in such a way that each word had a unique first letter. Across lists, words were matched on frequency and word length; the assignment of words to lists was kept constant for all participants. Across study-test cycles, order of the 18 to-be-studied lists was randomized. Within lists, both item order at study and stimulus order of item-specific first-letter retrieval probes (cues) at test were randomized.

Procedure

Participants were tested in a quiet surrounding, seated in front of a 15 in. computer screen with a distance of 1.25 m. They were informed about the general nature of the memory task. They were told that they should learn multiple lists of words and that their memory for the words of each list would be tested after study of each list. Eighteen study-test cycles were conducted, each consisting of a study phase, a distractor phase, and a test phase (Fig. 1).

In the study phase, a list's 12 words were presented visually one after another in the center of the screen. Words subtended a vertical visual angle of 0.6° and an average horizontal visual angle of 2.3°. Each word was presented for 2 s, preceded by a prestimulus fixation cross presented in the center of the screen with variable duration (1.8–2.2 s). In the distractor phase, participants counted backward in steps of threes from a random three-digit number for 30 s. Duration of the distractor phase was equal to the delay between study and test phases. In the test phase, a cued-recall test was conducted in which retrieval of the 12 words was cued with item-specific first-letter retrieval probes. Each probe (stimulus) was presented for 2 s, preceded by a precue fixation cross presented in the center of the screen with variable duration (1.8–2.2 s). Each stimulus presentation was followed by a 1 s blank-screen interval. Next, a question mark was exposed in the center of the screen for 4 s. Participants were instructed to give their oral response only after appearance of the question mark. The experimenter noted whether retrieval of an item was successful or not. Presentation and randomization were done with E-Prime software (v1.1.4, Psychology Software Tools, Sharpsburg, Pennsylvania, USA). A session was completed in approximately 75 min by all participants at which point participants were thanked for their participation, paid, and fully debriefed.

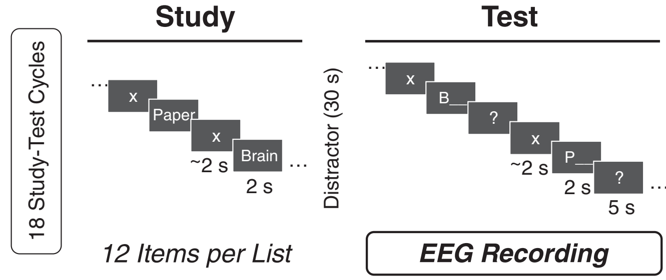

Fig. 1. Experimental procedure. Eighteen study-test cycles were conducted, each consisting of a study phase, a distractor phase, and a test phase. In the study phase, 12 words per list were presented visually one after another in the center of the screen. In the distractor phase, participants counted backward in steps of threes. In the test phase, a cued-recall test was conducted in which item retrieval was cued with item-specific first-letter probes. Participants were instructed to give their oral response only after appearance of the question mark. EEG data was collected in the test phase.

Recording of EEG data

EEG was recorded from 61 equidistant active electrodes mounted in elastic caps (ActiCAP, Montage 10, Brain Products, Gilching, Germany). ActiCAP with its active electrode system enables fast electrode placement and low electrode-skin impedance due to amplification circuitry built into the electrodes, boosting the signal and reducing the noise. Electrode-skin impedance was kept below 20 kΩ. Electrode Cz served as common reference. Signals were digitized with a sampling rate of 500 Hz and amplified between 0.15 and 100 Hz with a notch filter at 50 Hz, removing power line noise which has a 50 Hz frequency in Europe (BrainAmpMR plus, BrainVision Recorder, v1.20, Brain Products, Gilching, Germany).

Preprocessing of EEG data

EEG recordings were rereferenced offline against average reference and EOG corrected using calibration data and generating individual EOG artifact coefficients (Ille et al., 2002), as implemented in the BESA Research software package (v5.3.7, BESA Software, Gräfelfing, Germany). Retrieval data were segmented into 4 s epochs ranging from 1.5 s before to 2.5 s after stimulus onset. To avoid filter artifacts at the edges of the epochs, all further analyses were restricted to a 3 s interval ranging from 1 s before to 2 s after stimulus onset. Segments with remaining artifacts were marked by careful visual inspection and excluded from further analyses.