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Distinct slow and fast cortical theta dynamics in episodic memory retrieval

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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.

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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

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[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).

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
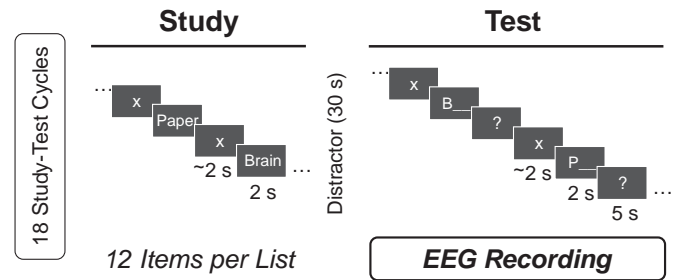
Fig. 1. Experimental procedure. Eighteen study-test cycles were conducted, each consisting of a study phase, a distractor phase, and a test phase. In the study phase, 12 words per list were presented visually one after another in the center of the screen. In the distractor phase, participants counted 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.

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.

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.

For each subject, numbers of segments for recalled (R) and not-recalled (NR) items from early (items 1–6: tested first) and late output positions (items 7–12: tested last) that went into further analysis were matched to be equal by randomly selecting, for each of the four item types (R_{1-6}, NR_{1-6}, R_{7-12}, NR_{7-12}) exactly the number of segments available for the item type with the smallest number of artifact-free segments. Across participants, mean number of segments for each item type that went into analysis was 30.6 ($SD = 7.0$), with a range from 20 to 41 segments per item type. Random selection of trials did not affect the results, as suggested by three additional independent samplings of the original dataset.

Time–frequency analysis of EEG data

EEG data were transformed into the time–frequency domain using the complex demodulation algorithm implemented in BESA Research (v5.3.7, Hoechstetter et al., 2004). The algorithm consists of a multiplication of the time-domain signal with a complex periodic exponential function, having a frequency equal to the frequency under analysis, and subsequent low-pass filtering. The low-pass filter is a finite impulse response filter of Gaussian shape in the time domain, which is related to the envelope of the moving window in wavelet analysis. The data were filtered in a frequency range from 1 to 20 Hz and exported in bins of 0.1 s and 0.5 Hz. Time resolution was set to 158.0 ms (full power width at half maximum, FWHM) and frequency resolution was set to 0.708 Hz (FWHM).

Event-related power changes in the test phase were examined by calculating the percentage of power decrease or increase in relation to a prestimulus baseline interval (Pfurtscheller and Aranibar, 1977; Pfurtscheller and Lopes da Silva, 1999), which was set from 1 s before to stimulus onset. Because the focus of the present study was on theta oscillations at retrieval, only low-frequency oscillations in the frequency range from 1 to 20 Hz were analyzed. A priori, data were analyzed with and without subtracting the evoked signal. As it turned out, subtracting the evoked signal did not affect the results, indicating that the present EM effects in slow and fast theta power primarily arose from modulations in induced, that is, non-phase-locked and non-time-locked, brain oscillations. The present results were based on time–frequency analysis without subtraction of the evoked signal.

Analysis of absolute, baseline-uncorrected slow and fast theta power in the baseline interval revealed no significant clusters of prestimulus differences between R and NR items. Note, however, that with the present bottom-up statistical approach (see below) small or regional effects in prestimulus theta power may have been missed in the present analysis (e.g., see Addante et al., 2011, for effects in prestimulus theta power related to successful source retrieval in item recognition memory).

Statistical analysis of time–frequency data

To control for problems of multiple comparisons, a rigorous bottom-up approach was chosen. Both random permutation and cluster analyses were calculated to test the significance of power differences at multiple electrode sites (Maris and Oostenveld, 2007). Analyses were calculated separately for slow and fast theta oscillations.

In random permutation analysis, the exact timing of significant stimulus-induced power changes was analyzed. For each 100-ms time windows (20), t-tests for all electrode sites (61) were calculated to assess how many electrodes exhibit a significant difference between R and NR items ($p < .01$). To evaluate whether a given number of electrodes exhibiting a significant difference between R and NR items in a specific time window was expected by chance, randomization tests using permutation runs shuffling the assignment of item types randomly for each participant were run (see Blair and Karniski, 1993). After each run, t-tests for all electrode sites were calculated returning the number of electrodes showing a significant difference between the randomly assigned item types. After 5000 permutation runs this procedure

yields a distribution of the number of significant electrodes in a sample with randomly assigned item types. This distribution then constitutes an approximation of the probability distribution under the null hypothesis. A significant difference between conditions is indicated, if the number of electrodes showing a significant difference between R and NR items is less likely than $p = .01$ according to the generated distribution. If the corrected p-value of the randomization test was below .01, then less than 1% of the permutation runs exhibited equal or more electrode sites with a significant difference between item types. If we found an effect to persist for two (or more) consecutive time windows (e.g., from 300 ms to 400 ms, from 400 ms to 500 ms, and from 500 ms to 600 ms), consecutive time windows were merged into an expanded time window of interest for further cluster analysis (e.g., from 300 ms to 600 ms; for similar procedures see Gruber et al., 2013; Pastötter et al., 2011).

In cluster analysis, we examined the clustering of effects in the (expanded) time windows of interest by calculating cluster-based random permutation analyses using BESA Statistics (v1.0, BESA Software, Gräfelfing, Germany). In each permutation analysis for each (expanded) time window of interest, t-tests were calculated for all electrode sites (61) to examine which electrodes show a reliable difference between R and NR items ($p < .01$). Clusters were identified by considering only those (at least four) contiguous electrode sites (with maximum distance of 45 mm between neighboring sites resulting in an average of 4.87 neighbors per electrode site) that fell below the p-value of .01 in the t-test. For each cluster, the sum of t-values of the single electrodes was calculated as a test statistic. In each permutation, this statistic was repeated for shuffled data in which data were randomly reordered across item types and the cluster with the highest sum of t-values was kept. By these means, a null distribution was created from 5000 permutations and the critical p-value for an empirically derived cluster was calculated.

Finally, averaged over electrodes of (a) significant cluster(s), two-way repeated measures analyses of variance (ANOVAs) on stimulus-induced theta power changes were calculated as a function of item type (R item, NR item) and output position (early: items 1–6, late: items 7–12). For correlational analyses, nonparametric Spearman correlations were calculated.

Results

Behavior

Participants recalled an average of 53.9% of the items of a list ($SD = 12.1\%$; minimum $= 34.6\%$; maximum $= 73.6\%$). Fig. 2 shows recall probability as a function of the items' serial output position at
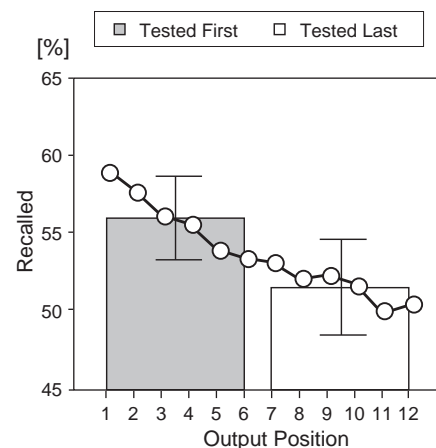
Fig. 2. Behavioral results. Recall probabilities decreased with increasing output position of the items. Participants recalled an average of 56.0% of the tested-fist items (output positions 1–6) and an average of 51.5% of the tested-last items (output positions 7–12). Error bars represent standard error of the mean.

test. Linear regression analysis of participants' individual recall rates regressed on items' serial output position revealed a best-fitting regression line ($F(1,238) = 7.05$, $p < .01$) with a negative slope significantly smaller than zero ($\beta = -.17$, $SE = .003$, $p < .01$). Consistently, comparison of recall rates for early (items 1–6) and late output positions (items 7–12) revealed a higher recall rate for tested-first than tested-last items (56.0% vs. 51.5%; $t_{19} = 2.45$, $p < .05$, $d = .55$). The behavioral results thus indicate a reliable effect of output position, which replicates the typical output interference effect (e.g., Roediger, 1978; Roediger and Schmidt, 1980).
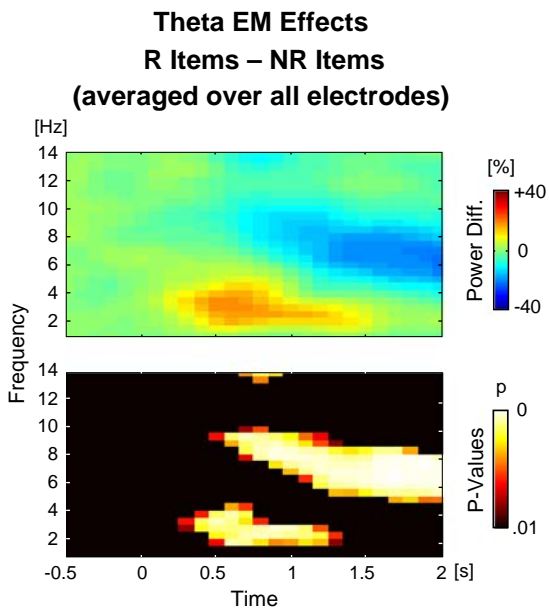
Electrophysiology

Overall analysis

Examination of differences in time–frequency power data between recalled (R) and not-recalled (NR) items averaged across all electrodes revealed two time–frequency clusters of significant EM effects in the theta frequency range: an early effect for slow theta power which was predominant from 2 to 4 Hz, and a later effect for fast theta power which was predominant from 5 to 7.5 Hz (Fig. 3). On the basis of this overall analysis, slow theta power data were collapsed from 2 to 4 Hz and fast theta power data were collapsed from 5 to 7.5 Hz for all further analyses of EM effects.

Slow theta power: 2–4 Hz

Examining the timing of EM effects in slow theta power, permutation analysis revealed a sustained positive EM effect from 0.3 s to 1.3 s after stimulus onset with a larger stimulus-induced increase of slow theta power for R items than for NR items. Cluster analysis revealed two significant spatial clusters showing positive EM effects: one fronto-central cluster ($p < .001$) and one right-parietal cluster ($p < .01$; Fig. 4A). Time–frequency spectrograms of stimulus-induced power changes, averaged across all significant electrodes from the two electrode clusters, indicate that the positive EM effect in slow theta power is well separable, with regard to both frequency and time, from the later negative EM effect in fast theta power (Fig. 4B). Time courses of slow theta power changes for R and NR items, averaged across all significant electrodes from the two spatial clusters, are depicted in Fig. 4C. It

Theta EM Effects
R Items – NR Items
(averaged over all electrodes)

Fig. 3. Overall analysis of episodic memory (EM) effects. Examination of time–frequency spectrograms of (significant) power differences between recalled (R) and not-recalled (NR) items, *averaged over all electrodes*, revealed two effects in the theta frequency range: an early positive EM effect for slow theta power (~3 Hz) and a later negative EM effect for fast theta power (~7 Hz).
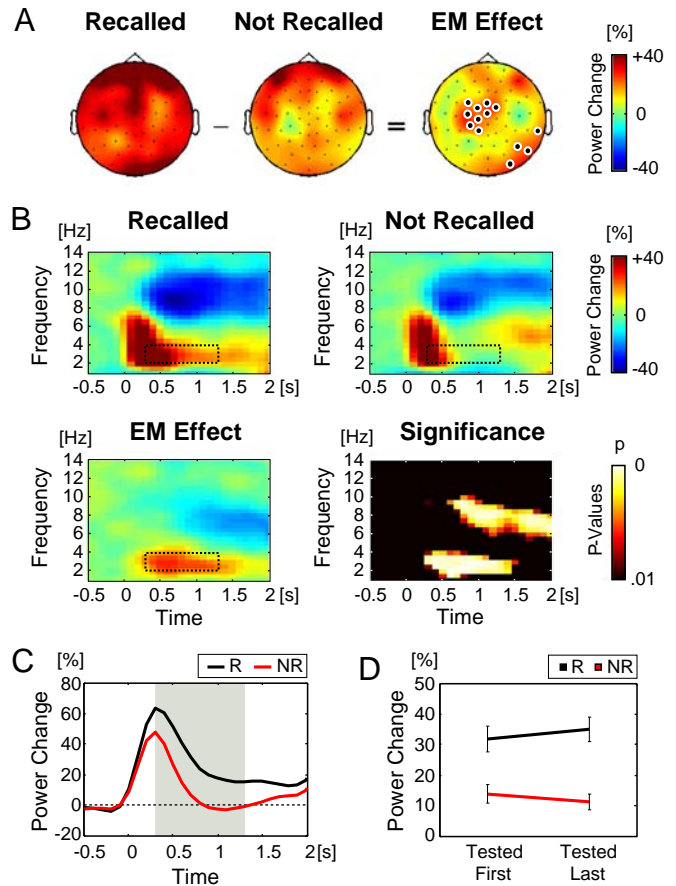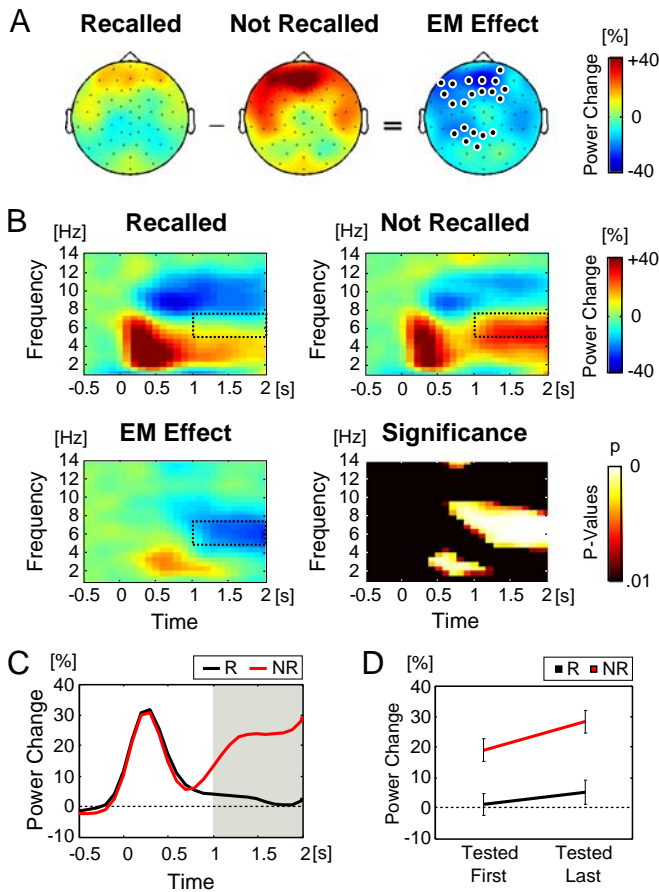

Fig. 4. Slow theta oscillations: 2–4 Hz. A, Topography and significant clusters of the positive EM effect in slow theta power. The difference in cue-induced slow theta power between R and NR items from 0.3 s to 1.3 s following onset of first-letter cues is shown. B, Time–frequency spectrograms of (significant) cue-induced power differences between R and NR items, *averaged over electrodes of the two significant slow theta clusters*. C, Time courses of slow theta power as a function of whether an item was recalled or not, averaged over electrodes of the two clusters. D, Slow theta power from 0.3 s to 1.3 s following cue onset as a function of item type and items' output position at test, averaged over electrodes of the two clusters; error bars represent standard error of the mean.

shows a sustained difference between R and NR items starting 0.3 s after stimulus onset.

To examine whether the EM effect in slow theta power differed between electrode clusters and output positions, an analysis of variance (ANOVA) with the factors of item type (R vs. NR), cluster (fronto-central vs. right-parietal), and output position (early vs. late) was calculated. This analysis revealed a main effect of item type due to the larger increase of slow theta power for R items than for NR items (33.9% vs. 13.1%; $F(1,19) = 58.83$, $p < .001$, partial $\eta^2 = .76$). Other main effects and interactions were nonsignificant (all $Fs(1,19) < 1$). The results indicate a positive EM effect in slow theta power that was equally present in the two electrode clusters and did not depend on items' output position. Slow theta power, averaged across all significant electrodes from the two electrode clusters, as a function of item type and output position is plotted in Fig. 4D.

Fast theta power: 5–7.5 Hz

Examining the timing of EM effects in fast theta power, permutation analysis revealed a sustained negative EM effect from 1 s to 2 s after stimulus onset with a larger increase of fast theta power for NR than for R items. Cluster analysis revealed two significant electrode clusters with negative EM effects: one mid-frontal cluster ($p < .001$) and one left-temporal cluster ($p < .01$; Fig. 5A). Fig. 5B shows that the negative EM effect in fast theta power was well separable, with regard to both frequency and time, from the earlier positive EM effect in slow theta

Fig. 5. Fast theta oscillations: 5–7.5 Hz. A, Topography and significant clusters of the negative EM effect in fast theta power. The difference in cue-induced fast theta power between R and NR items from 1 s to 2 s following onset of first-letter cues is shown. B, Time–frequency spectrograms of (significant) cue-induced power differences between R and NR items, *averaged over electrodes of the two significant fast theta clusters.* C, Time courses of fast theta power as a function of whether an item was recalled or not, averaged over electrodes of the two clusters. D, Fast theta power from 1 s to 2 s following cue onset as a function of item type and items' output position at test, averaged over electrodes of the two clusters; error bars represent standard error of the mean.

power. Time courses of fast theta power changes for R and NR items, averaged across all significant electrodes from the two electrode clusters, are depicted in Fig. 5C. It shows that the negative EM effect in fast theta power started around 1000 ms and increased until stimulus offset.

To examine whether the negative EM effect in fast theta power differed between clusters and output positions, an ANOVA with the factors of item type (R vs. NR), cluster (left-central vs. right-parietal), and output position (early vs. late) was calculated. It revealed a main effect of item type due to the larger increase of fast theta power for NR items than for R items (20.2% vs. 0.1%; $F(1,19) = 65.64$, $p < .001$, partial $\eta^2 = .78$), a main effect of cluster due to a larger increase in fast theta power in the mid-frontal cluster than in the left-temporal cluster (19.6% vs. 0.2%; $F(1,19) = 22.68$, $p < .001$, partial $\eta^2 = .54$), and a main effect of output position due to an increase of fast theta power from early to late output positions (7.7% vs. 13.6%; $F(1,19) = 65.64$, $p < .001$, partial $\eta^2 = .78$).

Moreover, the analysis revealed a significant interaction between the factors of item type and cluster ($F(1,19) = 6.04$, $p < .05$, partial $\eta^2 = .24$) and a marginally significant interaction between the factors of cluster and output position ($F(1,19) = 3.37$, $p = .08$, partial $\eta^2 = .15$). The former was due to a larger negative EM effect for the mid-frontal cluster (30.8% vs. 8.3%) than for the left-temporal cluster (9.8% vs. −6.2%), though significant for both ($t_{19} = 7.34$, $p < .001$, $d = 1.64$; $t_{19} = 6.83$, $p < .001$, $d = 1.52$). The latter was due to a marginally larger increase of fast theta power from early to late output positions for the mid-frontal cluster (15.5% vs. 23.6%) than for the left-

temporal cluster (−0.1% vs. 3.7%), though (marginally) significant for both ($t_{19} = 3.97$, $p < .001$, $d = .89$; $t_{19} = 1.85$, $p = .08$, $d = .41$). Other main effects and interactions were not significant ($Fs(1,19) < 1.6$), indicating that, in contrast to memory-related slow theta power, memory-related fast theta power increased with items' output position. Fast theta power, averaged across all significant electrodes from the two electrode clusters, as a function of item type and output position is shown in Fig. 5D.

Slow versus fast theta power

Correlational analysis showed that the positive EM effect in slow theta power was not related to the negative EM effect in fast theta power. Individual differences in fast theta power from 1 s to 2 s after stimulus onset between NR and R items, averaged across significant electrodes from the two fast-theta electrode clusters, and individual differences in slow theta power from 0.3 s to 1.3 s after stimulus onset between R and NR items, averaged across significant electrodes from the two slow-theta electrode clusters, were not related to each other across participants ($r = -.10$, $p = .66$).

Combined analysis of EM and output effects for slow and fast theta power (Figs. 4D and 5D) was calculated. In a three-way ANOVA, theta power was examined as a function of frequency (slow vs. fast), item type (R vs. NR), and output position (early vs. late). The analysis showed main effects of frequency (23.2% vs. 13.6%; $F(1,19) = 9.91$, $p < .01$, partial $\eta^2 = .34$) and output position (16.7% vs. 20.1%; $F(1,19) = 4.03$, $p = .059$, partial $\eta^2 = .17$), and an interaction between the factors of frequency and item type ($F(1,19) = 125.21$, $p < .001$, partial $\eta^2 = .87$), reflecting the concurrent positive and negative EM effects in slow and fast cortical theta power. More importantly, the analysis revealed a two-way interaction between the factors of frequency and output position ($F(1,19) = 9.31$, $p < .01$, partial $\eta^2 = .33$) and a three-way interaction between all three factors ($F(1,19) = 5.97$, $p < .05$, partial $\eta^2 = .24$), indicating that items' output position affected fast theta power, mainly for NR items, but not slow theta power. The main effect of item type and the interaction between the factors of item type and output position were nonsignificant (both $Fs(1,19) < 1$).

Discussion

The results of this study show that synchronizations of slow (~3 Hz) and fast (~7 Hz) cortical theta oscillations are differentially related to retrieval success in episodic memory retrieval. Increases of slow cortical theta power were positively related but increases of fast cortical theta power were negatively related to retrieval success. Concurrent positive and negative EM effects for slow and fast theta oscillations were dissociable in time and space, showing different time courses and different spatial locations on the scalp. The positive effect in slow theta power was predominant in the first half of the cue presentation interval and was localized over fronto-central and right-parietal electrodes. In contrast, the negative effect in fast theta power was predominant in the second half of the cue presentation interval and was localized over mid-frontal and left-temporal electrode sites. These results indicate distinct functional roles of slow and fast cortical theta oscillations in episodic memory retrieval.[2]

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[2] The present EM effects in slow and fast theta power arose in frequency ranges at the edges of the traditional theta frequency band. Therefore, it could be argued that stimulus-induced changes in delta (~2 Hz) and lower alpha (~8 Hz) power may have been missed in the present analyses because of the dominant effects in theta power. In addition, it could be argued that memory effects in delta and lower alpha power may have contributed, at least to some degree, to the present dominant effects in theta power, because of inevitable spatial blurring of time–frequency signals in the EEG data caused by volume conduction. Future iEEG work may examine this issue by recording data from electrodes placed in different cortical brain areas. The iEEG method is less susceptible to blurring of time–frequency signals and thus may be better able to pick up potential effects in frequency ranges nearby the traditional theta frequency band that could have been missed in the present analysis.

Slow and fast theta power did not only play a different role for retrieval success but were also differentially affected by items' output position at test. Whereas slow theta power was unaffected by items' output position, fast theta power increased from early to late output positions at test. This effect in fast theta oscillations was related to the behavioral effect of output interference, according to which recall chances decrease with items' increasing output position at test (Kahana, 1996; Roediger, 1973; Smith, 1971). Because output interference reflects an increase in interference and inhibition level that arises from the previous testing of other items (Bäuml and Samenieh, 2012; Roediger, 1978; Roediger and Schmidt, 1980; Verde, 2009), the finding suggests that increases of fast theta power, but not increases of slow theta power, reflect an increase in interference and inhibition level. Although a priori output interference might be due to fatigue, lack of concentration, waning of attention, or context change from early to late output positions at test, results of numerous studies show that it reflects a memorial effect (e.g., Malmberg et al., 2012; Roediger and Neely, 1982; Roediger and Schmidt, 1980; Smith, 1971).

Prior work on cortical oscillations in the traditional theta frequency band (3–8 Hz) demonstrated both positive and negative relationships between cortical theta power at retrieval and retrieval success. Work on recollection and conscious awareness in item recognition showed a positive relationship between theta power over fronto-central and parietal cortical brain regions and retrieval success (Addante et al., 2011; Gruber et al., 2008; Guderian and Düzel, 2005; Klimesch et al., 1997, 2001; Osipova et al., 2006), whereas work on interference and interference resolution showed a negative relationship between mid-frontal theta power, originating in the anterior cingulate cortex, and retrieval success (Hanslmayr et al., 2010; Khader and Rösler, 2010; Staudigl et al., 2010). Going beyond the prior work, the present study provides direct evidence for concurrent positive and negative EM effects in cortical theta power within the same task. It shows a positive EM effect arising for slow theta oscillations and a negative EM effect arising for fast theta oscillations. The present scalp localization of EM effects, with the slow theta effect over fronto-central and right-parietal electrodes and the fast theta effect dominant over mid-frontal electrodes, is in line with the view that the positive EM effect in slow theta power indexes processes related to recollection, whereas the negative EM effect in fast theta power indexes processes related to interference and interference resolution, an indication that may help in reconciling the different patterns of results in previous work on the role of theta oscillations in memory retrieval.[3]

Together with the recent findings of Lega et al. (2012), the present results suggest that, both in the hippocampus and in the neocortex, memory-related networks of slow and fast theta oscillations can be differentiated. This raises the question of the relationship between hippocampal and cortical theta oscillations in episodic memory retrieval. Based on animal research showing that learning in rodents is accompanied by increases of inter-regional theta phase synchronizations between hippocampal, entorhinal, and neocortical brain regions (Battaglia et al., 2011; Buzsáki and Moser, 2013; Jutras and Buffalo, 2014), research on human memory recently began to examine hippocampal–cortical theta phase coupling in iEEG data recorded from hippocampal and cortical electrodes in neurosurgical patients. Consistent with animal research, this work showed that increases of hippocampal–cortical theta phase coupling, both at encoding and retrieval, are positively related to retrieval success (Anderson et al., 2010; Burke et al., 2013; Fell et al., 2001, 2003; Lega et al., 2012; Watrous et al., 2013). In particular, in this recent work, the hippocampus has been suggested to be a hub region mediating inter-regional theta phase synchronizations between medial temporal, prefrontal and parietal brain regions during successful episodic memory retrieval (Anderson et al., 2010; Watrous et al., 2013). Following this suggestion, it seems likely that the present EM effects in cortical theta power for slow and fast theta oscillations in healthy participants may be synchronized with slow and fast memory-related theta oscillations in the hippocampus to some degree. Future work may show whether and how distinct networks of slow and fast theta oscillations across the human brain are linked to each other and mediated via inter-regional slow and fast theta phase synchronizations.

The present study revealed a dissociation of memory-related slow and fast cortical theta oscillations in episodic memory retrieval. However, this dissociation may not be restricted to episodic memory retrieval but may be generalized to episodic memory formation, working-memory maintenance, and working-memory retrieval. In prior work on the formation of episodic memories, concurrent subsequent-memory effects in theta power have been reported. Increases of theta power during encoding have been shown to be positively related to subsequent recall success in some studies (Hanslmayr et al., 2011; Klimesch et al., 1996; Osipova et al., 2006; Sederberg et al., 2003) but negatively in others (Burke et al., 2013; Pastötter et al., 2008; Sederberg et al., 2006; Serruya et al., 2014), indicating that distinct encoding networks of cortical theta oscillations may be related to different processes in episodic memory formation. Moreover, in prior work on working-memory maintenance and working-memory retrieval, theta power increases of frontal and parietal theta oscillations have been found to be differentially related to working-memory load (Meltzer et al., 2008), decision time (Jabobs et al., 2006), and retrieval success (Khader et al., 2010), indicating that distinct theta networks may be linked to different processes in working-memory maintenance and retrieval. On the basis of the present results, it may be speculated that these distinct encoding and working-memory networks of theta oscillations synchronize in distinct slow and fast theta frequencies.

In sum, this study showed that distinct cortical networks of slow and fast theta oscillations are differentially related to retrieval success in episodic memory retrieval. Power increases of slow theta oscillations were positively related to retrieval success, whereas power increases of fast theta oscillations were negatively related to retrieval success. The positive and negative EM effects in slow and fast theta power had different time courses and different locations on the scalp. In addition, analysis of the relationship between cortical theta dynamics and behavioral output interference revealed that fast theta but not slow theta power was related to the interference and inhibition level at test. Together with prior work, the results suggest that distinct cortical networks of slow and fast theta oscillations have distinct functional roles in episodic memory retrieval, with slow theta oscillations indexing processes related to recollection and conscious awareness and fast theta oscillations indexing processes related to interference and interference resolution.

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[3] The prior work on the role of theta oscillations in item recognition and interference studies did not show concurrent EM effects in slow and fast theta power within the same task. There may be two reasons for this. First, in prior item recognition studies, negative EM effects in fast theta power may have been missed because item recognition is much less susceptible to interference than recall is (Dennis and Humphreys, 2001). Second, in interference studies, positive EM effects in slow theta power may have been missed because no difference in theta activity between recalled and not-recalled items was calculated; moreover, theta activity was analyzed in a predefined (fast theta) frequency range (4 to 7 Hz, Hanslmayr et al., 2010; 5 to 7 Hz, Khader and Rösler, 2010; 5 to 9 Hz, Staudigl et al., 2010).

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