

Rhythmic Activity and Individual Variability in Recognition Memory: Theta Oscillations Correlate with Performance whereas Alpha Oscillations Correlate with ERPs

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Abstract

■ During study trials of a recognition memory task, alpha (~10 Hz) oscillations decrease, and concurrently, theta (4–8 Hz) oscillations increase when later memory is successful versus unsuccessful (subsequent memory effect). Likewise, at test, reduced alpha and increased theta activity are associated with successful memory (retrieval success effect). Here we take an individual-differences approach to test three hypotheses about theta and alpha oscillations in verbal, old/new recognition, measuring the difference in oscillations between hit trials and miss trials. First, we test the hypothesis that theta and alpha oscillations have a moderately mutually exclusive relationship; but no support for this hypothesis was found. Second, we test the hypothesis that theta oscillations explain not only memory effects within participants, but also individual differences. Supporting this prediction, durations of theta (but not alpha) oscillations

at study and at test correlated significantly with d' across participants. Third, we test the hypothesis that theta and alpha oscillations reflect familiarity and recollection processes by comparing oscillation measures to ERPs that are implicated in familiarity and recollection. The alpha-oscillation effects correlated with some ERP measures, but inversely, suggesting that the actions of alpha oscillations on memory processes are distinct from the roles of familiarity- and recollection-linked ERP signals. The theta-oscillation measures, despite differentiating hits from misses, did not correlate with any ERP measure; thus, theta oscillations may reflect elaborative processes not tapped by recollection-related ERPs. Our findings are consistent with alpha oscillations reflecting visual inattention, which can modulate memory, and with theta oscillations supporting recognition memory in ways that complement the most commonly studied ERPs. ■

INTRODUCTION

EEG oscillations are rhythmic brain activity, some of which are thought to play important roles in memory function. Broadly speaking, better memory is associated with more theta (4–8 Hz) activity but less alpha (~10 Hz) activity (Doppelmayr, Klimesch, Hodlmoser, Sauseng, & Gruber, 2005; Klimesch, Schack, & Sauseng, 2005; Jensen, Gelfand, Kounios, & Lisman, 2002; Doppelmayr, Klimesch, Schwaiger, Stadler, & Rohm, 2000; Klimesch, 1996, 1999; Doppelmayr, Klimesch, Schwaiger, Auinger, & Winkler, 1998; Klimesch, Schimke, & Schwaiger, 1994; Klimesch, Schimke, & Pfurtscheller, 1993; Klimesch, Schimke, Ladurner, & Pfurtscheller, 1990). To understand the specific roles of rhythmic activity in recognition memory, we ask three questions about how theta and alpha oscillations might contribute to memory in a verbal episodic, recognition task. Taking an individual differences approach, we seek evidence complementary to within-subject effects, about (1) how alpha and theta oscillations relate to one another, (2) how alpha and theta oscillations relate to memory performance, and (3) how alpha and theta oscillations relate to ERPs

whose functions in recognition memory have been well characterized.

Theme 1: The Relationship between Alpha and Theta Oscillations

As just described, theta and alpha activities have seemed to relate in opposite ways to successful memory during study and test in the context of some experimental manipulations. This raises the question: Is there always a push-and-pull relationship between these two rhythms? Because often, when theta oscillations increase, alpha oscillations decrease across a given manipulation; it is possible that alpha and theta rhythms are strictly mutually exclusive. Two specific ideas have been proposed, which might lead one to this prediction. Klimesch (1999) speculated that theta and alpha might be two dynamic modes of a single network that supports memory function, where the theta mode facilitates encoding of new information and the alpha mode facilitates retrieval of memory. In this sense, these measures of oscillations would reflect a switch in operating frequency of the network. What follows is that theta and alpha duration and power should have a strict opponent relationship with one another.

Alternatively, Klimesch, Freunberger, and Sauseng (2010) suggested that alpha and theta oscillations each reflect numerous, but different, cognitive processes relevant to memory. For example, alpha activity differentiates stimulus types (concrete vs. abstract words; Schack, Weiss, & Rappelsberger, 2003) and attentional demands (see Klimesch, 1999, for a review); on the other hand, theta activity is associated with rehearsal, retention, and working memory (see Kahana, Seelig, & Madsen, 2001; Klimesch, 1997, 1999, for review). Even if theta and alpha activity originate from different networks, if they reflect cognitive processes that tend to be even somewhat mutually exclusive, alpha oscillations would tend to decrease when theta oscillations increased, and vice versa. We adapted this logic to individual differences: If theta-oscillation measures are greater for a given participant, alpha-oscillation measures should be relatively smaller for that same participant; conversely, if alpha-oscillation measures are greater for a given participant, theta-oscillation measures should be relatively smaller for that same participant. Thus, we tested the mutual exclusivity hypothesis, which predicts a negative correlation across participants between measures of alpha and theta oscillations. Specifically, our approach was to measure the subsequent memory effect (remembered–not remembered items) at study and the retrieval success effect (remembered–not remembered items) at test at both alpha and theta frequencies for each participant and to compute the correlation between those oscillation measures across participants. By starting with the difference in activity between remembered and not remembered items, we restrict the analysis to activity that already distinguishes memory outcome within participants.

There are reasons one might not expect a negative correlation between duration or power of theta and alpha oscillations across participants. Instead of an inevitable opponent relationship between the two rhythms, it could be that many experimental manipulations happen to have opposite effects on alpha than on theta. Alpha and theta oscillations may just happen to respond in complementary ways to many experimental factors that have been studied. In this case, individual variability may not affect alpha and theta activities in opposite ways. The alternative prediction, then, is no significant correlation between theta and alpha measures across participants.

Yet other evidence leads one even to expect a positive correlation. Some studies have found that theta showed the same subsequent memory effect as alpha activity: Remembered trials had less alpha activity and less theta activity than forgotten trials (Burke et al., 2013; Depue et al., 2013; Lega, Jacobs, & Kahana, 2012; Fell et al., 2011). Lisman and Jensen (2013) and Hanslmayr and Staudigl (2014) argued that the proximity of theta and alpha frequencies might have contributed to their similar activity pattern, with alpha activity “bleeding in” to the theta band. Alternatively, Bonnefond and Jensen (2012) showed that increased alpha activity could enhance later memory performance by inhibiting external visual dis-

tractors. Furthermore, it has long been known that visual imagery is an effective strategy for word memory (Roediger, 1980; Paivio, 1969). Theta activity, in turn, has been linked to mental imagery tasks (Bhattacharya, 2009; Li et al., 2009; Kawasaki & Watanabe, 2007). Moreover, alpha oscillations may also become more prevalent during visual imagery (Bartsch, Hamuni, Miskovic, Lang, & Keil, 2015), because alpha oscillations often synchronize during internally directed attention (as reviewed by Klimesch, Sauseng, & Hanslmayr, 2007). It is possible that, when a participant employs an imagery-based strategy, both alpha and theta oscillations might increase to inhibit external stimuli and to engage in mental imagery, respectively. In this case, the third prediction is a significant positive correlation between measures of theta and alpha activities across participants.

Theme 2: Convergent Evidence for Relevance to Memory Performance

The logic of the subsequent memory effect and retrieval success effect is that these differences in brain activity could reflect processes related to memory function, because they identify activity that differs between successful (remembered) and unsuccessful (not remembered) memory outcomes. But, because oscillation measures, like all brain activity measures, are observational and correlational, it is always possible that theta and alpha oscillations are not necessary for memory performance and could be epiphenomenal; additional convergent evidence is desirable.

Phase coding and phase coherence of theta oscillations was proposed to be the neural mechanism for encoding of episodic memory (Summerfield & Mangels, 2005; Fell et al., 2001, 2003; Weiss & Rappelsberger, 2000). Put simply, theta oscillations are thought to play a crucial role in successful encoding, and the difference in theta activity should produce a behavioral difference—a difference in memory performance. Some previous researchers have taken within-subject effects further by splitting their participants into two groups based on their memory performance. Klimesch (1997) summarized numerous studies that found participants in a good memory group had a greater decrease in alpha power, during both study and test, than participants in a poor memory group. Complementing this, Doppelmayr et al. (1998) found parallel effects for theta power during test; participants in the good memory group had a larger increase in theta power than participants in the poor memory group. Those results show that both alpha and theta oscillations can differentiate groups of participants based on their memory performance; if alpha and theta oscillation measures could also be shown to explain variance in memory performance (d' or RTs of hits) across participants in a continuous manner, that would provide additional convergent evidence that would strengthen the argument for their behavioral relevance. If not, that would weaken

the argument and suggest that we might be looking at a spectator process or a process that is simply not relevant to the memory test we use. We expect to see a positive correlation between measures of theta activity and memory performance (d') and a negative correlation for measures of alpha activity.

However, it is important to note that a large body of research has also suggested that an increase in alpha activity could also be beneficial to memory performance. When participants were asked to retain information in their mind, there were increased alpha activity during retention (synchronization), and alpha desynchronizes after the retention (Sauseng et al., 2005; Herrman, Senkowski, & Rottger, 2004; Busch & Herrmann, 2003; Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Jensen et al., 2002; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; Schack & Klimesch, 2002). This active retention would lead to better memory performance later on. Thus, we might expect to see a positive correlation between measures of alpha activity and memory performance (d').

Theme 3: Using Prior Knowledge about ERPs to Query the Possible Cognitive Roles of Alpha and Theta Oscillations

Much of recognition memory research has centered around a specific ongoing cognitive process debate between single-process theory and dual-process theory. The dual-process position assumes that participants use two separable sources of information to make old versus new decisions: familiarity and recollection. Familiarity is supposed to be a relatively simple strength signal, whereas recollection is supposed to reflect additional, detailed contextual retrieval. In oscillation studies of recognition memory, it has been proposed that theta activity is involved specifically in recollection. Reviewed by Nyhus and Curran (2010), increased theta power is related to better recognition, but more so when participants respond correctly to source judgments or make correct “remember” responses (compared with “know” responses), two ways researchers have attempted to operationalize recollection (e.g., Guderian, Schott, Richardson-Klavehn, & Düzel, 2009; Gruber, Tsivilis, Giabbiconi, & Müller, 2008; Osipova et al., 2006; Guderian & Düzel, 2005). Other studies have implicated theta activity in familiarity-based retrieval. For example, Klimesch, Doppelmayr, Yonelinas, et al. (2001) found more theta power for “know” than “remember” responses. Moreover, Caplan and Glaholt (2007) measured oscillations during the study phase of a relational memory task (cued recall of word-pairs and triples), which is part of some definitions of recollection (Yonelinas, 2002). They found that anterior theta oscillations had greater duration for more accurate and faster participants. In short, theta oscillations are related to recognition memory, but it is not clear how this oscillation contributes to memory function and whether it is related to familiarity or recollection or both, or would be more

consistent with single-process theory, which we consider in the Discussion.

In contrast to oscillations, recognition memory has been studied extensively using ERPs. Thus, if a particular oscillation were found to correlate with a particular ERP feature across participants, that would suggest a possible functional link between them. Then, what we know about the corresponding ERP (its cognitive or behavioral role) might also apply to the corresponding oscillation, and if not, then we could infer that they do not relate to common cognitive demands of the task. The amplitude of the FN400 (frontal old/new effect) is sensitive to manipulations thought to affect familiarity, and the Left Parietal Positivity (parietal old/new effect) amplitude is sensitive to manipulations thought to affect recollection (see Rugg & Curran, 2007, for a review). Interestingly, Jacobs, Hwang, Curran, and Kahana (2006) noted that the timing of two bursts of theta activity coincided with the latencies of both the FN400 and the Left Parietal Positivity. They speculated that the earlier theta activity signals were related to familiarity, and the later, to recollection. This interpretation would lead one to predict that measures of theta oscillations should correlate with both the FN400 and the Late Parietal Positivity, which we test as well.

Although there is still debate about what cognitive processes memory-related ERPs really reflect, at least we can ask whether an oscillation might correspond to the same cognitive process as a given ERP measure or a different process. Chen, Lithgow, Hemmerich, and Caplan (2014) took a similar individual-differences approach to ask if ERPs during study and ERPs during test might explain any common variance across participants and found that earlier ERPs (the Late Positive Component at study and FN400 at test) were correlated. The later ERPs (the Slow Wave at study and the Left Parietal Positivity) were also correlated. Using the same logic and approach, we correlated, across participants, measures of trial-averaged oscillations related to memory success to measures of ERPs related to memory success. If, indeed, the same cognitive process is contributing to both an ERP feature and an oscillation measure, we should see a strong correlation between the two.

Quantifying Oscillatory Activity

We wanted to choose a measure that would be relatively selective for rhythmic activity and minimally influenced by nonrepeating signals. Most studies of memory-related oscillations have used windowed Fourier transform or wavelet transforms to quantify spectral power as a function of frequency. Measured this way, activity need not necessarily be rhythmic (Klimesch, 1999). Any signal, whether rhythmic or nonrhythmic, can produce nonzero power values (Fourier's theorem). Transient artifacts or (nonrepeating) ERPs may contribute to an increase in measured oscillatory power. Importantly, EEG signal, like most natural signals, has a colored noise form, meaning

that power decreases approximately as relationship $1/f^\alpha$, where the lower frequency signals have a larger amplitude than the higher frequency signals. The colored noise form is present even when oscillatory activity is not present. This means that the power not only measures the sum of power from the rhythmic genuine oscillations but also the nonrhythmic background signal that has energy in the corresponding frequency.

A method for detecting oscillations, known as BOSC (Better OSCillation detection; Whitten, Hughes, Dickson, & Caplan, 2011; Caplan, Madsen, Raghavachari, & Kahana, 2001), is conservative about what is treated as rhythmic activity, ensuring that, relative to conventional power measures, the results are more specific to oscillations and relatively less influenced by nonrepeating signals. Specifically, the BOSC method models the colored noise background signal to determine thresholds that enable one to detect when oscillations are present, so-called “oscillatory-episode detection.” In addition to the power threshold, the EEG signal is also subject to a duration threshold to ensure that the detected signal is sustained (see Methods). Thus, the most popular measure derived from the BOSC method is termed $P_{\text{episode}}(f)$, a measure of the proportion of time during which oscillations were detected at each frequency, f . P_{episode} , a duration measure, ensures that the results relate to sustained rhythmic activity and cannot be explained away by nonrepeating signals. A measure of duration rather than amplitude, P_{episode} values are immediately interpretable: a P_{episode} value of 0.5, for example, indicates that oscillations at the frequency of detection were deemed to be present during 50% of the recording.

This kind of measure of duration deviates from most approaches to quantifying oscillations, which measure power (amplitude squared). P_{episode} , therefore, is (by design) relatively insensitive to how large a rhythm is, measuring, instead, how long it lasts. That said, the BOSC method allows one to measure the power within oscillatory episodes, given that they were detected. Although duration of detected oscillations and average power measures may be related, there is evidence that they can be sensitive to quite different sources of brain activity (Caplan, Bottomley, Kang, & Dixon, 2015). Rather than quantify power within detected oscillations, we simply conducted parallel sets of analyses using the more conventional power measure, log-transformed power as measured with the Morlet wavelet transform. When the conventional power measure agreed with the P_{episode} measure derived from the BOSC method (which they nearly always did), that suggests either that the effects may be driven by duration rather than power or that power increases approximately along with duration. Where they differ, that may indicate either that the P_{episode} method missed an effect on power that does not influence the duration of occurrence of oscillations or that the conventional power measure is picking up some nonrhythmic signal or short-duration signal that we wish not to confidently call

rhythmic (recall that the BOSC criteria are designed to minimize Type I error; signal that fails to meet the strict criteria should therefore be viewed as indeterminate as to whether they reflect rhythmic or nonrhythmic activity).

Design of the Current Study

We used a verbal recognition memory procedure that was consistent with prior procedures and obtained both a large number of trials per participant (225 studied words and an equal number of unstudied items as lure probes) and a large sample size (66 participants). Because we wanted there to be sufficient individual variability in study and test, we did not instruct participants to study in any specific way. Yonelinas (2002) reviewed evidence that when participants are given Remember/Know, source, or confidence judgments in addition to old/new judgments, that could change the way they make the old/new response itself. Because our aim at this stage was to understand the contributions of oscillations to old/new recognition, not Remember/Know, nor source, nor confidence judgments, we stick to the standard, simple old/new judgment response procedure.

METHODS

Participants

Eighty-six (12 self-reported left-handed,¹ 74 self-reported right-handed; 32 women) undergraduate students from an introductory psychology course at the University of Alberta, aged 17–28 years (mean = 20, $SD = 2.29$) participated for course credit. Data from 20 participants were excluded from analyses: 7 were excluded from analyses because of low rates of misses (<11 trials, <5%), 11 because of excessive artifacts in the EEG, and 2 who presumably reversed the response key mapping (accuracy < 50%), for a total of 66 participants included. Of the final sample, 59 were part of the 64 participants included in Chen et al. (2014), but the broader filter (0.1–50 Hz) used here resulted in more participants being excluded because of uncorrectable artifacts. Therefore, to more closely equate the sample size with that of Chen et al. (2014), we ran an additional eight participants, all but one of whom (because of excessive artifacts) could be included in the present analyses. All participants were required to have English as their first language and had normal or corrected-to-normal vision. Written informed consent was obtained before the experiment, and the procedures were approved by the University of Alberta ethics review board.

Materials

The stimuli were nouns drawn from the Toronto Word Pool (Friendly, Franklin, Hoffman, & Rubin, 1982) composed of four to eight letters. Kucera–Francis frequency was

between 1 and 712 per million. Study items and test probes were presented in the center of the computer screen using Times New Roman 17 point font with the E-Prime presentation software version 2.0 (Psychology Software Tools, Pittsburgh, PA).

Procedure

The methods are the same as in Chen et al. (2014). The session took place in an electrically shielded, sound-attenuated chamber. Each study set comprised 25 words, displayed one at a time for intentional study. Each word was presented for 1500 msec with jittered uniform-pseudorandom intertrial interval between 300 and 500 msec. The end-of-list distractor task, included to reduce recency effects that can contribute nuisance variability to the memory measure, consisted of five equations of the form of $A (+ \text{ or } -) B (+ \text{ or } -) C =$, where A , B , and C were randomly selected digits from 1 to 9, and the addition and subtraction operation were randomly selected in the equation. The participant was asked to type the correct answer. Each equation remained in the center of the screen until the participant made a response. In the test phase, which immediately followed the distractor task, 50 words were presented, half (25 words) from the study phase (targets, or “old” items) and half (25 words) not previously presented (lures, or “new” items), drawn at random, without replacement, from the word pool. Each probe was a single word that remained on the screen until the participant made an old/new response by pressing key 1 for old (judged to be a target) and 2 for new (judged to be a lure). Nine blocks of study/test were presented for a total of 225 study trials and 450 probe trials (Figure 1). For each trial, RT and accuracy were recorded.

EEG Recording and Preprocessing

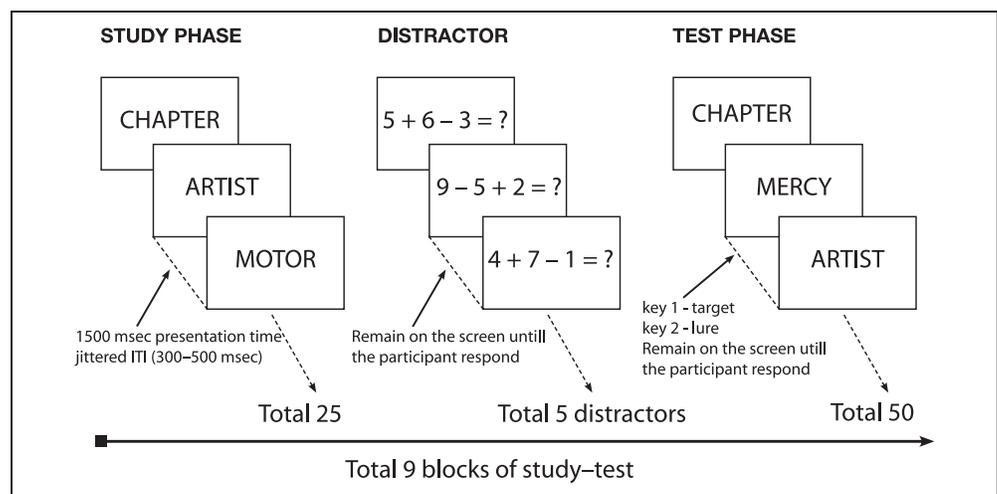
EEG was recorded using a high-density 256-channel Geodesic Sensor Net (EGI, Electrical Geodesics Inc., Eugene,

OR), amplified at a gain of 1000 and sampled at 250 Hz. Impedances were kept below 50 k Ω , and EEG was initially referenced to the vertex electrode (Cz). Data were analyzed by custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme & Makeig, 2004; scn.ucsd.edu/eeglab). Signal was bandpass filtered between 0.1 and 50 Hz and average rereferenced to a common average. Artifacts were corrected via independent component analysis, implemented in EEGLAB (Jung et al., 2000). The selection of components was based on visual inspection of the spatial topographies, time courses, and power spectral characteristics of all components. The components accounting for stereotyped artifacts including eye blinks, eye movements, and muscle movements were removed from the data. Event latencies were corrected with a time lag correction because of a known hardware calibration problem identified by EGI. Study trials were separated into subsequently remembered items (subsequent memory effect hits) and subsequently forgotten items (subsequent memory effect misses) based on the participants’ responses during the test phase and likewise for activity during test trials.

ERP Analysis

ERPs were analyzed as in Chen et al. (2014). ERP trials were time-locked to the onset of stimulus and referenced to a 100-msec prestimulus baseline. Electrodes and time windows were selected to be consistent with previous measurements of our ERP features of interest. The two subsequent memory effect components were analyzed at electrode Pz in the time window of 400–700 msec latency poststimulus for the Late Positive Component. Because of the longer time window of the Slow Wave (700–1200 msec) and variability in time windows in which the Slow Wave has been reported in the literature, we separated the Slow Wave into 700–900 msec (Slow Wave-Early) and 900–1200 msec (Slow Wave-Late) post-stimulus. For test activity, the two retrieval success effect

Figure 1. The experimental procedure. Each box illustrates the computer screen at a particular stage in the task (text has been enlarged relative to the screen size to improve clarity of the figure). There were nine blocks of study–test. Preprint from Chen et al. (2014). Copyright Springer. Reprinted with permission.



(hits–misses) components were analyzed in the time window of 300–500 msec poststimulus for the FN400 at electrode Fz and 500–800 msec poststimulus for the Left Parietal Positivity at electrode P3.

Oscillation Analysis

Oscillations were analyzed over the entire continuous EEG recording (without epoching to avoid edge effects) in both power and BOSC analysis. Oscillations occurring at all frequencies for each trial was calculated by averaging P_{episode} and power over the time window of 0–1200 msec poststimulus (which encompasses the timing of all the ERP measures of interest) for each trial. The frequency bands of interest comprised the following central frequencies: theta, 4.00 Hz, 4.78 Hz, 5.66 Hz, and 6.72 Hz; and alpha, 8.00 Hz, 9.51 Hz, and 11.31 Hz. For band-specific analyses, P_{episode} and log-power were averaged across the frequencies sampled within the band. Analysis was confined to the frontal and parietal midline electrodes, Fz, and Pz, with an emphasis on Fz for theta oscillations and Pz for alpha oscillations.

Conventional Power Analysis

The entire continuous EEG recording (without epoching to avoid edge effects) was analyzed with a Morlet wavelet transform, with a width of six cycles and sampled 24 frequencies logarithmically over the 1–45 Hz range. Wavelet power values were then log-transformed and normalized by dividing the given log-power by the sum of log-power across all frequencies. Frequencies within a band were collapsed by averaging the log-power within that particular band. Analysis was also confined to the same electrodes as in the BOSC analyses. For each participant, one power value was obtained at each frequency, at each electrode, averaging over all trials of a given condition.

BOSC Analysis

The BOSC method is based on the same wavelet transform as the power analysis. In applying this method (Whitten et al., 2011; Caplan et al., 2001); signals were only classified as rhythmic if they exceeded a particular power threshold for a given frequency for a minimum length of time (duration threshold). Briefly, the power threshold was set to the 95th percentile of the probability distribution of power values (the $\chi^2(2)$ distribution expected based on the fit mean power value, after fitting the power spectrum, estimated from the entire continuous record, with a linear regression in log–log coordinates) at a given frequency. The duration threshold was set at each frequency to three cycles. Activity was labeled rhythmic when both the power threshold and the duration threshold were exceeded. The proportion of time oscillations were detected within a time segment, denoted $P_{\text{episode}}(f)$ was calculated for each frequency, f . With the

power threshold, this method is not sensitive to changes in the amplitude of oscillations above the threshold; however, it is thus more selective for rhythmic (repeating) activity than other methods (Whitten et al., 2011; van Vugt, Sederberg, & Kahana, 2007; Caplan et al., 2001).

Finally, consider that the limits of frequency bands, like theta and alpha, have varied considerably across studies. This makes it important to examine each sampled frequency individually. To check the robustness of our frequency bands, we also examined our correlation analyses at all frequencies sampled over the 1–45 Hz range.

All statistical analyses were carried out using MATLAB and Statistic Toolbox Release 2008b (The MathWorks, Inc., Natick, MA) and IBM SPSS Statistics for Mac, Version 21.0. (IBM Corp., Armonk, NY).

RESULTS

Average accuracy was approximately midway between ceiling (100%) and floor (50%) levels (Table 1). This feature, combined with sizeable standard deviations for both accuracy and RT, suggests that there is meaningful variability across participants that might be explained in our analyses. First, we checked whether we could replicate the standard within-subject memory effects, analyzing the subsequent memory effects and retrieval success effects at both alpha and theta frequencies. Then we tested the hypothesis that there is a trade-off relationship between the two frequency bands, which, in turn, facilitate both encoding and retrieval (Theme 1). Next, we tested the behavioral relevance of alpha and theta oscillations by correlating memory outcome measures with the oscillation measures (Theme 2). Finally, we interrogated the possible cognitive functions of alpha and theta oscillations by correlating memory-related ERPs with the oscillation measures (Theme 3).

Replication of Subsequent Memory and Retrieval Success Effects

The subsequent memory effect was analyzed at electrodes Fz and Pz (Figure 2A, B). Paired-samples, two-tailed t tests comparing the duration of oscillatory activity (P_{episode}) between subsequent hits and subsequent misses were significant, where subsequent hits had theta oscillations at

Table 1. Accuracy (Percentage) and RT (msec) Values, along with Their Standard Deviations across Participants in Parentheses

Condition	[%]	RT [msec]
Hits (old)	76.7 (14.1)	953 (222)
Misses (old)	23.3 (10.2)	1313 (435)
Correct rejections (new)	85.3 (15.9)	1074 (299)
False alarms (new)	13.7 (11.4)	1507 (573)

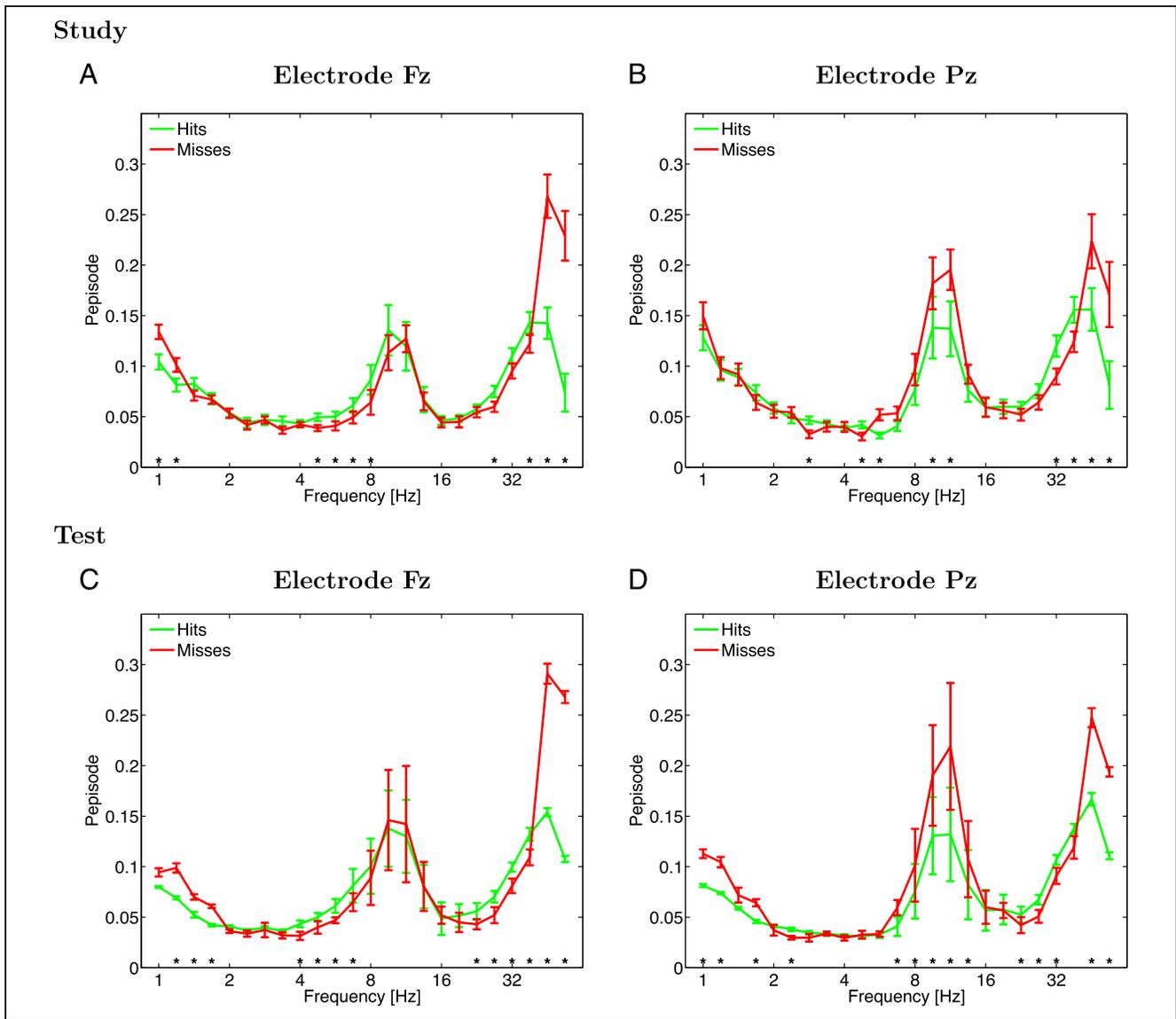


Figure 2. Average proportion of oscillatory activity ($P_{episode}$) is plotted as functions of frequency between hits (green) and misses (red) during study and test. Error bars represent 95% confidence intervals. * denotes significant ($p < .05$) differences between hits and misses.

electrode Fz more of the time than subsequent misses and subsequent hits had alpha oscillations at electrode Pz less of the time than subsequent misses in the alpha band (Table 2). A similar pattern was found at test when we conducted a retrieval success effect analysis, comparing theta and alpha activities for the hits to misses (Figure 2C, D). Paired-samples, two-tailed t tests comparing mean $P_{episode}$ values confirmed the retrieval success effect in both the theta (at Fz) and alpha (at Pz) bands (Table 2).

The mean power analysis produced the same pattern of results in the theta and alpha bands at both study (α : $t(65) = -5.60$; θ : $t(65) = 3.08$, $p < .05$) and test (α : $t(65) = -5.39$; θ : $t(65) = 3.08$, $p < .05$; Figure 3). In summary, both the duration of oscillatory activity ($P_{episode}$) and mean power analyses replicated previous within-subject findings of alpha activity decrease and theta activity increase during hits versus misses, at both study and test (Fell

Table 2. t Values from Paired-samples, Two-tailed t Tests ($df = 65$) Comparing Mean $P_{episode}$ between Subsequent Hits and Subsequent Misses during Study, and between Hits and Misses during Test for Alpha and Theta Oscillations at Electrodes of Interests

Electrodes	Study		Test	
	α	θ	α	θ
Fz	-0.89	3.37*	0.19	2.72*
Pz	-2.73*	-1.34	-5.23*	-0.21

* **Boldface** represents $p < .05$.

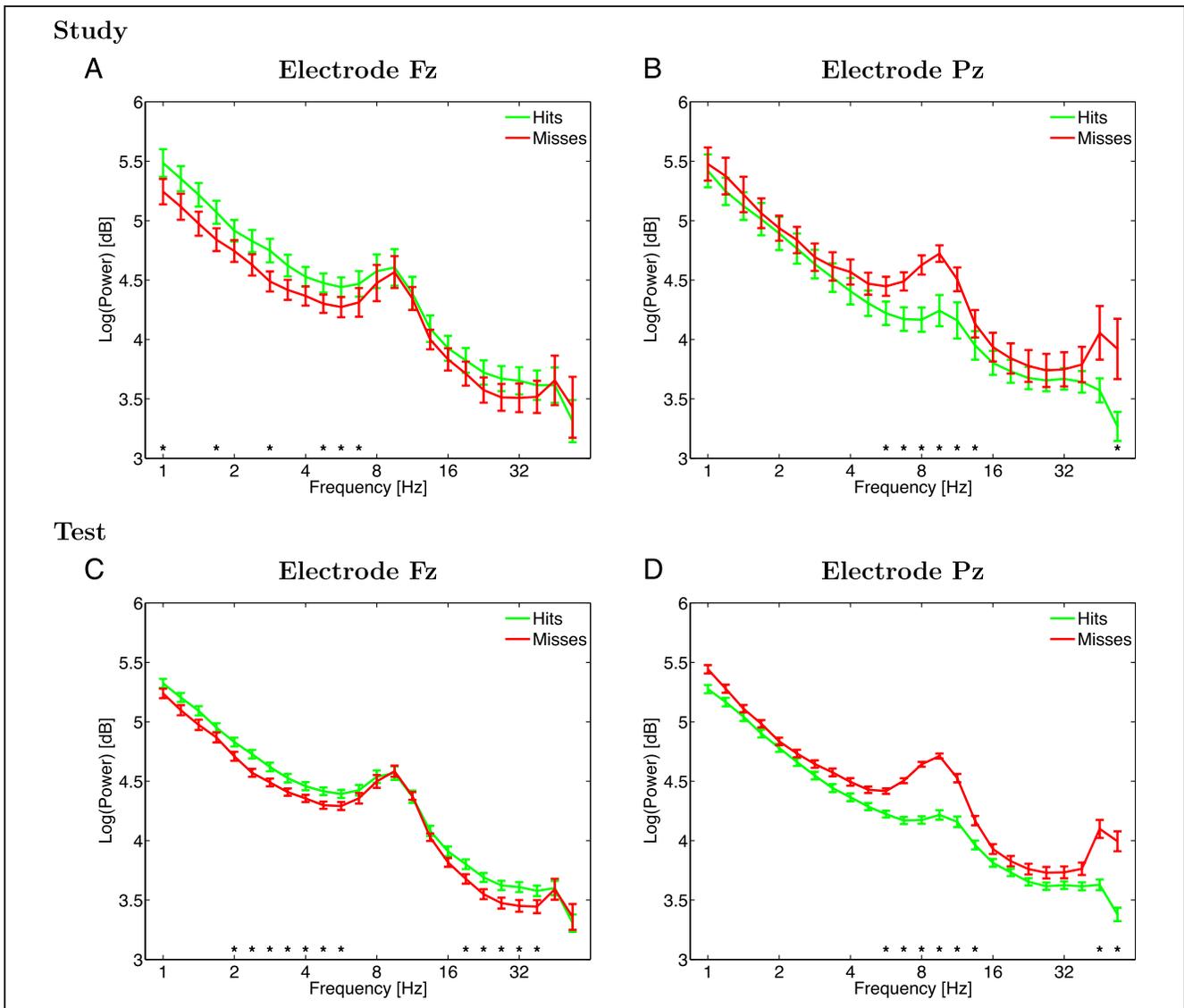


Figure 3. Average wavelet power (log-transformed) is plotted as functions of frequency between hits (green) and misses (red) during study and test. Error bars represent 95% confidence intervals. * denotes significant ($p < .05$) differences between hits and misses.

et al., 2011; Klimesch et al., 2010; Klimesch, 1999; Klimesch, Doppelmayr, Pachinger, & Ripper, 1997). This lays the groundwork for the individual-differences analyses that are the main focus of the study.

Finally, note that there were differences in the gamma band between hits and misses (Figure 2). This is in line with prior findings suggesting that gamma activity is related to memory function (Jensen, Kaiser, & Lachaux, 2007), although beyond the scope of our hypotheses.

Theme 1: Possible Inverse Relationship between Theta and Alpha Oscillations

We now turn to our first question, regarding the relationship between alpha and theta at both study and test. First, ignoring memory outcome, we evaluate the possibility that participants who generally have more alpha

activity, correspondingly, have less theta activity. We correlated, across participants, the P_{episode} values in the alpha band (measured at Pz) with the P_{episode} in the theta band (measured at Fz), at both study and test, averaged over trials, regardless of memory outcome. We found no significant correlation between alpha and theta oscillation durations at study ($r(64) = .16, p > .1, 95\% \text{ CI} [-0.09, 0.40]$) nor at test ($r(64) = .11, p > .1, 95\% \text{ CI} [-0.07, 0.37]$). Although the confidence intervals cannot exclude negative correlation values, they suggest that, if the underlying correlation is negative, it must be quite small in magnitude. Next, by incorporating memory outcome into the analysis, we correlated the subsequent memory effect and the retrieval success effect (P_{episode} difference measure of hits–misses for study and test activity, respectively) across participants. Again, no significant correlation was found at study ($r(64) = .18, p > .1, 95\% \text{ CI} [-0.07,$

0.42]) nor at test ($r(64) = .19, p > .1, 95\% \text{ CI } [-0.04, 0.39]$).

To assess the robustness of the correlation results to the choice of frequency limits of the theta and alpha bands and to address the possible bleed-in effect between alpha and theta measures mentioned in the Introduction (Hanslmayr & Staudigl, 2014; Lisman & Jensen, 2013), we plotted the full matrix, frequency-by-frequency, of correlation values between electrode Fz and Pz at both study and test in Figure 4. Frequencies nearby one another were correlated positively (see the bright color diagonal effect), as expected. There were significant correlations in other regions of the figure, beyond the frequencies of interests, which might be worth looking into for further follow-up studies; for example, delta- and gamma-frequency P_{episode} measures appeared to be correlated, as well as posterior gamma- with anterior theta-frequency oscillations, which might reflect a theta/gamma multiplexing process that has been suggested to support memory (Lisman & Jensen, 2013; Belluscio, Mizuseki, Schmidt, Kempter, & Buzsaki, 2012; Mormann et al., 2005; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Bragin et al., 1995). More importantly, the frequencies in the alpha and theta bands (outlined in the black box) showed no strong negative correlations, suggesting that averaging across frequencies within each band did not misrepresent the underlying pattern.

The mean power measure also produced a nonsignificant ($p > .1$) correlation between alpha and theta power at study ($r(64) = .16$) and at test ($r(64) = .20$) regardless of memory outcome. Moreover, by incorporating memory outcome into the analysis (subsequent memory effect and the retrieval success effect), no significant ($p > .1$) correlation was found at study ($r(64) = .08$) and at test ($r(64) = .11$). Thus, a trade-off relationship between alpha and theta activities did not appear to be present in our task.

Theme 2: Relationship between Oscillations and Individual Variability in Memory Outcome

We next examined the behavioral relevance of these memory-related oscillations. If oscillation measures could be shown to explain variance in memory performance across participants, that would corroborate the within-subject results and strengthen the role of theta and alpha oscillations in this recognition task. We first correlated the theta and alpha (P_{episode}) subsequent memory effects with the behavioral measures (d' and mean RT for hits) across participants and likewise for the retrieval success effects (Table 3). There was a significant correlation between d' and theta-oscillation durations at study (Figure 5) but not at test. Although speculative, it may be that theta oscillations are just more short-lived and thus harder to measure at test. Note that at least at the higher range of the theta band, the correlations were positive, just not significant.

The mean power measure produced the same pattern of results: a significant correlation between d' and theta power at study ($r(64) = .30, p < .05$) but not at test, and nonsignificant ($p > .1$) correlations between alpha power and RT (study: $r(64) = -.10$; test: $r(64) = -.03$), or d' (study: $r(64) = -.05$; test: $r(64) = .02$). Thus, more theta activity (measured by both P_{episode} and mean power measures) during study may lead to better recognition memory performance later on. On the other hand, there was no support for our prediction that alpha oscillations would inversely correlate with either behavioral measure. Although alpha oscillations (both measures) showed significant subsequent memory and retrieval success effects within participants, the individual differences in alpha oscillations (P_{episode} and mean power measures) may not reflect individual differences in performance.

Again, to assess the robustness of these results, we conducted a broadband version of this analysis and plotted correlation values as functions of all frequencies at electrodes

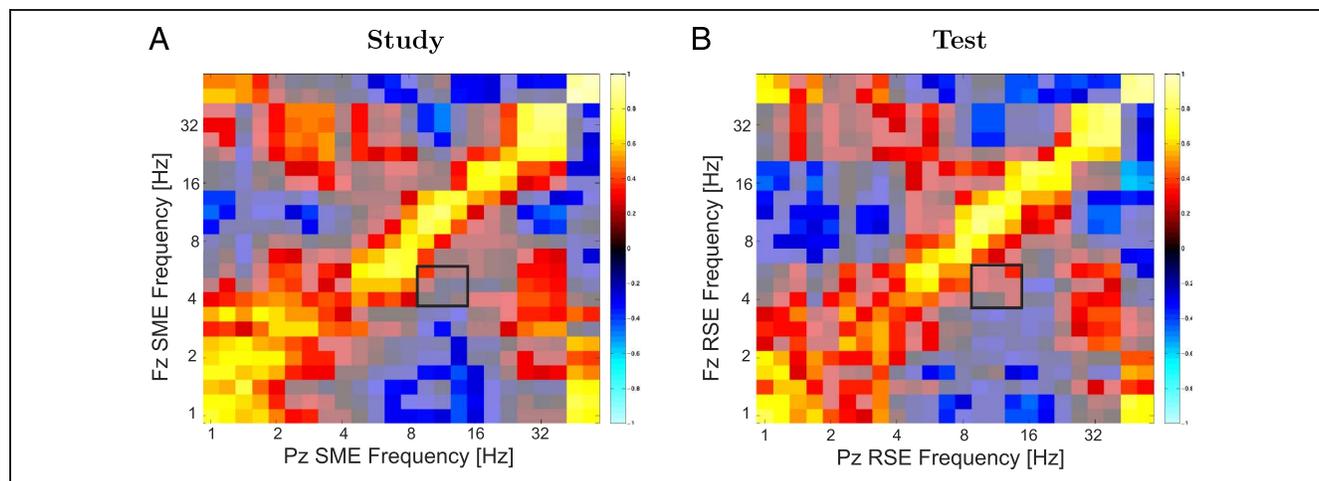


Figure 4. Pearson correlation ($df = 64$) plotted for all P_{episode} frequencies between electrode Fz and Pz at study and test. The semitransparent white screen masks out any nonsignificant points ($p > .05$). The black boxes on the figure indicate the frequencies selected for the main correlation analysis: theta (at Fz) and alpha (at Pz).

Table 3. Pearson Correlation ($df = 64$) between (1) Mean P_{episode} Alpha (Recorded at Pz) and Theta (Recorded at Fz) Oscillations with Behavioral Measures (d' and RT), (2) Study Mean P_{episode} Alpha and Theta Oscillations with Study ERPs (the Subsequent Memory Effect), and (3) Retrieval Mean P_{episode} Alpha and Theta Oscillations with Retrieval ERPs (Retrieval Success Effect)

	Study		Test	
	α	θ	α	θ
d'	-0.06 (-0.31, 0.2)	0.30* (0.04, 0.52)	-0.12 (-0.36, 0.14)	0.09 (-0.17, 0.34)
RT	0.08 (-0.19, 0.33)	-0.07 (-0.31, 0.20)	0.03 (-0.23, 0.28)	-0.21 (-0.45, 0.05)
Late Positive Component	[0.33* (0.08, 0.54)]	-0.12 (-0.36, 0.14)	-	-
Slow Wave-Early	[0.31* (0.07, 0.54)]	-0.08 (-0.33, 0.18)	-	-
Slow Wave-Late	0.46* (0.23, 0.64)	0.07 (-0.18, 0.32)	-	-
FN400	-	-	0.29* (0.04, 0.51)	0.02 (-0.24, 0.27)
Left Parietal Positivity	-	-	-0.15 (-0.39, 0.11)	0.06 (-0.20, 0.32)

Reported along with 95% confidence interval; [] indicates that this significant correlation become nonsignificant after the multiple regression model (see main text).

***Boldface** represents $p < .05$.

Fz and Pz (Figure 6). In general, the broadband analyses confirmed the results of the band-averaged analyses. Although there was no significant correlation between RT and band-averaged retrieval oscillation measures, 4.7 Hz oscillations at electrode Fz correlated negatively with RT (significantly, uncorrected). This appeared to be washed out by other frequencies when averaged across frequencies within the theta band (Figure 6D).

Theme 3: Relationship between Oscillations and Memory-related ERPs

We aimed to inform our understanding of the possible functions of the alpha and theta oscillations to recognition

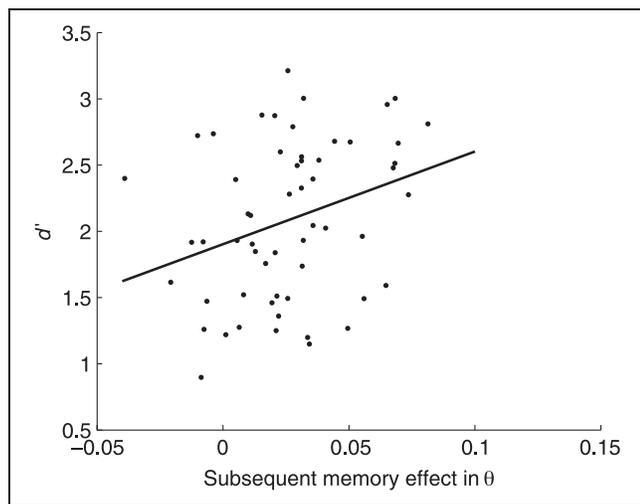


Figure 5. Relationship between d' and the size of the subsequent memory effect in the theta band ($r(64) = .30$). Each point represents a single participant. The subsequent memory measure is the proportion of oscillations (P_{episode}) for hits minus misses.

memory by seeking possible relationships between well-studied memory-related ERPs and oscillation measures. Using the P_{episode} measure, we thus correlated, across subjects, each oscillation measure with mean voltage measures of the most commonly reported ERPs implicated in recognition memory, as laid out in the Introduction. Surprisingly, the theta-band subsequent memory effect was not correlated with any of the three ERP subsequent memory effects. However, the alpha-band subsequent memory effect was correlated with all three: the Late Positive Component, the Slow Wave-Early, and the Slow Wave-Late time windows (Table 3). The broadband analysis at study confirmed this; alpha-band oscillation durations (subsequent memory effect) were correlated with the Late Positive, Slow Wave-Early, and Slow Wave-Late (Figure 7).

The mean power analyses produced the same pattern of results: significant ($p < .05$) correlation between subsequent memory effect alpha power with the Late Positive Component ($r(64) = .34$), the Slow Wave-Early ($r(64) = .36$), and the Slow Wave-Late ($r(64) = .52$).

It is important to note that Chen et al. (2014) found the subsequent memory effect ERPs in all three time windows to be mutually correlated with one another. To resolve this ambiguity, multiple regression was run with P_{episode} (alpha) as the measure and the Late Positive Component, the Slow Wave-Early, and the Slow Wave-Late as the three predictors. This model explained 18% of the variance. The only significant predictor was the Slow Wave-Late, $\beta = 0.38$, $t = 2.63$, $p < .05$ (Figure 8A). The Late Positive Component, $\beta = 0.14$, $t = 0.79$, $p > .1$, and the Slow Wave-Early, $\beta = 0.01$, $t = 0.08$, $p > .1$, were not significant predictors. These results suggested that the Slow Wave-Late was the main predictor for P_{episode} (alpha); the positive correlation between alpha duration and the Late Positive Component, and the Slow Wave Early might be due to the positive correlation with the Slow Wave-Late.

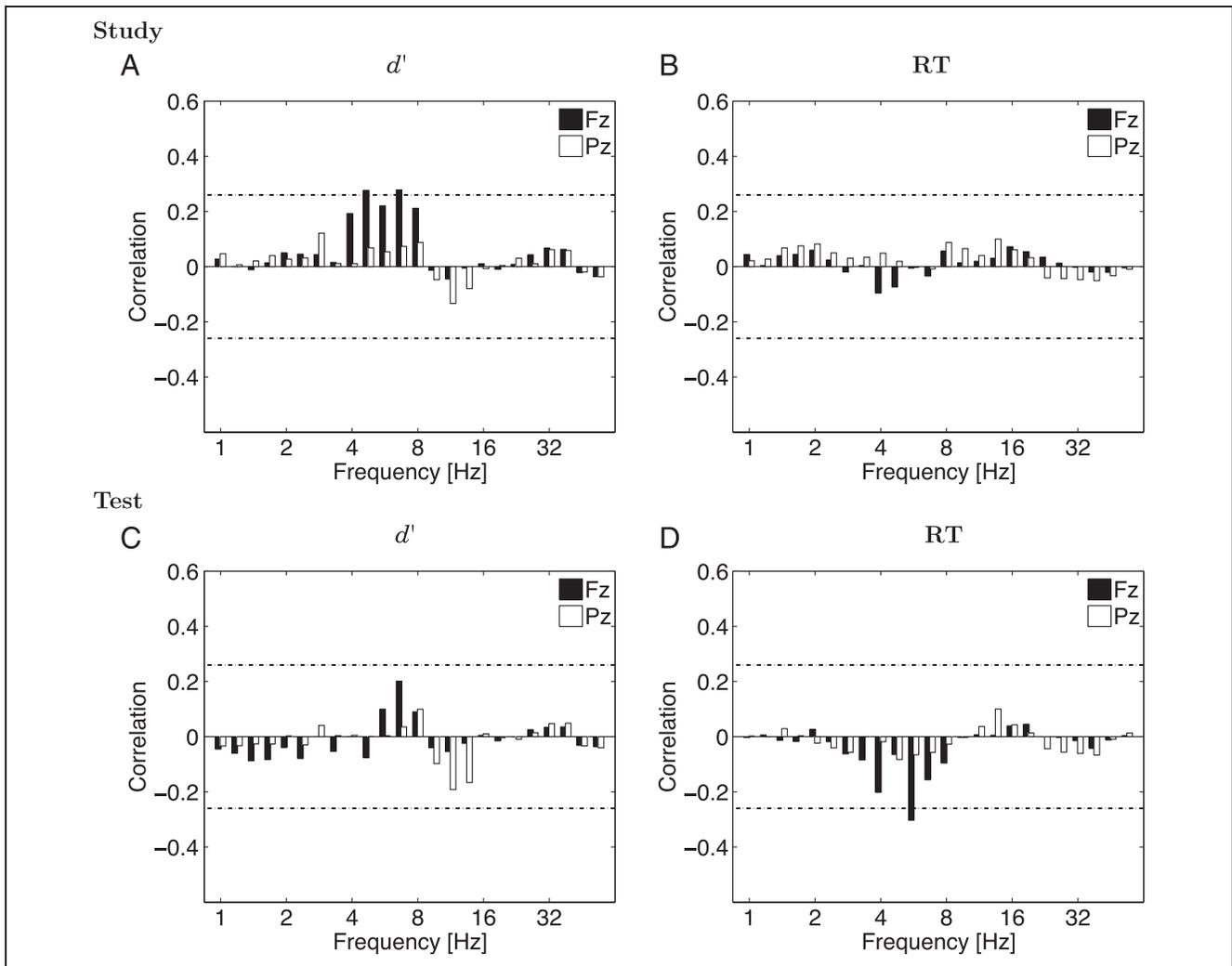


Figure 6. Pearson correlation ($df = 64$) plotted for all P_{episode} frequencies at study (A, B) and test (C, D) correlating with d' (A, C) and RT (B, D). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < .05$, two-tailed).

This same multiple regression was run with alpha-band mean power as the measure and the Late Positive Component, the Slow Wave-Early, and the Slow Wave-Late as the three predictors. As above, we found that the Slow Wave-Late, $\beta = 0.41$, $t = 3.13$, $p < .05$, was the only significant predictor.

It may seem logically backwards that later activity could explain away earlier activity. Quite likely, activity is already ramping up at the times of the two earlier ERP signals, but this early activity is only coupled with alpha activity if it either is sustained throughout the entire window of analysis or appears during the time frame of the Slow Wave-Late. Initially, we predicted that increase in alpha activity might correlate with memory-related ERP negatively. Rather, the positive correlation between alpha oscillation measures and Slow Wave-Late indicates that if a participant has more alpha suppression (less alpha activity), then the amplitude difference is smaller for the Slow Wave-Late. Researchers have functionally distinguished the Late Positive Component from the Slow Wave,

where the former is thought to index the encoding of item information or “shallower” processing and the latter is thought to index “deeper” levels of processing (Fabiani, Karis, & Donchin, 1990; Karis, Fabiani, & Donchin, 1984). It would follow that when participants use deeper strategies (such as visual imagery), we should expect to see a bigger subsequent memory effect during the Slow Wave. Another line of research also found that when participants turned their attention inward or engaged in mental imagery, increased alpha power was observed (Bartsch et al., 2015). Taken together, we speculate that our participants were employing strategies that tapped into the deeper processes indexed by the Slow Wave, this was also reflected in increased alpha oscillations (both measures).

During test, we found a positive correlation between $P_{\text{episode}}(\text{alpha})$ and the FN400, but not with the Late Parietal Positivity. $P_{\text{episode}}(\text{theta})$, again, did not correlate with any retrieval ERP measure (Table 3). We also conducted the broadband analysis to assess the robustness of the

correlation results. No frequencies showed any significant relationships with the FN400 except within the alpha band. Moreover, we found no significant correlations between any frequencies and the Left Parietal Positivity (Figure 9).

Using the mean power measure, the correlation between the alpha-band retrieval success effect and the FN400 was not significant, although it was in the same direction as found for P_{episode} (mean power: $r(64) = .18, p > .1$).

The Old/New Effect versus the Retrieval Success Effect

We have argued (Chen et al., 2014) that it makes most sense to compare study activity and test activity using the subsequent memory effect and retrieval success effect measures, because they both take into account memory success versus failure. However, the bulk of published research regarding ERPs during recognition test has measured the so-called “old/new effect,” contrast-

ing correct-old versus correct-new items (hits–correct rejections). Indeed, Chen et al. (2014) found that, for ERPs, although the within-subject effects appeared similar for retrieval success effect and old/new effect comparisons, the individual differences effects were quite different. We thus asked if our results would be different if we substituted the old/new effect for the retrieval success effect. The paired-samples, two-tailed t test, comparing mean P_{episode} between hits and correct rejections during test, was significant for the theta band at electrode Fz ($t(65) = 2.73, p < .05$), with theta oscillations more of the time during hits than correct rejections, but was not significant for the alpha band ($t(65) = -0.68, p > .1$) at electrode Pz, replicating prior results (Klimesch, Doppelmayr, Stadler, et al., 2001; Klimesch, 1999).

In addition, we tested the possible relationship between the P_{episode} (theta) old/new effect and the ERP old/new effects (FN400 and Left Parietal Positivity) across participants (Table 4). There was a significant correlation between the theta-band old/new effect and d' (Figure 11) but

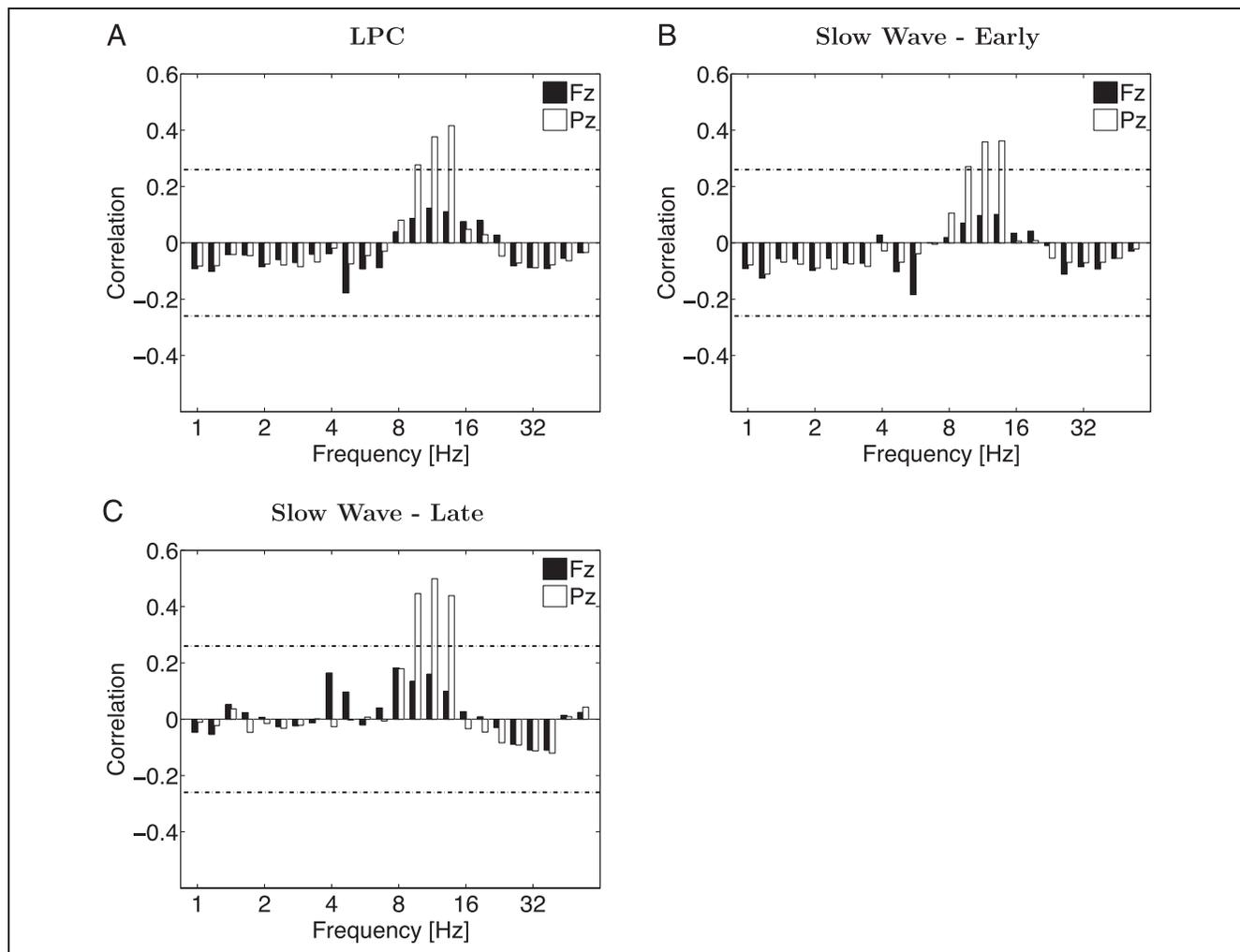


Figure 7. Pearson correlation ($df = 64$) plotted for all P_{episode} frequencies at study correlating with subsequent memory effect ERPs (A, LPC; B, Slow Wave-Early; C, Slow Wave-Late). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < .05$, two-tailed).

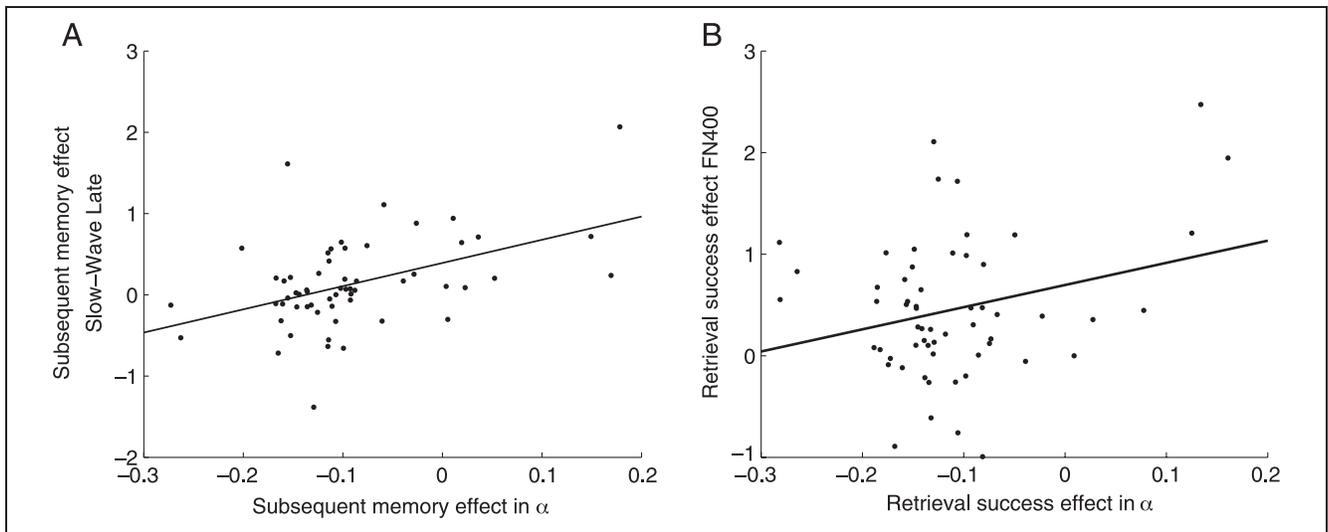


Figure 8. Relationship between (A) Slow Wave-Late and the size of the subsequent memory effect in the alpha band ($r(64) = .46$), and (B) FN400 and the size of the retrieval success effect in the alpha band ($r(64) = .29$). Each point represents a single participant. The subsequent memory measure is the proportion of oscillations (P_{episode}) for hits minus misses at study, and the retrieval success measure is the proportion of oscillations (P_{episode}) for hits minus misses at test.

not RT. The theta-band old/new effect was not significantly correlated with the FN400 nor with the Left Parietal Positivity. Checking the robustness of correlation, in the broadband analysis, one can also see a strong correlation with d' of the old/new effect at several frequencies within the theta band (Figure 10).

Checking the key findings with the mean power measure, the old/new effect was also significant in the theta-band at electrode Fz ($t(65) = 2.53, p < .05$). The correlation between the theta-band old/new effect and d' did not reach significance using the mean power measure, although it was still nominally positive ($r(64) = .16, p > .1$; Figure 11).

In summary, the results concerning alpha oscillations (P_{episode} and mean power measures) are consis-

tent with alpha oscillations reflecting attention. In the old/new effect, hits are contrasted with correct rejections; because a correct rejection is a correct response, it is plausible that visual attention is as elevated during correct rejections as during hits (in contrast to during misses, which might, sometimes, reflect lapses in visual attention). The positive correlation between d' and theta oscillations (P_{episode} but not mean power measure) also strengthens the behavioral relevance of theta oscillations for old/new recognition. This raised the question whether theta oscillations might be related to differentiation effects in recognition (Shiffrin & Steyvers, 1997), which motivated the following additional analyses.

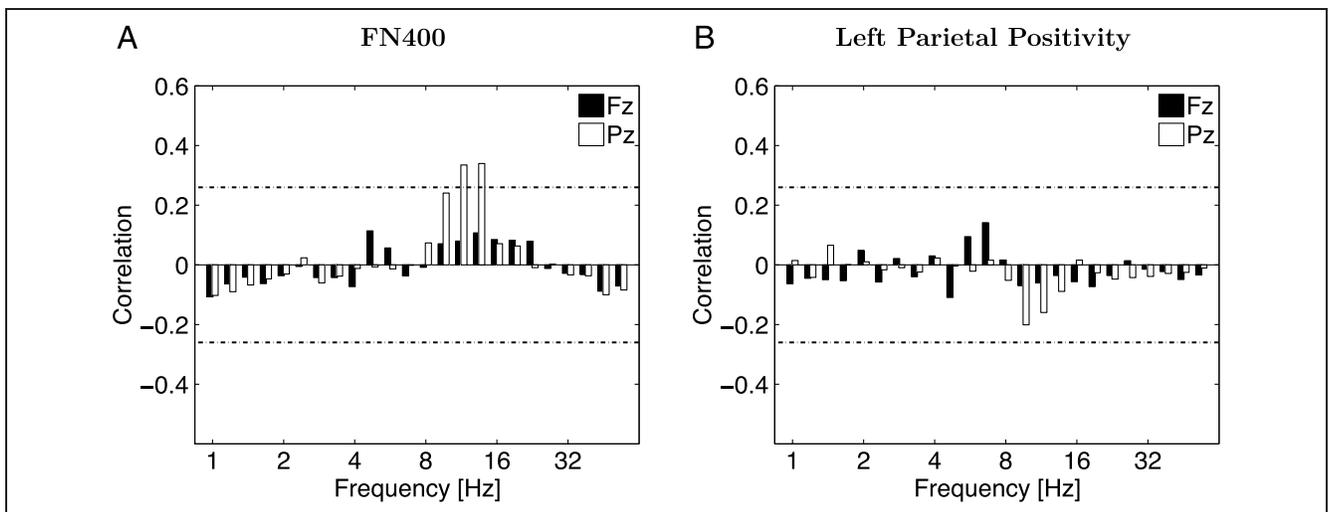


Figure 9. Pearson correlation ($df = 64$) plotted for frequencies showing retrieval success effect at retrieval correlating with retrieval success effect ERPs (A, FN400; B, LPP). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < .05$, two-tailed).

Table 4. Pearson Correlation ($df = 64$) between Retrieval Theta Oscillations (Old/New Effect: Hits–Correct Rejections) with Behavioral Measures (d' and RT) and with Retrieval ERPs (Old/New Effect); Theta Recorded at Electrode Fz

	d'	RT	FN400	Left Parietal Positivity
θ	0.29* (–0.08, 0.51)	–0.17 (–0.28, 0.41)	–0.03 (–0.29, 0.22)	0.11 (–0.14, 0.36)

***Boldface** represents $p < .05$.

Follow-up Analysis of Theta Oscillations and Memory Outcome

The finding that theta oscillation duration covaried with d' during test, only when we contrasted hits with correct rejections (old/new effect), but not hits–misses, led us to move beyond the difference measures. A multiple regression was run with d' as the measure and $P_{\text{episode}}(\text{theta})$ during study for later-hits, during study for later-misses, during hits at test, during misses at test, and during correct rejections at test as the five predictors² (Table 5). The model explained 17% of the variance. The significant predictors were theta-oscillation durations during study for later-hits, during hits at test, and during correct rejections at test. Theta oscillations during study for later-misses and misses at test were not significant predictors. Thus, theta-oscillation durations associated with successful memory (hits at both study and test) were the main predictors of d' , along with theta oscillations during correct rejections, with a negative β . This suggests that theta oscillations help to encode items well but also support the discrimination of old from new items. In differentiation models, such as Retrieving Effectively from Memory (Shiffrin & Steyvers, 1997), when an item is studied, a memory trace is formed; later a test item is compared with those formed memory traces to make an old/new decision. The better list items are studied; not only will studied items match better, but unstudied items will match

memory of the list worse, leading to strength-based mirror effect. Theta oscillations at study might index the formation of memory traces which, later on, lead to reduction of the degree to which new items match memory. Likewise, theta oscillations at test may reflect the strength of the match of the probe item to memory. Studied items that are correctly identified (hits) may thereby be more likely to evoke theta oscillations, matching memory better, than lure items that are correctly identified (correct rejections), matching memory less. Note that the correlation between the theta-band old/new effect and d' did not reach significance using the mean power measure. Thus, it was not warranted to conduct the multiple regression analysis with mean power.

Robustness to the Selection of Time Windows

To assess the robustness of the correlation results to the choice of time-windows of analysis, we reran our analyses for the theta and alpha bands, using the P_{episode} measures, varying the time window following stimulus onset, in 200-msec segments. The full 1200-msec window, therefore, was broken down into six segments. Importantly, the BOSC analysis had been run over the continuous recording, and was only then calculated by averaging the P_{episode} values during each of the time windows: 1–200 msec,

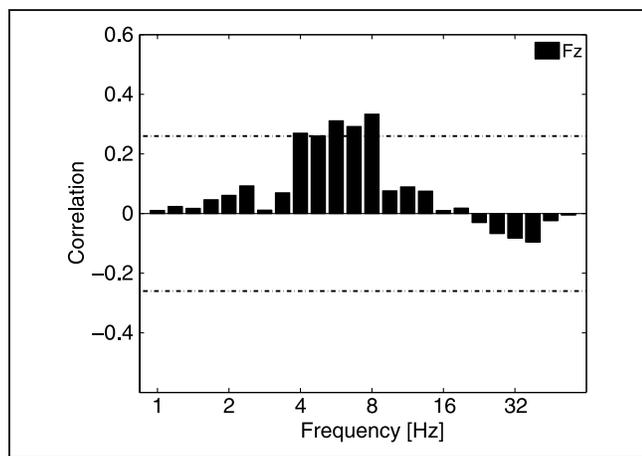


Figure 10. Pearson correlation ($df = 64$) plotted for frequencies showing old/new effect at retrieval correlating with the d' . Oscillations were recorded at electrode Fz. The dashed lines denote the significance thresholds ($p < .05$, two-tailed).

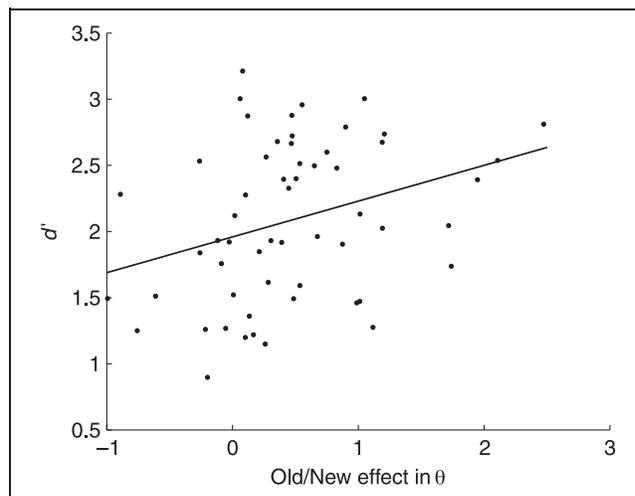


Figure 11. Relationship between d' and the size of the old/new effect in the theta band ($r(64) = .29$). Each point represents a single participant. The theta old/new effect measure is the proportion of oscillations (P_{episode}) for hits minus correct rejections, recorded at electrode Fz.

Table 5. Regression Model for Theta Activity Predicting d'

Predictors	Beta	<i>t</i>
θ Hits (study)	0.61	2.36*
θ Misses (study)	0.21	0.42
θ Hits (test)	0.88	2.21*
θ Misses (test)	0.09	0.35
θ Correct rejections (test)	-0.62	-2.61*

The theta activity measure is the proportion of oscillations (P_{episode}) for hits and misses during study and hits, misses, and correct rejection during test, recorded at electrode Fz.

* $p < .05$.

201–400 msec, 401–600 msec, 601–800 msec, 801–1000 msec, and 1001–1200 msec. It is important to note that P_{episode} , just as with any measure of power, integrates over signal before and after the 200-msec window of interest. Thus, the final 200-msec windows of analysis should not be taken as instantaneous estimates of oscillatory activity; rather, our objective here was to test whether our effects might depend critically on the selection of the time window. In general, the smaller time window results were similar to the full 1–1200 msec window. Across all six time windows, the pattern of significance (and sign) that were the same as the full-window analysis, for alpha oscillations, were the nonsignificant correlation between the alpha subsequent memory effect and both d' and RT, the significant correlation with Late Positive Component and Slow Waves, and the nonsignificant correlation between the alpha retrieval success effect and behavioral measures and the Left Parietal Positivity. For theta oscillations, the unchanged findings were the nonsignificant correlation between the theta subsequent memory effect and RT, as well as all subsequent memory effect ERP measures; the nonsignificant correlation between the theta retrieval success effect and behavioral measures, the FN400 and the Left Parietal Positivity; the significant correlation between theta old/new effect and d' ; and the nonsignificant correlation between the theta old/new effect and the FN400, and the Left Parietal Positivity. There were three results that were significant within 1–1200 msec time window analyses but nonsignificant (although the correlations were unchanged in sign) at some of the shorter time windows: (1) the theta subsequent memory effect significantly correlated with d' at the first four time windows but was nonsignificant at 801–1000 msec ($r(64) = .19, p > .1$) and 1001–1200 msec ($r(64) = .19, p > .1$); (2) the theta old/new effect significantly correlated with d' at the first four time windows but was nonsignificant at 801–1000 msec ($r(64) = .19, p > .1$) and 1001–1200 msec ($r(64) = .18, p > .1$); and (3) the alpha retrieval success effect significantly correlated with FN400 across all except the 601–800 msec window ($r(64) = .21, p > .1$). Still, the signs of the effects were all unchanged from the full window to all subwindows. The mean power analyses pro-

duced the same pattern of results as the mean power full-window analyses. Thus, overall, the pattern of results appears robust to choice of time window.

DISCUSSION

Exploiting individual variability, we correlated measures of alpha and theta oscillations with each other, with behavioral memory outcomes and with memory-related ERPs. This approach revealed new evidence regarding the possible functions of alpha and theta oscillations in recognition memory, as we elaborate next.

Theme 1: A Possible Trade-off Relationship between Alpha and Theta Oscillations

Our first goal was to test whether alpha and theta oscillations are inversely correlated across participants, in a simple recognition task. We did observe the subsequent memory and retrieval success effects in both alpha and theta oscillations as reported by Klimesch (1997), Klimesch et al. (1990, 1993, 1994, 1997, 2010), and Rugg and Dickens (1982). However, our correlation results offer no support for any trade-off relationship. Alpha and theta oscillations may play different roles in memory encoding and retrieval, but these cognitive functions appear independent and, in this experiment, do not display a straight-forward trade-off relationship with one another, at least with respect to individual variability and old/new recognition memory. It is likely that the individual variability in our study may not affect alpha and theta activity in opposite ways. Thus, prior findings of alpha and theta oscillations changing in opposite directions may be specific to those experimental manipulations, rather than reflecting an inevitable push-and-pull relationship between the two rhythms.

Theme 2: Relevance of Alpha and Theta Oscillations to Recognition Memory Outcome

Measures of alpha oscillations did not correlate with either d' or RT, suggesting that alpha oscillations are not major drivers of old/new recognition. Prior research has suggested that the amount of theta activity at test can index memory performance (Doppelmayr et al., 1998, 2000). In our data set, theta activity at study was correlated with d' , and theta activity at test was only correlated with d' using the old/new effect contrast (but not with retrieval success effect). Caplan and Glaholt (2007) found that theta-oscillation duration was correlated, across individuals, with accuracy and RT of a relational memory task. Theta oscillations might thus support item-memory encoding and retrieval via relational memory strategies, such as formation of interactive imagery or sentences.

Theme 3: Memory-related Oscillations and Memory-related ERPs

ERPs have been studied more extensively than oscillations in relation to recognition memory. Prior research has suggested many possible functional roles those ERP features could reflect. Although this is still under debate, at least we can ask whether an oscillation might correspond to the same cognitive process as an ERP or a different process. At study, measures of alpha-band oscillations were correlated with features of the ERP subsequent memory effect, most robustly, with the Slow Wave-Late. In contrast, measures of theta-band oscillations at study did not correlate with any ERP measure. The Slow Wave has been thought to index elaborative memorization strategies (Fabiani et al., 1990), which could include “deep” levels of processing as well as relational or imagery-based strategies. Interestingly, reviewing a large body of research, Nyhus and Curran (2010) thought it likely that theta oscillations are engaged in relational and association-memory encoding, in item-memory as well as relational memory tasks. This suggested a clear hypothesis: Theta oscillations and the Slow Wave reflect a common, relational process, in which case they should correlate with one another during study. This correlation, however, was not significant. This raises the possibility that, if theta oscillations are involved in associative or relational encoding, they do so in a very different way than the Slow Wave.

There was a strong correlation between measures of alpha oscillations and the Slow Wave-Late. It is plausible that one’s level of visual attention during study could influence the quality of later memory. Klimesch et al. (1993) asked if attention was the only relevant factor for the suppression of the alpha during successful memory encoding. Klimesch et al. (1993) presented participants with a list of characters to remember, after a short delay participants were presented with a target and lure to select which one was from the study list. Importantly, the study lists were manipulated in two ways: varying list length and varied versus consistent mapping. In the “varied mapping” condition where the characters comprising each list were randomly drawn from a larger stimulus pool. In the “consistent mapping” condition, the set of characters in each list within a block was identical, thus demanding less attention than the varied mapping condition. Alpha power decreased more in the varied mapping condition than the consistent mapping condition, suggesting that alpha (decrease) indexed attention. More importantly, within each mapping condition, the later-remembered encoding trials also had less alpha power. In line with these results, Gevins, Smith, McEvoy, and Yu (1997) found that alpha power decreased during an *n*-back task, but more so for the more challenging condition than a simpler control condition (3-back vs. 1-back). This result suggested that as memory load increased, alpha activity decreased. Our results were consistent with these findings that alpha activity decreases more during remembered trials than the forgotten trials

(at both study and test). In other words, it is possible that decreased alpha activity might not only index attention, but perhaps memory-relevant cognitive processes.

Furthermore, alpha activity has also been suggested to index inward attention; when a participant focuses more on their internal thoughts, alpha activity may increase. The positive correlation between measures of alpha oscillations and the Slow Wave-Late is also consistent with that idea, presuming that the Slow Wave reflects such deep levels of processing. It is possible that the increase in alpha duration and power captured the inward attention required for making mental visual representations of items during encoding, which may also be indexed by the Slow Wave-Late.

At test, the FN400 and the Left Parietal Positivity have been suggested to index familiarity-based and recollection-based retrieval, respectively (Rugg & Curran, 2007). There are several reasons to expect theta oscillations support recollection-based recognition judgments (Nyhus & Curran, 2010), which leads one to predict a positive correlation between theta oscillations and the Late Parietal Positivity. However, we did not see a straight-forward mapping of the theta activity onto the Left Parietal Positivity, nor even the FN400. Instead, the retrieval success measure of alpha oscillations correlated with the FN400. These correlations remained nonsignificant when measured with the old/new effect contrast (although, recall that the theta-band old/new effect did correlate significantly with d'). In other words, theta oscillations may be important for recognition memory at test, perhaps in distinguishing old from new items, but not in the same way as the Late Parietal Positivity. We did see a significant correlation between alpha activity and the FN400, adding to other evidence that alpha activity is important for memory retrieval (Klimesch et al., 1990) and may contribute to a common retrieval process as the FN400, perhaps familiarity or conceptual or semantic priming (Voss & Federmeier, 2011; Rugg & Curran, 2007).

Yet other alternative accounts to dual-process theory remain viable. For example, Wixted (2007) proposed that familiarity and recollection may both coexist in the brain, but that they summate to drive the old/new decision. Dunn (2008) went even further, showing that even remember and know judgments may be driven by only a single underlying decision dimension (which could be the sum of two or more sources of evidence, but they still summate to drive responses). Thus, it is also possible that theta (as well as alpha) oscillations reflect memory quality or strength but do not map clearly onto recollection and familiarity.

Our results added more evidence that alpha activity might index visual attention, because alpha oscillations differed between hits and misses but not between hits and correct rejections. Namely, it is possible that participants weren’t paying attention during those trials that led to a miss response later on. More importantly, this result also converges with previous research on alpha power

and performance on various tasks (Mathewson et al., 2012; Klimesch et al., 2007; Doppelmayr et al., 2000, 2005; Klimesch, Vogt, & Doppelmayr, 2000; Klimesch, 1999). In addition, correlations between measures of alpha oscillations and memory-related ERPs during both study and test are also consistent with previous research on alpha power (Jensen et al., 2002; Klimesch et al., 1990, 1993). Furthermore, the regression model suggested that theta duration during hits (both at study and test) and during correct rejections were the main predictors of d' . Criss, Wheeler, and McClelland (2013) conducted an fMRI study that examined brain activity between hits and correct rejections during the test phase of an old/new recognition task. They found that more percent signal change in angular gyrus region was correlated with d' . In other words, the bigger the signal change difference in angular gyrus, the bigger the d' , the better a participant could discriminate old from new items. Criss et al. (2013) suggested that the activity in angular gyrus could reflect memory strength differentiation. Adopting the same logic here, the cognitive process we captured in the theta old/new contrast (hits–correct rejections) might also reflect matching of the probe to memory, which can differentiate old and new items.

Prior research has suggested that parietal lobe contributions to memory retrieval are more closely linked to metamemory processes, such as confidence rating judgments of recollection, than to veridical recognition itself (Woroch & Gonsalves, 2010; Ally, Simons, McKeever, Peers, & Budson, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). Chen et al. (2014) suggested that the Left Parietal Positivity may not reflect recognition success, but rather discriminating the old from new items. Moreover, the theta-oscillation old/new effect contrast did not correlate with the Left Parietal Positivity. If, indeed, both the theta oscillations and the Left Parietal Positivity reflect some process involved in differentiating memory strength between old and new items, at least they contribute to the process differently. In addition, it is possible that measures of theta oscillations do reflect recollection processes (correlation with d') in a way that the Left Parietal Positivity does not.

In summary, a pattern emerges from the correlation results whereby alpha oscillations are correlated with memory-related ERPs but not with memory performance and theta oscillations, on the other hand, are correlated with memory performance but not with memory-related ERPs. Both the alpha and theta oscillations are evidently important for successful encoding and retrieval of memory; our replications of the significant subsequent memory effect and retrieval success effect, with the BOSC method, confirm that reduced alpha oscillations and increased theta oscillations indicate successful memory. Although the precise functions of these two oscillations in recognition memory still require further investigation, our results suggest that alpha oscillations might index

the participant's attention level. This could include both visual attention and inward attention that could each facilitate encoding and retrieval in different ways. Those cognitive processes indexed by alpha oscillations are also reflected in the memory-related ERP amplitude; however, the duration and power of alpha oscillations do not translate directly to better memory performance, at least as measured with old/new judgments.

Prior research has built a strong case for theta oscillations supporting memory. We have shown that the theta oscillations not only differ between remembered and forgotten words but also correlate with memory performance across participants. Intriguingly, we find no correlation between theta oscillations and memory-related ERPs, even those thought to reflect the same or similar cognitive processes (the Slow Wave and Late Parietal Positivity). It is plausible that theta oscillations would correlate with other ERP measures that we did not test; it is equally possible that our understanding of these ERP features and theta oscillations requires refinement.

Comparison with Conventional Measures of Power

We focused on a measure derived from the BOSC method to be conservative about classifying measured activity as rhythmic. Thus, results obtained with the P_{episode} measure may be more susceptible to Type II than to Type I error. In addition, P_{episode} measures duration of oscillations, given that power exceeds the tuned threshold; thus, any modulation of power within those detected oscillatory episodes is ignored by P_{episode} . To check whether our emphasis on this selective oscillation duration measure may have hidden any pertinent results, we conducted parallel analyses using mean power as the measure. If amplitude modulations showed any of the effects of interest, we would have found significant effects using mean power that were not significant with P_{episode} as the measure. We found no such cases. On the other hand, mean power is not selective for oscillatory activity; if oscillations are present, large in amplitude and/or long lasting, they will tend to dominate the power measure, but if they are sporadic, mean power will be weighted more by nonoscillatory signal such as one expects from the colored noise background spectrum. This may explain why some results were statistically less robust using mean power than P_{episode} . These exceptions were still in the same direction: (1) the correlation between the alpha-band retrieval success effect and the FN400 (mean power: $r(64) = .18, p > .1$) and (2) the correlation between the theta-band old/new effect and d' (mean power: $r(64) = .16, p > .1$). Thus, using mean power as an alternative measure produced no results that contradicted the results obtained with P_{episode} . Although no conflict between the two measures was found in the current data set, it is still advisable, in future studies, to analyze both, especially to test the possibility that modulations of power within oscillations may track behavioral or cognitive functions even when oscillation

durations do not change. Together, including both P_{episode} and mean power measures could provide us with more comprehensive picture of oscillation functions.

Conclusion

We used a large sample size to exploit individual variability by correlating measures of memory-related oscillations, in the alpha and theta bands, with behavioral outcomes and memory-related ERPs. Alpha and theta oscillations appear to play crucial roles in recognition memory; however, they seem to contribute to memory differently. The correlations between measures of alpha oscillations and memory-related ERPs suggested that alpha oscillations help engage participants in effective memory encoding and retrieval. The correlation between measures of theta oscillations at study and d' provided convergent evidence that the theta oscillations help to support successful encoding of new information in recognition memory. Moreover, durations of theta oscillations at test (with the old/new contrast, but not with the retrieval success contrast) correlating with memory outcome provided support for differentiation models, suggesting that the prevalence of theta oscillations may reflect differentiation. Furthermore, this effect did not overlap with the function of the Left Parietal Positivity, which may also contribute to differentiation. Theta oscillations might support item-memory encoding and retrieval by contributing to relational memory processes; however, the involvement of theta oscillations in relational memory must be different from those indexed by ERP measures.

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Notes

1. When we excluded these 12 participants from the analyses, the pattern of results was not affected.
2. We could not include false alarms because of low trial counts.

REFERENCES

Ally, B. A., Simons, J. S., McKeever, J. D., Peers, P. V., & Budson, A. E. (2008). Parietal contributions to recollection: Electrophysiological evidence from aging and patients with parietal lesions. *Neuropsychologia*, *46*, 1800–1812.

- Bartsch, F., Hamuni, G., Miskovic, V., Lang, P. J., & Keil, A. (2015). Oscillatory brain activity in the alpha range is modulated by the content of word-prompted mental imagery. *Psychophysiology*, *52*, 727–735.
- Belluscio, M. A., Mizuseki, K., Schmidt, R., Kempster, R., & Buzsáki, G. (2012). Cross-frequency phase-phase coupling between theta and gamma oscillations in the hippocampus. *Journal of Neuroscience*, *32*, 423–435.
- Bhattacharya, J. (2009). Increase of universality in human brain during mental imagery from visual perception. *PLoS One*, *14*, e4121.
- Bonnefond, M., & Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology*, *22*, 1969–1974.
- Bragin, A., Jando, G., Nádasdy, Z., Hetke, J., Wise, K., & Buzsáki, G. (1995). Gamma (40–100 Hz) oscillation in the hippocampus of the behaving rat. *Journal of Neuroscience*, *15*, 47–60.
- Burke, J. F., Zaghoul, K. A., Jacobs, J., Williams, R. B., Sperling, M. R., Sharan, A. D., et al. (2013). Synchronous and asynchronous theta and gamma activity during episodic memory formation. *Journal of Neuroscience*, *33*, 292–302.
- Busch, N. A., & Herrmann, C. S. (2003). Object-load and feature-load modulate EEG in a short-term memory task. *NeuroReport*, *14*, 1721–1724.
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*, *9*, 613–625.
- Caplan, J. B., Bottomley, M., Kang, P., & Dixon, R. A. (2015). Distinguishing rhythmic from non-rhythmic brain activity during rest in healthy neurocognitive aging. *NeuroImage*, *112*, 341–352.
- Caplan, J. B., & Glaholt, M. G. (2007). The roles of EEG oscillations in learning relational information. *NeuroImage*, *38*, 604–616.
- Caplan, J. B., Madsen, J. R., Raghavachari, S., & Kahana, M. J. (2001). Distinct patterns of brain oscillations underlie two basic parameters of human maze learning. *Journal of Neurophysiology*, *21*, 3175–3183.
- Chen, Y. Y., Lithgow, K., Hemmerich, J. A., & Caplan, J. B. (2014). Is what goes in what comes out? Encoding and retrieval event-related potentials together determine memory outcome. *Experimental Brain Research*, *232*, 3175–3190.
- Cooper, N. R., Croft, R. J., Dominey, S. J., Burgess, A. P., & Gruzelier, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*, *47*, 65–74.
- Criss, A. H., Wheeler, M. E., & McClelland, J. L. (2013). A differentiation account of recognition memory: Evidence from fMRI. *Journal of Cognitive Neuroscience*, *25*, 412–435.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics. *Journal of Neuroscience Methods*, *134*, 9–21.
- Depue, B. E., Ketz, N., Mollison, M. V., Nyhus, E., Banich, M. T., & Curran, T. (2013). Rps and neural oscillations during volitional suppression of memory retrieval. *Journal of Cognitive Neuroscience*, *25*, 1624–1633.
- Doppelmayr, M., Klimesch, W., Hodlmoser, K., Sauseng, P., & Gruber, W. (2005). Intelligence related upper alpha desynchronization in a semantic memory task. *Brain Research Bulletin*, *66*, 171–177.
- Doppelmayr, M., Klimesch, W., Schwaiger, J., Auinger, P., & Winkler, T. (1998). Theta synchronization in the human EEG and episodic retrieval. *Neuroscience Letters*, *257*, 41–44.
- Doppelmayr, M., Klimesch, W., Schwaiger, J., Stadler, W., & Rohm, D. (2000). The time locked theta response reflects

- interindividual difference in human memory performance. *Neuroscience Letters*, *278*, 141–144.
- Dunn, J. C. (2008). The dimensionality of the remember-know task: A state-trace analysis. *Psychological Review*, *115*, 426–446.
- Fabiani, M., Karis, D., & Donchin, E. (1990). Effect mnemonic strategy manipulation in a von Restorff paradigm. *Electroencephalography Clinical Neurophysiology*, *75*, 22–35.
- Fell, J., Klaver, P., Elfadil, H., Schaller, C., Elger, C. E., & Fernandez, G. (2003). Rhinal-hippocampal theta coherence during declarative memory formation: Interaction with gamma synchronization? *European Journal of Neuroscience*, *17*, 1081–1088.
- Fell, J., Klaver, P., Lehnertz, K., Grunwald, T., Schaller, C., Elger, C. E., & Fernandez, G. (2001). Human memory formation is accompanied by rhinal-hippocampal coupling and decoupling. *Nature Neuroscience*, *4*, 1259–1264.
- Fell, J., Ludowig, E., Staresina, B. P., Wagner, T., Kranz, T., Elger, C. E., et al. (2011). Medial temporal theta/alpha power enhancement precedes successful memory encoding: Evidence based on intracranial EEG. *Journal of Cognitive Neuroscience*, *31*, 5392–5397.
- Friendly, M., Franklin, P. E., Hoffman, D., & Rubin, D. C. (1982). The Toronto word pool: Norms for imagery, concreteness, orthographic variables, and grammatical usage for 1,080 word. *Behavior Research Methods & Instrumentation*, *14*, 375–399.
- Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, *7*, 374–385.
- Gruber, T., Tsviliv, D., Giabbiconi, C., & Müller, M. M. (2008). Induced electroencephalogram oscillations during source memory: Familiarity is reflected in the gamma band, recollection in the theta band. *Journal of Cognitive Neuroscience*, *20*, 1043–1053.
- Guderian, S., & Düzel, E. (2005). Induced theta oscillations mediate large-scale synchrony with mediotemporal areas during recollection in humans. *Hippocampus*, *15*, 901–912.
- Guderian, S., Schott, B. H., Richardson-Klavehn, A., & Düzel, E. (2009). Medial temporal theta state before an event predicts episodic encoding success in humans. *Proceedings of the National Academy of Sciences, U.S.A.*, *106*, 5365–5370.
- Hanslmayr, S., & Staudigl, T. (2014). How brain oscillations form memories—A processing based perspective on oscillatory subsequent memory effects. *Neuroimage*, *85*, 648–655.
- Herrman, C. S., Senkowski, D., & Rottger, S. (2004). Phase-locking and amplitude modulations of EEG alpha: Two measures reflect different cognitive processes in a working memory task. *Journal of Experimental Psychology*, *51*, 311–318.
- Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: Theta correlates of memory retrieval and decision making. *Neuroimage*, *32*, 978–987.
- Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, *12*, 877–882.
- Jensen, O., Kaiser, J., & Lachaux, J.-P. (2007). Human gamma-frequency oscillations associated with attention and memory. *Trends in Neuroscience*, *30*, 317–324.
- Jung, T.-P., Makeig, S., Humphries, C., Lee, T.-W., McKeown, M. J., Iragui, V., et al. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*, *37*, 163–178.
- Kahana, M. J., Seelig, D., & Madsen, J. R. (2001). Theta returns. *Current Opinion Neurobiology*, *6*, 739–744.
- Karis, D., Fabiani, M., & Donchin, E. (1984). “P300” and memory: Individual difference in the von Restorff effect. *Cognitive Psychology*, *16*, 177–216.
- Kawasaki, M., & Watanabe, M. (2007). Oscillatory gamma and theta activity during repeated mental manipulations of a visual image. *Neuroscience Letters*, *422*, 141–145.
- Klimesch, W. (1996). Memory processes, brain oscillations and EEG synchronization. *International Journal of Psychophysiology*, *24*, 61–100.
- Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, *26*, 319–340.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29*, 169–195.
- Klimesch, W., Doppelmayr, M., Pachinger, T., & Ripper, B. (1997). Brain oscillations and human memory: EEG correlates in the upper alpha and theta band. *Neuroscience Letters*, *238*, 9–12.
- Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. (1999). ‘Paradoxical’ alpha synchronization in a memory task. *Cognitive Brain Research*, *7*, 493–501.
- Klimesch, W., Doppelmayr, M., Stadler, W., Pollhuber, D., Sauseng, P., & Rohm, D. (2001). Episodic retrieval is reflected by a process specific increase in human electroencephalographic theta activity. *Neuroscience Letters*, *302*, 49–52.
- Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N. E. A., Lazzara, M., Rohm, D., et al. (2001). Theta synchronization during episodic retrieval: Neural correlates of conscious awareness. *Cognitive Brain Research*, *111*, 781–793.
- Klimesch, W., Freunberger, R., & Sauseng, P. (2010). Oscillatory mechanisms of process binding in memory. *Neuroscience and Biobehavioral Reviews*, *34*, 1002–1014.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillation: The inhibition-timing hypothesis. *Brain Research Reviews*, *53*, 63–88.
- Klimesch, W., Schack, B., & Sauseng, P. (2005). The functional significance of theta and upper alpha oscillations. *Experimental Psychology*, *52*, 99–108.
- Klimesch, W., Schimke, H., Ladurner, G., & Pfurtscheller, G. (1990). Alpha frequency and memory performance. *Psychophysiology*, *4*, 381–390.
- Klimesch, W., Schimke, H., & Pfurtscheller, G. (1993). Alpha frequency, cognitive load and memory performance. *Brain Topography*, *5*, 1–11.
- Klimesch, W., Schimke, H., & Schwaiger, J. (1994). Episodic and semantic memory: An analysis in the EEG theta and alpha band. *Electroencephalography and Clinical Neurophysiology*, *91*, 428–441.
- Klimesch, W., Vogt, F., & Doppelmayr, M. (2000). Interindividual differences in alpha and theta power reflect memory performance. *Intelligence*, *27*, 347–362.
- Lega, B. C., Jacobs, J., & Kahana, J. (2012). Human hippocampal theta oscillations and the formation of episodic memories. *Hippocampus*, *22*, 748–761.
- Li, Y., Umeno, K., Hori, E., Takakura, H., Urakawa, S., Ono, T., et al. (2009). Global synchronization in the theta band during mental imagery of navigation in human. *Neuroscience Research*, *65*, 44–52.
- Lisman, J. E., & Jensen, O. (2013). The theta-gamma neural code. *Neuron*, *77*, 1002–1016.
- Mathewson, K. E., Basak, C., Maclin, E. L., Low, K. A., Boot, W. R., Kramer, A. F., et al. (2012). Different slopes for different folks: Alpha and beta EEG power predict subsequent video game learning rate and secondary task improvement. *Psychophysiology*, *49*, 1558–1570.
- Mormann, F., Fell, J., Axmacher, N., Weber, B., Lehnertz, K., Elger, C. E., et al. (2005). Phase/amplitude reset and theta-gamma interaction in the human medial temporal lobe

- during a continuous word recognition memory task. *Hippocampus*, *15*, 890–900.
- Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and Biobehavioral Reviews*, *34*, 1023–1035.
- Osipova, D., Takashima, A., Oostenveld, R., Fernández, G., Maris, E., & Jensen, O. (2006). Theta and gamma oscillations predict encoding and retrieval of declarative memory. *Journal of Neuroscience*, *26*, 7523–7531.
- Paivio, A. (1969). Mental imagery in associative learning and memory. *Psychological Review*, *76*, 241–263.
- Roediger, H. L. (1980). The effectiveness of four mnemonics in ordering recall. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 558–567.
- Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Neuroscience*, *11*, 251–257.
- Rugg, M. D., & Dickens, A. M. J. (1982). Dissociation of alpha and theta activity as a function of verbal and visuospatial tasks. *Electroencephalography and Clinical Neurophysiology*, *53*, 201–207.
- Sauseng, P., Klimesch, W., Doppelmayr, M., Pecherstorfer, T., Freunberger, R., & Hanslmayr, S. (2005). EEG alpha synchronization and functional coupling during top-down processing in a working memory task. *Brain Mapping*, *26*, 148–155.
- Schack, B., & Klimesch, W. (2002). Frequency characteristic of evoked and oscillatory electroencephalographic activity in a human memory scanning task. *Neuroscience Letters*, *331*, 107–110.
- Schack, B., Weiss, S., & Rappelsberger, P. (2003). Cerebral information transfer during word processing: Where and when does it occur and how fast is it? *Human Brain Mapping*, *19*, 18–36.
- Sederberg, P. B., Kahana, M. J., Howard, M. W., Donner, E. J., & Madsen, J. R. (2003). Theta and gamma oscillations during encoding predict subsequent recall. *Journal of Neuroscience*, *23*, 10809–10814.
- Shiffrin, R. M., & Steyvers, M. (1997). A model for recognition memory: REM—Retrieving effectively from memory. *Psychonomic Bulletin & Review*, *4*, 145–166.
- Summerfield, C., & Mangels, J. A. (2005). Coherent theta-band EEG activity predicts item-context binding during encoding. *Neuroimage*, *24*, 692–703.
- van Vugt, M. K., Sederberg, P. B., & Kahana, M. J. (2007). Comparison of spectral analysis methods for characterizing brain oscillations. *Journal of Neuroscience Methods*, *162*, 49–63.
- Voss, J. L., & Federmeier, K. D. (2011). FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. *Psychophysiology*, *48*, 532–546.
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Neuroscience*, *9*, 445–453.
- Weiss, S., & Rappelsberger, P. (2000). Long-range EEG synchronization during word encoding correlates with successful memory performance. *Cognitive Brain Research*, *9*, 299–312.
- Whitten, T. A., Hughes, A. M., Dickson, C. T., & Caplan, J. B. (2011). A better oscillation detection method robustly extracts EEG rhythms across brain state changes: The human alpha rhythm as a test case. *Neuroimage*, *54*, 860–874.
- Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, *114*, 152–176.
- Woroch, B., & Gonsalves, B. D. (2010). Event-related potential correlates of item and source memory strength. *Brain Research*, *1317*, 180–191.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*, 441–517.