

Alpha Oscillations during Incidental Encoding Predict Subsequent Memory for New “Foil” Information

David A. Vogelsang¹, Matthias Gruber^{2,3}, Zara M. Bergström⁴,
Charan Ranganath², and Jon S. Simons¹

Abstract

■ People can employ adaptive strategies to increase the likelihood that previously encoded information will be successfully retrieved. One such strategy is to constrain retrieval toward relevant information by reimplementing the neurocognitive processes that were engaged during encoding. Using EEG, we examined the temporal dynamics with which constraining retrieval toward semantic versus nonsemantic information affects the processing of new “foil” information encountered during a memory test. Time–frequency analysis of EEG data acquired during an initial study phase revealed that semantic compared with nonsemantic processing was associated with alpha decreases in a left frontal electrode cluster from around 600 msec after stimulus onset. Successful encoding of semantic versus nonsemantic foils during a subsequent memory test was related to decreases in alpha oscillatory activity in the same left frontal

electrode cluster, which emerged relatively late in the trial at around 1000–1600 msec after stimulus onset. Across participants, left frontal alpha power elicited by semantic processing during the study phase correlated significantly with left frontal alpha power associated with semantic foil encoding during the memory test. Furthermore, larger left frontal alpha power decreases elicited by semantic foil encoding during the memory test predicted better subsequent semantic foil recognition in an additional surprise foil memory test, although this effect did not reach significance. These findings indicate that constraining retrieval toward semantic information involves reimplementing semantic encoding operations that are mediated by alpha oscillations and that such reimplementation occurs at a late stage of memory retrieval, perhaps reflecting additional monitoring processes. ■

INTRODUCTION

Memory retrieval often requires goal-directed control processes to optimize retrieval success. One possible strategy people use to facilitate memory retrieval is to reimplement the neurocognitive processes that were involved during encoding (Rugg, Johnson, Park, & Uncapher, 2008). This idea has been manifested in the Transfer Appropriate Processing Framework, which states that the likelihood of retrieval success is dependent on the overlap between encoding and retrieval operations (Roediger, Weldon, & Challis, 1989; Morris, Bransford, & Franks, 1977). Accordingly, the most effective encoding strategy depends on the specific conditions at retrieval, and conversely, what constitutes an optimal retrieval strategy depends on the conditions under which the information was encoded (Rugg et al., 2008). In line with this principle, previous behavioral studies have shown that recognition memory is enhanced when mental operations at encoding are recapitulated during a subsequent memory test (Dewhurst & Brandt, 2007; Morris et al., 1977).

Jacoby, Shimizu, Daniels, and Rhodes (2005) developed a behavioral “memory for foils” paradigm that enabled

such encoding–retrieval overlap to be investigated more directly. In an initial study phase (Phase 1 of the paradigm), participants studied nouns in two separate blocks, one of which involved a semantic task (pleasant/unpleasant judgment) and the other involved a nonsemantic task (letter judgment). In a subsequent recognition memory test (Phase 2), studied and nonstudied words were intermixed, and participants undertook blocks in which they judged whether they had previously encountered the words in the pleasantness judgment task or whether they were new (the memory test for semantically encoded words), or judged whether they had previously seen the words in the letter judgment task or whether they were new (the memory test for nonsemantically encoded words). Of special interest were the new words (so called “foils”) in the semantic and nonsemantic memory test blocks. The semantic and nonsemantic foils were subsequently mixed together with completely new words in a final foil recognition test (Phase 3) in which participants were again instructed to make an old/new judgment, this time about whether the words had been encountered at any time during the experiment or were completely novel. Jacoby et al. found that the “foil” words were differentially memorable depending on the type of test in which they had been originally encountered: Recognition memory was significantly

¹University of Cambridge, ²University of California at Davis, ³Cardiff University, ⁴University of Kent

higher for semantic compared with nonsemantic foils. Because semantic encoding typically leads to more accurate memory compared with nonsemantic encoding, this “foil effect” implies that participants strategically orient their retrieval toward a semantic processing mode when attempting to retrieve semantic encoded information and a nonsemantic processing mode when retrieving nonsemantic information, resulting in better incidental encoding of semantic compared with nonsemantic foils. Jacoby and colleagues interpreted this foil finding in light of the transfer appropriate processing principle by emphasizing the importance of the overlap in study–test operations for optimizing retrieval success (see also Zawadzka, Hanczakowski, & Wilding, 2017; Gray & Gallo, 2015; Kantner & Lindsay, 2013; Alban & Kelley, 2012; Halamish, Goldsmith, & Jacoby, 2012; Danckert, MacLeod, & Fernandes, 2011; Marsh et al., 2009).

Recently, we collected fMRI data in a “memory for foils” paradigm and applied subsequent memory analysis (also known as “difference due to memory” or “DM effect”) to study the neural mechanisms underlying the enhanced encoding of foils in a semantic compared with nonsemantic recognition test. The results revealed that the left inferior frontal gyrus (LIFG) exhibited significantly greater subsequent memory effects for semantic compared with nonsemantic foils (Vogelsang, Bonnici, Bergström, Ranganath, & Simons, 2016). A conjunction analysis revealed significant overlap in activity between semantic processing in the initial study phase and semantic foil encoding during the first memory retrieval test in the LIFG; however, this overlap in activation was not observed for the nonsemantic condition. The LIFG has previously been associated with semantic processing and semantic encoding strategies across many studies (Kim, 2011; Fletcher, Stephenson, Carpenter, Donovan, & Bullmore, 2003; Poldrack et al., 1999; Wagner et al., 1998). Together with the behavioral result that semantic foils were recognized more accurately than nonsemantic foils on the final surprise foil recognition test, these neuroimaging data support the hypothesis that directing retrieval toward new semantic versus nonsemantic information leads to the recruitment of distinct neural mechanisms that are predictive of subsequent memory (Vogelsang et al., 2016).

A key element of the foil paradigm is the proposal that retrieval is strategically oriented toward the relevant processing mode to facilitate memory search before information is retrieved. It has been hypothesized that there are two ways that control can be exerted over retrieval: “front-end” and “back-end” processes. Front-end control processes are engaged shortly after a memory cue is encountered to guide retrieval attempts (Jacoby, Shimizu, Velanova, & Rhodes, 2005). Alternatively, strategic control processes can also be recruited later on in the trial when retrieval attempts have failed or have produced ambiguous information and additional monitoring or verification is required, which has been referred to as back-end control (Halamish et al., 2012) or “late correction strategy” (Jacoby,

Kelley, & McElree, 1999). Front-end control processes are similar to the concept of retrieval orientation, which refers to the type of processing participants engage in when they are prompted with a retrieval cue to increase the likelihood of retrieval success (Rugg & Wilding, 2000). However, when such early control processes result in retrieved information that is vague or ambiguous, participants may engage back-end control processes, correcting their strategy, to increase the likelihood of recollecting accurately more contextual details about the encoded event (Jacoby et al., 1999). Previous fMRI research was unable to distinguish “front-end” and “back-end” accounts (Vogelsang et al., 2016) because the low temporal resolution of the BOLD precludes investigation of at which stage of retrieval (early vs. late) LIFG activity is reinstated for semantic compared with nonsemantic foils. Therefore, in the current study, we recorded EEG oscillations during performance of the “memory for foils” paradigm. The fine-grained temporal resolution of neural oscillations can provide more information with regard to the question of “when” the neural activity associated with initial encoding operations during a study phase reoccur during the incidental encoding of foils in a subsequent recognition test.

Neural oscillations and their relationship with memory functions have gained considerable interest in recent years (Fell & Axmacher, 2011). In the memory encoding literature, there is evidence that a decrease in alpha power might be related to semantic processing (Hanslmayr & Staudigl, 2014; Zion-Golombic, Kutas, & Bentin, 2010; Hanslmayr, Spitzer, & Bäuml, 2009; Bastiaansen, van der Linden, ter Keurs, Dijkstra, & Hagoort, 2005; for a review, see Klimesch, 1999). For example, Hanslmayr and colleagues (2009) contrasted deep semantic encoding with shallow nonsemantic encoding and found power decreases in alpha (and beta) frequency bands that were related to successful semantic encoding. Fellner, Bäuml, and Hanslmayr (2013) showed that alpha and beta decreases predicted subsequent memory in a semantic condition, but not in a nonsemantic but still highly efficient encoding condition (in this case, a survival processing task), thereby suggesting that alpha decreases are likely a reflection of semantic processing in particular, rather than of efficient encoding strategies in general. Furthermore, alpha decreases have been observed over left frontal electrodes in tasks requiring high semantic processing demands (Hanslmayr & Staudigl, 2014; Klimesch, 1999) but have also been associated with subsequent memory effects (Klimesch, Doppelmayr, Schimke, & Ripper, 1997), consistent with the idea that the left prefrontal cortex is important for successful encoding (Vogelsang et al., 2016; Wagner et al., 1998).

The main aim of the present experiment was to investigate the temporal dynamics of EEG oscillations associated with encoding of new “foil” words during a memory retrieval test. We focused our analysis on alpha EEG frequencies (8–10 Hz) because previous research has shown that alpha plays a role in both semantic processing (Bakker,

Takashima, van Hell, Janzen, & McQueen, 2015) and subsequent memory effects (Hanslmayr et al., 2009). We first examined alpha power associated with semantic versus nonsemantic processing during the initial study phase. We then investigated whether alpha power differences were again observed during successful encoding of semantic versus nonsemantic foils in the first memory test, which would support the hypothesis that the incidental encoding of foils in a memory test involves the reimplementation of the neurocognitive processes that were involved during initial encoding (Vogelsang et al., 2016; Bergström, Vogelsang, Benoit, & Simons, 2015; Jacoby, Shimizu, Daniels, et al., 2005; Jacoby, Shimizu, Velanova, et al., 2005). Most importantly, the high temporal resolution of EEG oscillations allowed us to examine whether alpha reinstatement during foil encoding occurred early or late in the trial, which we hypothesized would indicate that participants used “front-end” or “back-end” control strategies, respectively. We also tested whether those individuals who showed the largest alpha power differences during semantic versus nonsemantic processing in the study phase also showed the largest alpha power differences during semantic encoding of foils in the retrieval test, which would support the hypothesis that the alpha effects during study and test were functionally related. Finally, we tested the hypothesis that if alpha frequencies mediate semantic foil encoding during the first recognition test, then individuals who showed larger alpha differences for successfully encoded foils during the first test should also exhibit better foil recognition performance in the final foil recognition test.

METHODS

Participants

Fifty-three right-handed healthy English native speakers with normal or corrected-to-normal vision participated in this experiment. Written informed consent was obtained before commencement of the experiment, and all participants received £15 for their participation. Data from 17 participants were excluded because they did not produce enough trials of each type for the subsequent memory analysis (see “Time–Frequency Analysis” section for details). In addition, data from two participants were excluded because of excessively noisy EEG data. The final data set thus consisted of 34 participants (21 women, mean age = 21.9 years, range 18–33 years). The study was approved by the University of Cambridge psychology research ethics committee.

Materials

The stimuli consisted of 552 nouns (e.g., “book”) derived from the MRC psycholinguistic database (Wilson, 1988; also used in Vogelsang et al., 2016). The 552 words were split into six lists that were matched for concreteness,

familiarity, Kucera–Francis frequency, word length, and number of syllables, and we counterbalanced the assignment of lists to the experimental conditions across participants.

Procedure

Participants were fitted with an EEG cap and were seated in a sound- and light-attenuated room. Participants completed three phases: (1) a study phase (henceforth referred to as “Phase 1”), (2) an initial memory test (henceforth referred to as “Phase 2”), and (3) a final surprise memory test that assessed foil recognition (henceforth referred to as “Phase 3”). Throughout all phases, participants provided their responses on a button box with either their left or right hand (counterbalanced across participants).

Phase 1 consisted of two separate incidental encoding blocks during which participants were instructed to make a simple judgment. In a semantic judgment study block, participants made a pleasantness judgment (“Is this word pleasant?”). In a nonsemantic study block, participants made a letter judgment (“Is there a letter O or U in the word?”). Each trial in the study phase started with a 500-msec fixation cross followed by the stimulus that was presented in the center of the screen for 2000 msec. Both the semantic and nonsemantic judgment blocks consisted of 92 trials each. The order of semantic and nonsemantic judgment blocks was counterbalanced across participants. Participants were instructed to respond while the words were on the screen.

In Phase 2, participants’ memory for the stimuli encountered during Phase 1 was assessed in an old/new recognition test, which aimed to manipulate whether participants oriented retrieval toward semantic or nonsemantic information. In the semantic test phase, 92 old words from the semantic study phase were intermixed with 92 new words (semantic foils). In the nonsemantic test phase, 92 old words from the nonsemantic study phase were intermixed with 92 new words (nonsemantic foils). For both blocks, participants were told in which specific Phase 1 task any old words had been shown to encourage them to engage different retrieval orientations for the two blocks. The order of test block (semantic and nonsemantic) was counterbalanced across participants. Each test trial began with a 500-msec fixation cross, followed by the presentation of the stimulus centrally on the screen for 2000 msec. Participants were instructed to provide their response as to whether each word was old or new while the stimulus was still on the screen.

In the final phase, a surprise old/new foil recognition test (Phase 3) was administered in which participants were asked to distinguish between the semantic and nonsemantic foils and completely new words. Participants were instructed that they were “going to be presented with a word that is either old or new. ‘Old’ in this case means that you saw the word at some point earlier in

the experiment in any study or test phase. ‘New’ words are words you have not seen at all in today’s experiment.” This foil recognition test consisted of 368 words (92 semantic foils, 92 nonsemantic foils, and 184 completely new words, which were randomly intermixed). Each trial in the final foil recognition test began with a 500-msec fixation cross followed by the stimulus presented centrally for 2000 msec.

EEG Recording and Preprocessing

EEG data were acquired during all phases of the experiment and were recorded with an Electrical Geodesic (Eugene, OR) Netamps 200 system with a 128-channel HydroCel Geodesic Sensor Net (GSN 200; Tucker, 1993). The recorded EEG data were referenced to Cz and were filtered with a bandwidth of 0.01–70 Hz (250 Hz sampling rate). The EEG data were analyzed in EEGLab 13 (Delorme & Makeig, 2004). The continuous EEG data from the study phase and first retrieval test were rereferenced to an average mastoid reference and high-pass filtered with a cutoff of 0.5 Hz (two-way least-squares finite impulse response filter), and the continuous data were divided into epochs ranging from –500 msec before cue onset until 2000 msec thereafter. Artifact correction was applied using extended info-max independent component analysis (Bell & Sejnowski, 1995, in Delorme & Makeig, 2004) using Runica from the EEGLab toolbox, with default mode training parameters (Delorme & Makeig, 2004). Independent components reflecting eye movements and other sources of noise were identified by visual inspection of component scalp topographies, time courses, and activation spectra and were discarded from the data by back-projecting all but these components to the data space. Trials that still contained artifacts after running independent component analysis correction were removed after visual inspection, resulting in only 5–10% of the trials being excluded.

Time–Frequency Analysis

Time–frequency analysis in EEGLab was applied using Morlet wavelets (Percival & Walden, 1993) with six cycles in a frequency range of 4–30 Hz, with steps of 1 Hz between each wavelet center frequency. These wavelets were applied in a sliding window with 20-msec increments in the 0–2000 msec interval. To minimize edge effects (distortions that occur at the edge of the time window of analysis), we concatenated mirrored (i.e., time inverted) segments at the left and right edge of the original epochs. We then performed the wavelet transform on these extended epochs and discarded the concatenated segments from the final analysis (for detailed explanation of this “reflection approach,” see Cohen, 2014; see Fell et al., 2011, for example of a paper using this approach). The results reported here were not corrected for baseline in the frequency domain because we were interested in oscillatory differences between the semantic and nonsemantic

conditions, and therefore, baseline correction is not necessary (see, for similar approaches, Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013).

To identify the neural oscillations associated with semantic and nonsemantic processing, we first examined the power spectra of epoched data from Phase 1. For each of the 34 participants, EEG data during the study phase were binned according to the type of processing (semantic vs. nonsemantic). In this way, we could isolate the EEG frequencies that were elicited by semantic and nonsemantic processing to later examine whether these frequencies were reinstated during the encoding of foils in the first test phase (Phase 2). Mean trial numbers were the following: semantic study mean = 90, range 46–92; nonsemantic study mean = 92, range 88–92.

To analyze the neural oscillations during Phase 2, we binned the EEG data for each participant according to condition (semantic vs. nonsemantic) and subsequent memory (remembered vs. forgotten). Mean trial numbers for each condition were as follows: semantic foils remembered mean = 65, range 25–81; semantic foils forgotten mean = 25, range 12–67; nonsemantic foils remembered mean = 55, range 15–79; and nonsemantic foils forgotten mean = 35, range 13–77.

Time–frequency analysis was conducted on EEG that was averaged within nine electrode clusters (frontal vs. central vs. posterior; left vs. middle vs. right; see Figure 1) based on a previous study by Hsieh, Ekstrom, and Ranganath (2011). These clusters included the following: left frontal cluster (Channels 33, 24, 26; equivalent to F3, F7, AF7), mid frontal cluster (Channels 19, 11, 4; equivalent to Fz, F1, F2), right frontal cluster (Channels 124, 2, 122; equivalent

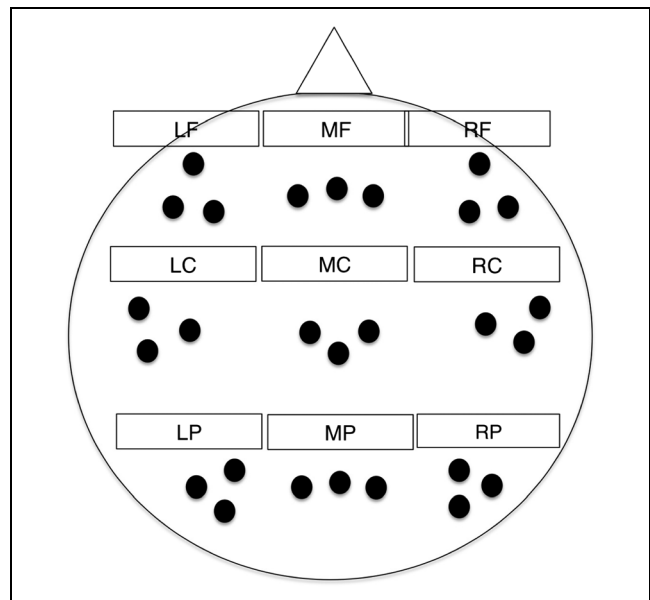


Figure 1. Locations of the electrode clusters, which included left frontal (LF), mid frontal (MF), right frontal (RF), left central (LC), mid central (MC), right central (RC), left posterior (LP), mid posterior (MP), and right posterior (RP).

Table 1. Accuracy (Hits and FAs) and RT (for Hits and Correct Rejections) for Phase 2

| | <i>Hits</i> | | <i>FA</i> | | <i>RT (msec)</i> | | | |
|-------------|-------------|-----------|-------------|-----------|--------------------|------------------|----------------------------------|--------------------------------|
| | <i>Mean</i> | <i>SD</i> | <i>Mean</i> | <i>SD</i> | <i>Hits (Mean)</i> | <i>Hits (SD)</i> | <i>Correct Rejections (Mean)</i> | <i>Correct Rejections (SD)</i> |
| Semantic | 0.88 | 0.07 | 0.13 | 0.11 | 890 | 113 | 938 | 117 |
| Nonsemantic | 0.50 | 0.15 | 0.26 | 0.13 | 981 | 138 | 982 | 161 |

to F4, F8, AF8), left central cluster (Channels 35, 36, 41; equivalent to C5, C3, T7), mid central cluster (Channels 31, 55, 80; equivalent to Cz, C1, C2), right central cluster (Channels 109, 104, 110; equivalent to C4, C6, T8), left posterior cluster (Channels 52, 53, 60; equivalent to P3, P1, PO3), mid posterior cluster (Channels 61, 62, 78; equivalent to CP1, Pz, CP2), and right posterior cluster (Channels 85, 86, 92; equivalent to P2, P4, PO4).

Statistical Analysis

Across-trial permutation tests were conducted to test for significant effects in alpha power related to the semantic versus nonsemantic processing in Phase 1 and successful encoding of semantic versus nonsemantic foils in Phase 2. For both phases, the 2000-msec epoch was split into time windows of 200 msec each.

The permutation testing procedure consisted of three steps. First, for Phase 1, permutation testing was conducted on the mean power alpha (8–10 Hz) frequencies per condition for each time window and electrode cluster (see Gruber et al., 2013, for similar procedure). We first conducted two-tailed paired *t* tests on the relevant electrode clusters comparing the two conditions. Second, the two conditions were then interchanged randomly for each participant and each randomization run, so that pseudoconditions were created in which systematic differences between the conditions were eliminated. For each permutation, we selected the largest negative and positive *t* value across all nine electrode clusters. This step was repeated 1000 times so that a null distribution of largest negative and positive *t* values across all clusters was created and the two tails of the null *t* distribution were used as critical *t* values. Using an alpha level of .05 with 1000 permutations, we used the 25th and 975th values to represent the critical *t* values, and values below or higher than these values were considered to be significant effects. This stringent permutation method corrects for multiple comparisons and was based on Blair and Karniski (1993; for similar approaches, see Gruber et al., 2013; Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Staudigl, Hanslmayr, & Bäuml, 2010; Hanslmayr et al., 2009).

For Phase 2, we conducted the permutation testing only in those electrode clusters that showed a significant alpha effect in Phase 1. Thus, the electrode clusters that showed a significant effect in Phase 1 were taken as “elec-

trode clusters of interest” for the analysis for Phase 2 data, to examine alpha activity reimplementation during encoding of foils in the same electrode clusters that showed significant alpha effects in Phase 1. To test our hypothesis that reimplementation of semantic processes facilitate successful encoding of foils, we focused the Phase 2 analysis on the interaction between condition (semantic vs. nonsemantic) and subsequent memory in Phase 2 (remembered vs. forgotten) by comparing the difference between remembered and forgotten semantic foils versus the difference between remembered and forgotten nonsemantic foils. We also tested the simple effects of subsequent memory for semantic versus nonsemantic conditions separately. The rest of the permutation procedure was the same as for the Phase 1 data.

RESULTS

Behavioral Results

Recognition accuracy for Phase 2 was calculated using the discrimination measure $p(\text{Hits}) - p(\text{False alarms [FA]})$ (Snodgrass & Corwin, 1988) and the results are presented in Table 1. Recognition memory for semantic trials was significantly more accurate compared with nonsemantic trials ($t(33) = 25.4, p < .001, 95\% \text{ CI } [0.47, 0.56]$, Cohen’s $D_z = 4.4$). Furthermore, RTs were faster for old semantic items compared with old nonsemantic items ($t(33) = 4.39, p < .001, 95\% \text{ CI } [49, 134]$, Cohen’s $D_z = 0.75$). Foils presented in the semantic condition were also endorsed as new significantly more quickly than foils presented in the nonsemantic condition ($t(33) = 2.23, p = .033, 95\% \text{ CI } [4, 84]$, Cohen’s $D_z = 0.38$).

The behavioral results of Phase 3 are presented in Table 2. Note that we conducted the Phase 3 analysis on accuracy scores (proportion correct) rather than Hits–FAs because in the final foil recognition test completely new

Table 2. Accuracy (Proportion Correct) and RT for Phase 3

| | <i>Accuracy</i> | | <i>RT (msec)</i> | |
|-------------------|-----------------|-----------|------------------|-----------|
| | <i>Mean</i> | <i>SD</i> | <i>Mean</i> | <i>SD</i> |
| Semantic foils | 0.72 | 0.16 | 887 | 122 |
| Nonsemantic foils | 0.61 | 0.16 | 910 | 118 |
| New items | 0.77 | 0.12 | 921 | 127 |

Semantic vs. Nonsemantic Processing

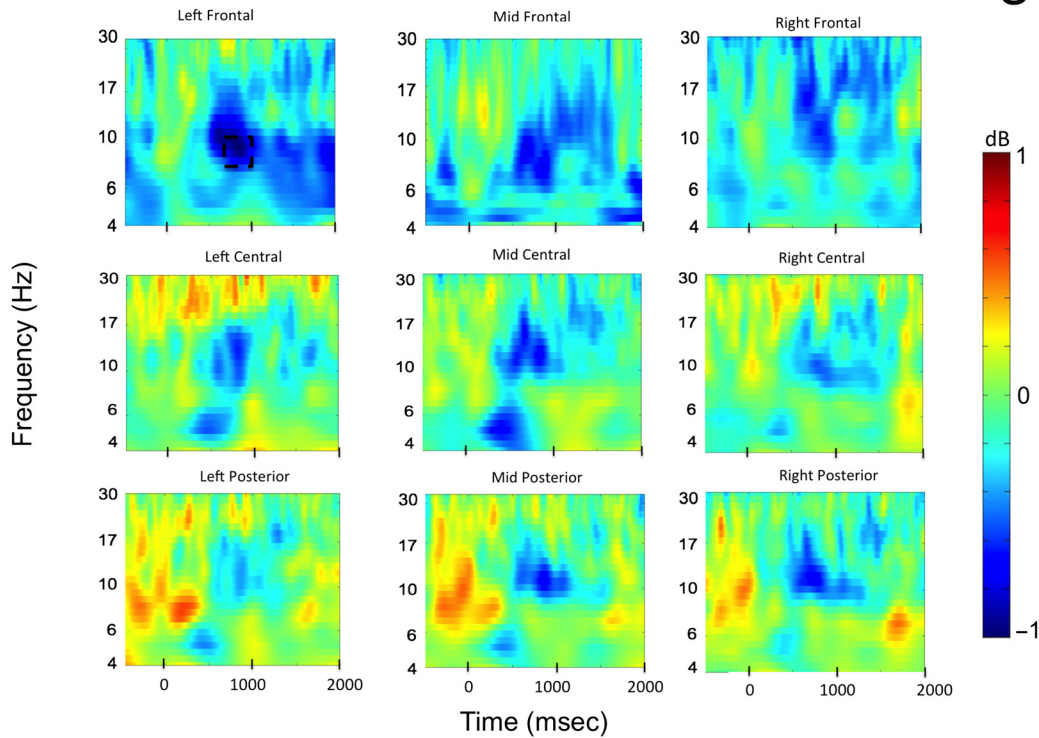


Figure 2. Time–frequency plots for semantic versus nonsemantic processing in the study phase. Significant decreases in alpha frequencies were observed in left frontal and mid and right posterior electrode sites. The dotted boxes represent the significant alpha time window.

items were intermixed with semantic and nonsemantic foils, so a proper Hits–FAs analysis cannot be conducted here. In line with our main prediction, semantic foils were recognized significantly more accurately than nonsemantic foils ($t(35) = 5.18, p < .001, 95\% \text{ CI } [0.066, 0.15]$, Cohen’s $D_z = 0.89$) and significantly faster ($t(33) = 3.42, p = .002, 95\% \text{ CI } [9, 37]$, Cohen’s $D_z = 0.59$). There was no significant difference in RT between nonsemantic foils and new items ($t(33) = 1.5, p = .15$); however, RT was faster for recognizing semantic foils compared with new items ($t(33) = 4.03, p < .001, 95\% \text{ CI } [17, 52]$, Cohen’s $D_z = 0.69$). These results replicate earlier findings of the “foil effect” obtained in previous studies (Vogelsang et al., 2016; Bergström et al., 2015; Jacoby, Shimizu, Daniels, et al., 2005; Jacoby, Shimizu, Velanova, et al., 2005).

Time–Frequency Results

Phase 1: Semantic versus Nonsemantic Processing

The time–frequency analysis of Phase 1 focused on a direct comparison between all semantic and all nonsemantic trials. The results are presented in Figure 2. Significant decreases in alpha power were observed over the left frontal electrode cluster between 800 and 1000 msec after word onset ($t(33) = -3.13, p = .004, 95\% \text{ CI } [-1.4, -0.3]$, Cohen’s $D_z = 0.54$). No other significant effects were observed in any of the other electrode clusters. The time

course of the alpha power changes in the left frontal electrode cluster is presented in Figure 3, and the t values in the alpha band across all electrode clusters is presented in Figure 4.

Subsequent Memory Effect for Foils in Phase 2

The second part of the time–frequency analysis focused on the temporal dynamics of subsequent memory effects (DM effect) for foils during Phase 2 to investigate when alpha activity was reinstated in a way that facilitated

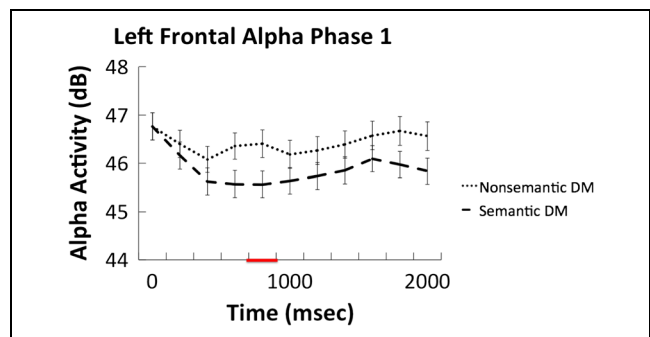


Figure 3. Average alpha (8–10 Hz) frequency–time courses (in decibel) for semantic and nonsemantic processing in the left frontal cluster. Red line on x axis represents significant time window.

Semantic vs. Nonsemantic Processing

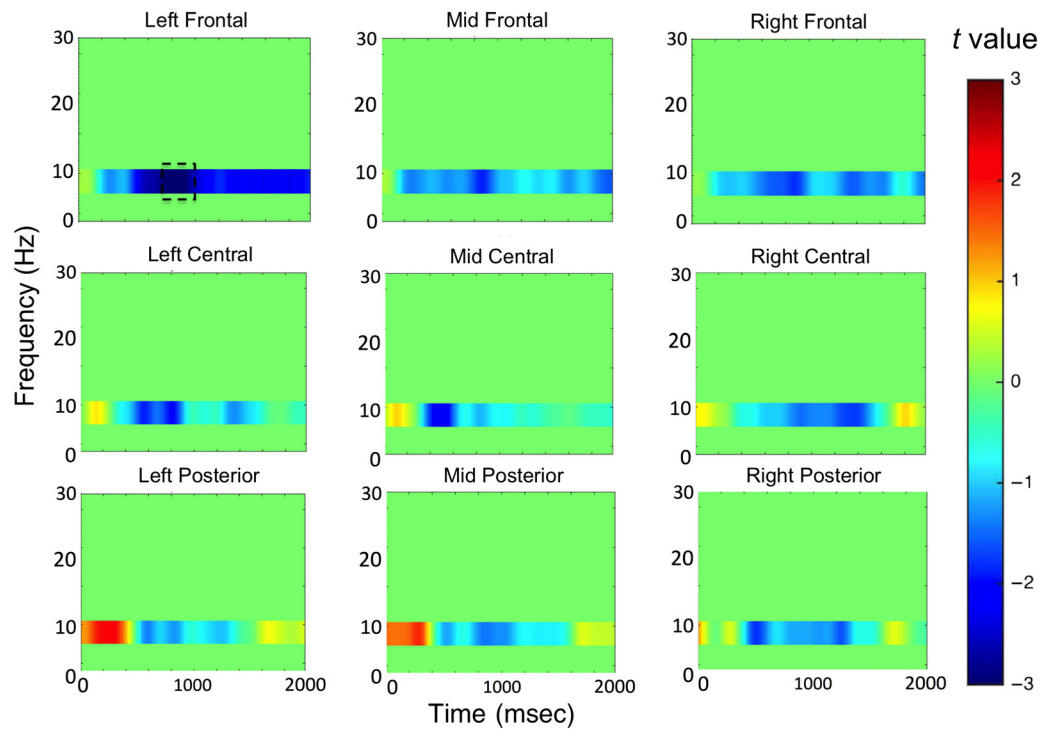


Figure 4. t values for semantic versus nonsemantic processing in all electrode clusters.

encoding of semantic foils. The time–frequency plot of the interaction term (DM effect for semantic foils – DM effect for nonsemantic foils) for all electrode clusters is presented in Figure 5. Because significant alpha effects in Phase 1 were only observed in the left frontal electrode cluster, only this cluster was used to conduct the permutation analysis in Phase 2, which allowed us to directly test the reimplementation hypothesis.

The left frontal electrode cluster showed a significant interaction in the alpha band between 1000 and 1200 msec after word onset ($t(33) = -3.57, p = .001, 95\% \text{ CI} [-1.54, -0.42]$, Cohen’s $D_z = 0.61$; see dashed box in Figure 5). Time–frequency plots comparing EEG oscillations associated with successful encoding of each type of foils separately are presented in Figure 6, and the time courses for alpha frequencies in the left frontal cluster for the semantic and nonsemantic subsequent memory effect as well as the t values for the left frontal electrode cluster are presented in Figure 7. These comparisons indicated that the significant interaction arose because power differences between remembered and forgotten items were observed in the semantic but not in the nonsemantic condition. For successful encoding of semantic foils, alpha in the 1000–1200 msec time window ($t(33) = -4.19, p = .0001, 95\% \text{ CI} [-1.30, -0.45]$, Cohen’s $D_z = 0.72$) power was significant depending on whether a word was later remembered or forgotten. However, no significant differences between remembered and forgotten words were observed

for nonsemantic foils (1000–1200 msec alpha: $t(33) = 0.72, p = .47, 95\% \text{ CI} [-0.19, 0.40]$, Cohen’s $D_z = 0.12$). Thus, the subsequent memory effects observed here became apparent over left frontal electrodes around 1000 msec after stimulus presentation, which is at a relatively late stage in the trial.

Relationship between Phase 1 and Phase 2 Alpha Frequencies

The third part of the analysis assessed the relationship between alpha decreases in Phase 1 during semantic versus nonsemantic processing and alpha decreases in Phase 2 during semantic (subsequently remembered vs. forgotten) foil encoding to test whether these effects were functionally related, which would support the hypothesis that the neurocognitive processes engaged during initial encoding are reimplemented when attempting to retrieve information. To examine the relationship between Phase 1 and Phase 2 alpha activity, we extracted the mean alpha signal that showed a significant effect in the Phase 1 (800–1000 msec) and Phase 2 (1000–1200 msec) time windows for each participant and conducted an across-participant Pearson correlation. A Pearson correlation is appropriate here because the time–frequency data were normally distributed.

There was a significant correlation ($r = 0.37, p = .03$; two-tailed) between Phase 1 alpha activity associated

DM effect: Semantic vs. Nonsemantic Foils

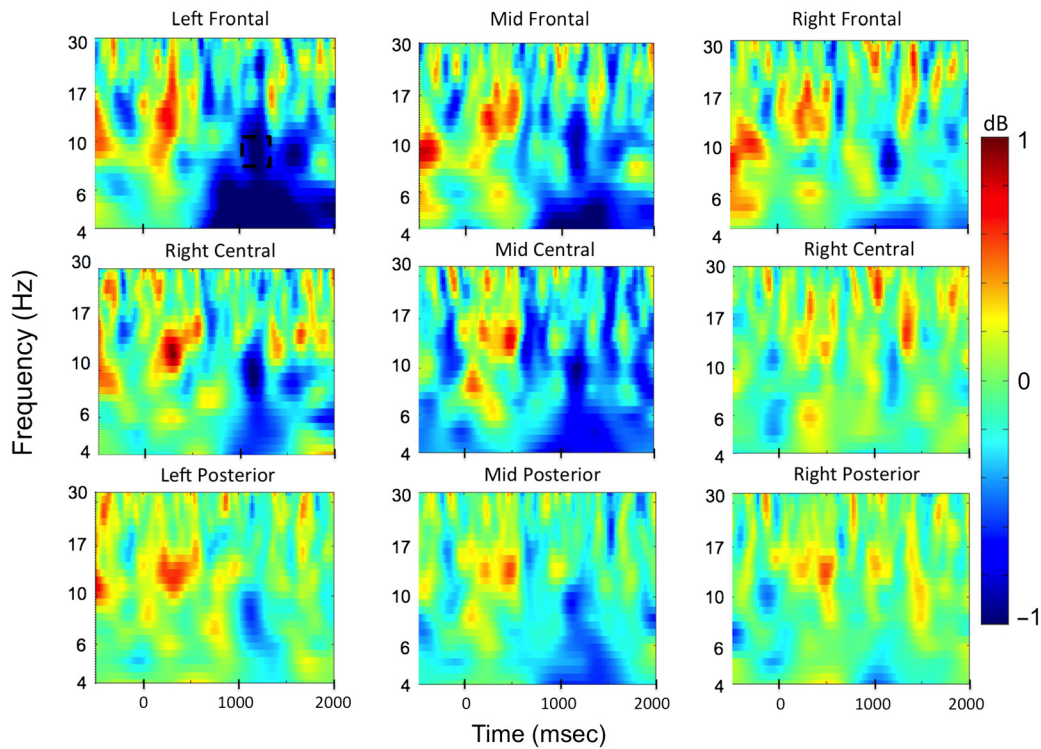


Figure 5. Time–frequency plots from the left frontal cluster illustrating EEG oscillation differences associated with successful encoding (DM effect) of semantic versus nonsemantic foils during the first memory test (Phase 2). The plot represents the difference of semantic foils later remembered–forgotten versus nonsemantic foils later remembered–forgotten. Permutation testing conducted on the left frontal electrode cluster (indicated by black squares) revealed a significant alpha decrease for subsequently remembered versus forgotten semantic versus nonsemantic foils in the left frontal cluster. The dotted box represents the significant alpha time window that survived correction for multiple comparisons.

with semantic versus nonsemantic processing and Phase 2 alpha activity associated with semantic subsequent memory effect, indicating that those participants who showed a large alpha effect in Phase 1 also showed an alpha effect for semantic foil encoding in Phase 2. The results of the correlation analysis are presented in Figure 8.

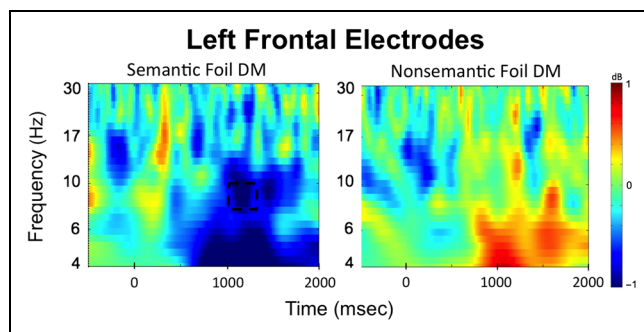


Figure 6. Time–frequency plots from the left frontal cluster illustrating semantic and nonsemantic foil subsequent memory (DM) EEG oscillation effects (remembered–forgotten). Successful encoding of semantic foils was uniquely associated with a left frontal alpha power decrease. The dotted box represents the significant alpha time window.

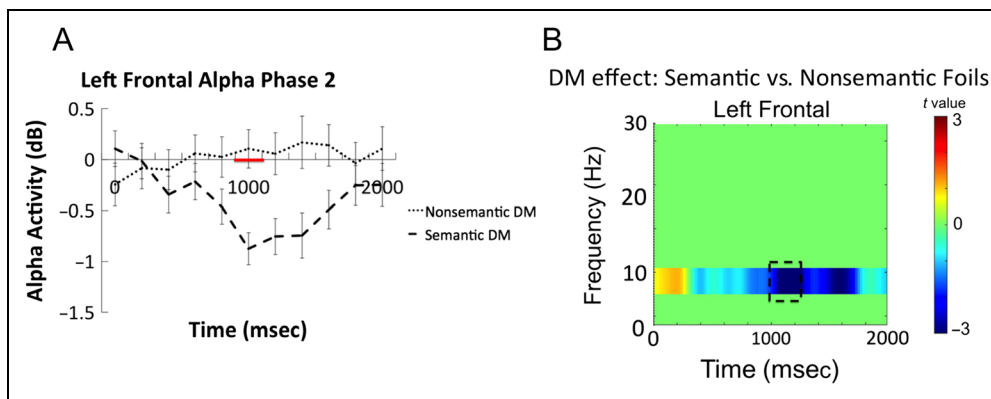
Relationship between Alpha Frequencies and Subsequent Foil Recognition

Finally, we examined whether individual differences in Phase 2 alpha activity associated with semantic foil encoding correlated with individual differences in behavioral semantic foil recognition in Phase 3, which would provide additional evidence that alpha power is functionally related to semantic encoding success. We used the Phase 2 alpha power from the 1000–1200 msec time window associated with semantic foils that were later remembered versus forgotten and correlated this with Phase 3 semantic foil recognition accuracy (proportion of correct responses). A negative correlation was observed between Phase 2 alpha power associated with later remembered semantic foils and Phase 3 semantic foil recognition accuracy; however, this correlation was not significant ($r = -0.26$, $p = .13$; two-tailed). This correlation is displayed in Figure 9.

DISCUSSION

The aim of the current experiment was to investigate the neural oscillations involved in the successful encoding of new “foil” information presented during a recognition test

Figure 7. (A) Time courses of left frontal alpha (average of 8–10 Hz) differences associated with successful encoding of semantic versus nonsemantic foils. Red line on *x* axis represents significant time window that survived correction for multiple comparisons. (B) *t* Values for semantic versus nonsemantic subsequent memory effect in the left frontal electrode cluster.



when participants engage a semantic versus nonsemantic processing mode. We tested the hypothesis that attempting to retrieve information from memory involves the reimplementation of the neurocognitive processes that were engaged during initial encoding (Vogelsang et al., 2016; Bergström et al., 2015; Jacoby, Shimizu, Daniels, et al., 2005; Jacoby, Shimizu, Velanova, et al., 2005). More specifically, we used the excellent temporal resolution of EEG to examine the temporal dynamics of the encoding of foils to obtain a better understanding of when reimplementation processes occur. It has previously been suggested that the foil effect can be explained by source constrained retrieval processes that reimplement encoding processes in the early stage of a memory test trial to guide memory search as a form of “front-end control” (Kantner & Lindsay, 2013; Jacoby, Shimizu, Daniels, et al., 2005), predicting that the neural activity associated with such reimplementation should be apparent shortly after a recognition cue is presented. An alternative, though not mutually exclusive, proposal is that control processes may be engaged at a later stage of processing, for example, to monitor whether retrieved information is correct (Halamish et al., 2012; Jacoby et al., 1999) or to elicit recollection if initial unconstrained retrieval attempts are

unsuccessful as a “late correction” or “back-end control” strategy (Jacoby et al., 1999).

Our behavioral findings replicated earlier studies in demonstrating the typical foil effect: Semantic foils were remembered significantly more accurately than nonsemantic foils, supporting the idea that participants implemented a semantic processing mode during the semantic memory test (Vogelsang et al., 2016; Kantner & Lindsay, 2013; Alban & Kelley, 2012; Halamish et al., 2012; Danckert et al., 2011; Marsh et al., 2009; Jacoby, Shimizu, Daniels, et al., 2005; Jacoby, Shimizu, Velanova, et al., 2005). Time–frequency analysis of EEG data collected during the initial study phase revealed a power decrease in alpha frequencies over left frontal electrodes between 800 and 1000 msec during the semantic as opposed to nonsemantic task, consistent with prior literature highlighting a role for alpha oscillations in semantic processing (e.g., Bastiaansen et al., 2005; for a review, see Klimesch, 1999). Importantly, the EEG data from the first recognition test revealed decreases in alpha oscillatory activity in the left frontal electrode cluster between 1000 and 1200 msec that predicted subsequent recognition of semantic, but not nonsemantic,

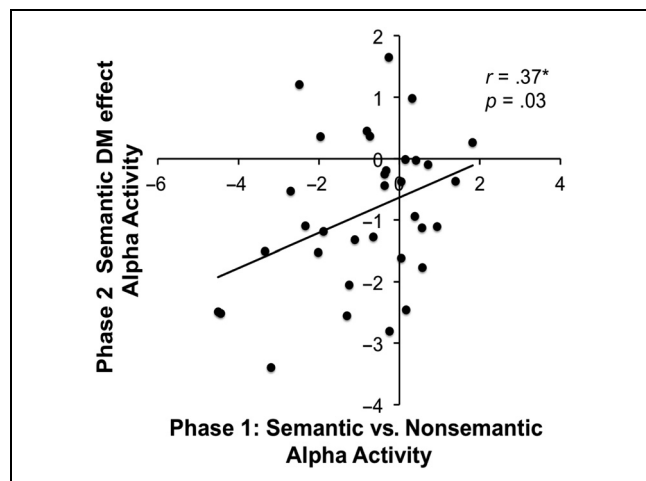


Figure 8. Correlations between Phase 1 (800–1000 msec) and Phase 2 (1000–1200 msec) alpha activity.

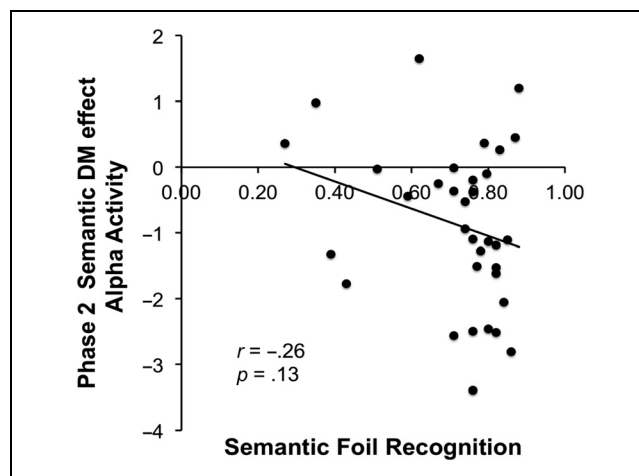


Figure 9. Correlations between Phase 2 alpha related activity for remembered versus forgotten semantic foils (1000–1200 msec) and subsequent semantic foil recognition accuracy (proportion correct responses).

foils during the final surprise recognition test. Thus, similar oscillatory activity was associated with semantic processing during initial study and during foil encoding while participants were trying to retrieve semantic information. Furthermore, individual differences in alpha activity during the semantic study phase (Phase 1) were significantly correlated with individual differences in alpha activity for successfully encoded foils during the semantic recognition test (Phase 2), suggesting that the semantic neurocognitive processes that were engaged during initial study were reimplemented during the encoding of foils during the Phase 2 recognition test. Finally, we tested whether alpha decreases in phase semantic foil encoding during Phase 2 were negatively correlated with behavioral semantic foil recognition during Phase 3; however, this analysis did not reach significance, leaving the question open as to whether alpha power is functionally related to semantic foil encoding success.

Interestingly, alpha power decreases associated with semantic foil encoding became apparent after the average time when participants provided their response, at about 900 msec after stimulus presentation, suggesting that alpha oscillations may reflect an implementation of encoding operations at a relatively late processing stage, contrary to what would be predicted if such reinstatement was conducted as part of a front-end control strategy (Gray & Gallo, 2015; Jacoby, Shimizu, Daniels, et al., 2005; Jacoby, Shimizu, Velanova, et al., 2005). In a recent fMRI study, we found that the LIFG was significantly more active during successful encoding of semantic as opposed to nonsemantic foils (Vogelsang et al., 2016). The LIFG has been widely associated with semantic processing (Poldrack et al., 1999; Wagner et al., 1998), but the low temporal resolution of fMRI precluded us from determining whether LIFG activation reflected mentally reenacting a semantic processing mode early or later in the trial. The timing of the current EEG results suggest that the left frontal alpha decreases, which we tentatively interpret as possibly generated by the LIFG (Vogelsang et al., 2016), may reflect strategic processes that are engaged during a later decision stage of retrieval, which facilitates the incidental semantic encoding of foils.

The main underlying finding of the “foil effect” is that “deep” semantic foils are recognized significantly better than “shallow” nonsemantic foils despite the only difference between the foils being the type of information that was oriented toward when they were first encountered. There is nothing intrinsically “semantic” or “nonsemantic” about the foils themselves. Instead, the instructions at the start of the memory test determines which type of encoding context (semantic vs. nonsemantic) participants need to retrieve, appears in some manner to initiate “deeper” retrieval for the semantic test and “shallower” retrieval for the nonsemantic test (Jacoby, Shimizu, Velanova, et al., 2005), resulting in better incidental encoding of semantic compared with nonsemantic foils. Furthermore, this encoding difference occurs spontaneously,

because participants are not explicitly asked to use different retrieval strategies. The “foil effect” can be interpreted as evidence for the source constrained retrieval hypothesis as put forth by Jacoby, Shimizu, Daniels, et al. (2005) and indicates that sought after information can be used to guide information processing during recognition memory. In this way, memory retrieval can be considered an encoding event, determining whether information will be remembered in the future (Dudukovic, Dubrow, & Wagner, 2009).

Why did the neural markers of semantic encoding of foils occur so late? Because reinstating encoding operations is an effortful, self-initiated process (Alban & Kelley, 2012), it is possible that participants chose to engage such a strategy to elicit recollection only if an initial unconstrained retrieval attempt was unsuccessful. A related account suggests that participants may reinstate encoding operations to verify and possibly correct their initial more automatic retrieval assessments, and such a monitoring strategy may contribute to enhanced encoding of semantic foils together with earlier “front-end” control processes (Halamish et al., 2012). According to Jacoby et al. (1999), participants engage in such late correction strategies primarily when the retrieved information is vague or ambiguous (perhaps eliciting a sense of familiarity without recollection of decisive contextual information). The current oscillatory findings are consistent with reinstatement of encoding operations occurring at a late retrieval stage but do not rule out the possibility that encoding operations were also reinstated to constrain retrieval at the front-end without being reflected in our EEG results (EEG oscillations of course only capture certain aspects of neural activity).

Our oscillatory findings are consistent with prior literature highlighting a role for alpha frequencies in successful semantic encoding (Hanslmayr & Staudigl, 2014; Zion-Golumbic et al., 2010; Hanslmayr et al., 2009) and semantic processing (Long, Burke, & Kahana, 2014; Klimesch, Doppelmayr, & Hanslmayr, 2006). In the oscillations literature, alpha frequencies have been linked with a wide variety of cognitive functions ranging from inhibitory processes during memory suppression (Park et al., 2014), to fine-grained resolution of visual processing (Samaha & Postle, 2015), working memory (Myers, Stokes, Walther, & Nobre, 2014; Sauseng et al., 2009), and active inhibition of a not-to-be applied rule (Buschman, Denovellis, Diogo, Bullock, & Miller, 2012). One of the first studies that found a relationship between decreases in alpha and later memory performance was conducted by Klimesch (1997), who observed that decreases in alpha frequencies over parietal electrodes during semantic encoding were positively correlated with later memory retrieval. Hanslmayr et al. (2009) contrasted deep semantic encoding with shallow nonsemantic encoding and found power decreases in alpha (and beta) frequency bands that were related to successful semantic encoding only, and Fellner et al. (2013) showed that alpha likely reflects semantic processing specifically, rather than elaborative and efficient encoding

strategies in general. In our experiment, individual differences in alpha power decreases during the semantic recognition test for foils that were later remembered did not correlate significantly with individual differences in semantic foil recognition accuracy during the final surprise memory test. Therefore, we were not able to obtain additional converging evidence that alpha power decreases reflect successful semantic encoding.

Jacoby and colleagues (Jacoby, Shimizu, Daniels, et al., 2005; Jacoby, Shimizu, Velanova, et al., 2005) have hypothesized that a possible explanation for the enhanced encoding of semantic versus nonsemantic foils in the memory for foils paradigm might lie in the Transfer Appropriate Processing Framework and the related Encoding Specificity Principle, both of which predict that retrieval success depends on the amount of overlap between encoding and retrieval processes (Roediger, 1990; Morris et al., 1977; Tulving & Thomson, 1973). While attempting to retrieve words that had either been semantically or nonsemantically encoded, participants may mentally reenact the original study task, resulting in all recognition probes (both old items and foils) being processed semantically during the semantic test block and nonsemantically during the nonsemantic test block. Semantic retrieval attempts might involve thinking about the meaning of a foil word (e.g., “do I think a strawberry is pleasant?”), whereas nonsemantic retrieval attempts might involve examining the letters of the word in the hope that such a strategy will help to decide whether the word is old or new. Such reenactment may be a relatively late strategy that participants engage in after an initial heuristic familiarity assessment and may therefore be expressed in neural activity around the time or even after participants have made their memory judgment.

The current time–frequency results in combination with previous research indicate that neural oscillations are a useful tool for studying the temporal dynamics of encoding–retrieval overlap (Staresina et al., 2016; Waldhauser, Braun, & Hanslmayr, 2016; Staudigl, Vollmar, Noachtar, & Hanslmayr, 2015; Jafarpour, Fuentemilla, Horner, Penny, & Duzel, 2014; Staudigl & Hanslmayr, 2013; Waldhauser, Johansson, & Hanslmayr, 2012). Burke et al. (2013), for example, found that high gamma activity (44–100 Hz) during successful encoding of information is also observed in similar brain areas during the memory test phase in which previously studied items need to be recalled. Waldhauser and colleagues (2012) observed that decreases in alpha/beta frequencies during retrieval were associated with reactivation of encoded target information, whereas increases in alpha/beta power were associated with the inhibition of encoded distracter information. Cortical reinstatement has also been identified in an entrainment study in which participants studied words presented on flickering backgrounds of either 6 or 10 Hz (Wimber, Maaß, Staudigl, Richardson-Klavehn, & Hanslmayr, 2012). EEG measurements during successful retrieval of studied words exhibited 6- and 10-Hz frequency oscillations similar to the background flicker rates in which the words had been studied and the strength of

this reactivation was related to whether a word was remembered or forgotten (Wimber et al., 2012). More work needs to be done, however, to examine what mechanisms underlie the principle of encoding reimplementation and how that facilitates retrieval. One prominent view is that, during retrieval, a cue reactivates only a part of the encoded memory and that activity of a fraction of the original pattern triggers the reactivation of the entire trace (Rugg et al., 2008). This “pattern completion” process has been linked with the hippocampus, and a role for gamma power increases and alpha power decreases has been proposed as a neural mechanism underlying pattern completion (Staresina et al., 2016). However, there is also evidence that suggests that alpha and beta frequency bands in the cortex are important for content-specific processing (Hanslmayr, Staresina, & Bowman, 2016), which is in line with our current findings of alpha frequencies representing semantic processing.

To conclude, we investigated the neural oscillations involved in the encoding of new “foil” information presented during a retrieval test as a function of whether the test required participants to retrieve semantic versus nonsemantic information. Our findings show that semantic encoding during retrieval attempts was associated with power decreases in left frontal alpha oscillations, which may originate from the LIFG (Vogelsang et al., 2016). Consistent with previous findings, our results support the view that participants reimplement the distinct neurocognitive operations that were engaged during initial encoding, and we extend previous research by identifying that the time course of this reimplementation may be at a relatively late processing stage. Thus, retrieving memories does not only involve recollecting events from the past but may also determine what type of information will be remembered in the future.

Acknowledgments

This study was supported by a James S. McDonnell Foundation Scholar Award to J. S. S. and was carried out within the University of Cambridge Behavioural and Clinical Neuroscience Institute, funded by a joint award from the Medical Research Council and the Wellcome Trust.

Reprint requests should be sent to Jon S. Simons, Department of Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, United Kingdom, or via e-mail: jss30@cam.ac.uk.

REFERENCES

- Addante, R. J., Watrous, A. J., Yonelinas, A. P., Ekstrom, A. D., & Ranganath, C. (2011). Prestimulus theta activity predicts correct source memory retrieval. *Proceedings of the National Academy of Sciences, U.S.A.*, *108*, 10702–10707.
- Alban, M. W., & Kelley, C. M. (2012). Variations in constrained retrieval. *Memory and Cognition*, *40*, 681–692.
- Bakker, I., Takashima, A., van Hell, J. G., Janzen, G., & McQueen, J. M. (2015). Changes in theta and beta oscillations as signatures of novel word consolidation. *Journal of Cognitive Neuroscience*, *27*, 1286–1297.

- Bastiaansen, M. C. M., van der Linden, M., ter Keurs, M., Dijkstra, T., & Hagoort, P. (2005). Theta responses are involved in lexical-semantic retrieval during language processing. *Journal of Cognitive Neuroscience*, *17*, 530–541.
- Bell, A. J., & Sejnowski, T. J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural Computation*, *7*, 1129–1159.
- Bergström, Z. M., Vogelsang, D. A., Benoit, R. G., & Simons, J. S. (2015). Reflections of oneself: Neurocognitive evidence for dissociable forms of self-referential recollection. *Cerebral Cortex*, *25*, 2648–2657.
- Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology*, *30*, 518–524.
- 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*, 292–304.
- Buschman, T. J., Denovellis, E. L., Diogo, C., Bullock, D., & Miller, E. K. (2012). Synchronous oscillatory neural ensembles for rules in the prefrontal cortex. *Neuron*, *76*, 838–846.
- Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*. Cambridge, MA: MIT Press.
- Danckert, S. L., MacLeod, C. M., & Fernandes, M. A. (2011). Source-constrained retrieval influences the encoding of new information. *Memory and Cognition*, *39*, 1374–1386.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21.
- Dewhurst, S. A., & Brandt, K. R. (2007). Reinstating effortful encoding operations at test enhances episodic remembering. *Quarterly Journal of Experimental Psychology*, *60*, 543–550.
- Dudukovic, N. M., Dubrow, S., & Wagner, A. D. (2009). Attention during memory retrieval enhances future remembering. *Memory Cognition*, *37*, 953–961.
- Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. *Nature Reviews Neuroscience*, *12*, 105–118.
- 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 Neuroscience*, *31*, 5392–5397.
- Fellner, M.-C., Bäuml, K.-H., & Hanslmayr, S. (2013). Brain oscillatory subsequent memory effects differ in power and long-range synchronization between semantic and survival processing. *Neuroimage*, *79*, 361–370.
- Fletcher, P. C., Stephenson, C. M., Carpenter, T. A., Donovan, T., & Bullmore, E. T. (2003). Regional brain activations predicting subsequent memory success: An event-related fMRI study of the influence of encoding tasks. *Cortex*, *39*, 1009–1026.
- Gray, S. J., & Gallo, D. A. (2015). Disregarding familiarity during recollection attempts: Content-specific recapitulation as a retrieval orientation strategy. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *41*, 134–147.
- Gruber, M. J., Watrous, A. J., Ekstrom, A. D., Ranganath, C., & Otten, L. J. (2013). Expected reward modulates encoding-related theta activity before an event. *Neuroimage*, *64*, 68–74.
- Halamish, V., Goldsmith, M., & Jacoby, L. L. (2012). Source constrained recall: Front-end and back-end control of retrieval quality. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*, 1–15.
- Hanslmayr, S., Spitzer, B., & Bäuml, K.-H. (2009). Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cerebral Cortex*, *19*, 1631–1640.
- Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and episodic memory: Addressing the synchronization/desynchronization conundrum. *Trends in Neurosciences*, *39*, 16–25.
- Hanslmayr, S., & Staudigl, T. (2014). How brain oscillations form memories—A processing based perspective on oscillatory subsequent memory effects. *Neuroimage*, *85*, 648–655.
- Hsieh, L.-T., Ekstrom, A. D., & Ranganath, C. (2011). Neural oscillations associated with item and temporal order maintenance in working memory. *Journal of Neuroscience*, *31*, 10803–10810.
- Jacoby, L. L., Kelley, C. M., & McElree, B. D. (1999). The role of cognitive control: Early selection vs. late correction. In S. Chaiken & Y. Trope (Eds.), *Dual-process theories in social psychology* (pp. 383–400). New York: Guilford Press.
- Jacoby, L. L., Shimizu, Y., Daniels, K. A., & Rhodes, M. G. (2005). Modes of cognitive control in recognition and source memory: Depth of retrieval. *Psychonomic Bulletin & Review*, *12*, 852–857.
- Jacoby, L. L., Shimizu, Y., Velanova, K., & Rhodes, M. G. (2005). Age differences in depth of retrieval: Memory for foils. *Journal of Memory and Language*, *52*, 493–504.
- Jafarpour, A., Fuentemilla, L., Horner, A. J., Penny, W., & Duzel, E. (2014). Replay of very early encoding representations during recollection. *Journal of Neuroscience*, *34*, 242–248.
- Kantner, J., & Lindsay, D. S. (2013). Top-down constraint on recognition memory. *Memory and Cognition*, *41*, 465–479.
- Kim, H. (2011). Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies. *Neuroimage*, *54*, 2446–2461.
- 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., & Hanslmayr, S. (2006). Upper alpha ERD and absolute power: Their meaning for memory performance. *Progress in Brain Research*, *159*, 151–165.
- Klimesch, W., Doppelmayr, M., Schimke, H., & Ripper, B. (1997). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology*, *34*, 169–176.
- Long, N. M., Burke, J. F., & Kahana, M. J. (2014). Subsequent memory effect in intracranial and scalp EEG. *Neuroimage*, *84*, 488–494.
- Marsh, R. L., Meeks, J. T., Cook, G. I., Clark-Foos, A., Hicks, J. L., & Brewer, G. A. (2009). Retrieval constraints on the front end create differences in recollection on a subsequent test. *Journal of Memory and Language*, *61*, 470–479.
- Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior*, *16*, 519–533.
- Myers, N. E., Stokes, M. G., Walther, L., & Nobre, A. C. (2014). Oscillatory brain state predicts variability in working memory. *Journal of Neuroscience*, *34*, 7735–7743.
- Park, H., Lee, D. S., Kang, E., Kang, H., Hahn, J., Kim, J. S., et al. (2014). Blocking of irrelevant memories by posterior alpha activity boosts memory encoding. *Human Brain Mapping*, *35*, 3972–3987.
- Percival, D. B., & Walden, A. T. (1993). *Spectral analysis for physical applications: Multitaper and conventional univariate techniques*. Cambridge, UK: Cambridge University Press.
- Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage*, *10*, 15–35.

- Roediger, H. L., III. (1990). Implicit memory: Retention without remembering. *American Psychologist*, *45*, 1043–1056.
- Roediger, H. L., III, Weldon, M. S., & Challis, B. H. (1989). Explaining dissociations between implicit and explicit measures of retention: A processing account. In H. L. Roediger III & F. I. M. Craik (Eds.), *Variations of memory and consciousness: Essays in honor of Endel Tulving* (pp. 3–41). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Rugg, M. D., Johnson, J. D., Park, H., & Uncapher, M. R. (2008). Encoding–retrieval overlap in human episodic memory: A functional neuroimaging perspective. *Progress in Brain Research*, *169*, 339–352.
- Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Science*, *4*, 108–115.
- Samaha, J., & Postle, B. R. (2015). The speed of alpha-band oscillations predicts the temporal resolution of visual perception. *Current Biology*, *25*, 2985–2990.
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., et al. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology*, *19*, 1846–1852.
- Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology: General*, *117*, 34–50.
- Staresina, B. P., Michelmann, S., Bonnefond, M., Jensen, O., Axmacher, N., & Fell, J. (2016). Hippocampal pattern completion is linked to gamma power increases and alpha power decreases during recollection. *eLife*, *5*, e17397.
- Staudigl, T., & Hanslmayr, S. (2013). Theta oscillations at encoding mediate the context-dependent nature of human episodic memory. *Current Biology*, *23*, 1101–1106.
- Staudigl, T., Hanslmayr, S., & Bäuml, K.-H. (2010). Theta oscillations reflect the dynamics of interference in episodic memory retrieval. *Journal of Neuroscience*, *30*, 11356–11362.
- Staudigl, T., Vollmar, C., Noachtar, S., & Hanslmayr, S. (2015). Temporal-pattern similarity analysis reveals the beneficial and detrimental effects of context reinstatement on human memory. *Journal of Neuroscience*, *35*, 5373–5384.
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, *87*, 154–163.
- Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, *80*, 352–373.
- Vogelsang, D. A., Bonnici, H. M., Bergström, Z. M., Ranganath, C., & Simons, J. S. (2016). Goal-directed mechanisms that constrain retrieval predict subsequent memory for new “foil” information. *Neuropsychologia*, *89*, 356–363.
- Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., et al. (1998). Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, *281*, 1188–1191.
- Waldhauser, G. T., Braun, V., & Hanslmayr, S. (2016). Episodic memory retrieval functionally relies on very rapid reactivation of sensory information. *Journal of Neuroscience*, *36*, 251–260.
- Waldhauser, G. T., Johansson, M., & Hanslmayr, S. (2012). Alpha/beta oscillations indicate inhibition of interfering visual memories. *Journal of Neuroscience*, *32*, 1953–1961.
- Wilson, M. (1988). The MRC psycholinguistic database: Machine-usable dictionary, version 2.00. *Behavior Research Methods, Instruments, and Computers*, *20*, 6–10.
- Wimber, M., Maaß, A., Staudigl, T., Richardson-Klavehn, A., & Hanslmayr, S. (2012). Rapid memory reactivation revealed by oscillatory entrainment. *Current Biology*, *22*, 1482–1486.
- Zawadzka, K., Hanczakowski, M., & Wilding, E. L. (2017). Late consequences of early selection: When memory monitoring backfires. *Journal of Memory and Language*, *92*, 114–127.
- Zion-Golub, E., Kutas, M., & Bentin, S. (2010). Neural dynamics associated with semantic and episodic memory for faces: Evidence from multiple frequency bands. *Journal of Cognitive Neuroscience*, *22*, 263–277.