

Brain Oscillations Dissociate between Semantic and Nonsemantic Encoding of Episodic Memories

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Prior studies, mostly using intentional learning, suggest that power increases in theta and gamma oscillations and power decreases in alpha and beta oscillations are positively related to later remembering. Using incidental learning, this study investigated whether these brain oscillatory subsequent memory effects can be differentiated by encoding task. One group of subjects studied material performing a semantic (deep) encoding task, whereas the other group studied the same material performing a nonsemantic (shallow) encoding task. Successful encoding in the semantic task was related to power decreases in the alpha (8–12 Hz) and beta (12–20 Hz) frequency band, and a power increase in the gamma band (55–70 Hz). In the shallow task, successful encoding was related to a power decrease in the alpha band and a power increase in the theta frequency band (4–7 Hz). A direct comparison of results between the 2 encoding tasks revealed that semantic subsequent memory effects were specifically reflected by power decreases in the beta (0.5–1.5 s) and the alpha frequency band (0.5–1.0 s), whereas nonsemantic subsequent memory effects were specifically reflected by a power increase in the theta frequency band (0.5–1.0 s).

Keywords: alpha, beta, EEG, gamma, strategy, subsequent memory, theta

Introduction

During each day of our life we experience many different episodes of which we can later remember some but forget others. The neural mechanisms mediating later remembering and forgetting during encoding of episodic events can be studied by subsequent memory or differences in memory paradigms. In these paradigms, the differences in neural activity during encoding of episodic events are investigated. In particular, the neural activity at encoding of episodic events (e.g., words) recalled on a later test is compared with the neural activity of events which are later forgotten.

The subsequent memory paradigm has been known for more than 20 years (Sanquist et al. 1980; Paller et al. 1987), and has attracted a lot of interest since then. Many studies have been carried out in order to unravel the neural mechanisms of subsequent memory by applying a variety of methods, such as event-related potentials (ERPs; Paller et al. 1987) and functional magnetic resonance imaging (fMRI) (Brewer et al. 1998; Wagner et al. 1998). ERP studies, for example, have identified a number of components emerging around 250 ms being more positive for later remembered than for later forgotten items (Paller et al. 1987). Exploring the locus of subsequent memory effects, fMRI studies have consistently shown that stronger activation of regions in the inferior prefrontal cortex and the medial temporal cortex are positively related to performance

on a later memory test (see Paller and Wagner 2002; for a review).

Due to their critical role in establishing synchronized firing between distant cortical cell assemblies and thereby promoting proper communication within a neural network (Fries 2005), brain oscillations have also been investigated intensively in memory research (Klimesch 1999; Werkle-Bergner et al. 2006). Typically, brain oscillations are divided into different frequency bands, for example, ranging from theta (4–7 Hz), alpha (8–12 Hz), beta (12–30 Hz), to gamma (>30 Hz). Oscillatory activity in these frequency bands has been shown to be differentially related to successful episodic encoding. For example, theta oscillations have been reported to be higher in amplitude for subsequently remembered than for subsequently forgotten words (Klimesch, Doppelmayr, et al. 1996; Summerfield and Mangels 2005; Caplan and Glaholt 2007) and pictures (Osipova et al. 2006). Similarly, gamma oscillations have also been shown to be higher for later remembered in contrast to later forgotten items (Gruber et al. 2004; Osipova et al. 2006). With respect to alpha oscillations, the opposite pattern was observed, with a stronger decrease in power during encoding predicting remembering on a later memory test (Klimesch, Schimke, et al. 1996; Weiss and Rappelsberger 2000). Similar results were obtained for the beta frequency band, showing that beta power for later recalled words is lower than for later not recalled words (Sederberg et al. 2007). Not all of the previous studies investigated the role of brain oscillations by analyzing the whole frequency range, however. A study which investigated power in all frequency ranges was carried out by Sederberg et al. (2003), who recorded intracranial electroencephalography (EEG) in epilepsy patients. Their results showed all of the above-described effects, with high power in the theta and gamma band but low power in the alpha and beta band to be related to subsequent recall on a later memory test.

Most of the previous studies examining oscillatory correlates of encoding processes used intentional learning instructions, with only a minority of studies employing incidental learning (Klimesch et al. 1996b; Gruber et al. 2004). During intentional learning, subjects typically engage in processing more conducive to learning the material and thus tend to encode the study material more semantically than during incidental learning (e.g., Anderson 1995). This may hold particularly if word lists are presented for study, which is the common procedure in most of the memory studies. In order to disentangle semantic from nonsemantic encoding processes, incidental learning tasks with different encoding strategies can be used. The results from such studies typically show that orienting subjects toward semantic (or deep) encoding leads to superior memory performance over deep orienting subjects toward phonological (or

shallow) encoding of material (Craik and Lockhart 1972; Craik and Tulving 1975).

Using fMRI, Otten and Rugg (2001a) demonstrated that the neural subsequent memory effect depends on the nature of the encoding task. They showed that successful encoding in a semantic task is related to activation of left inferior prefrontal regions, whereas successful encoding in a shallow task is related to activation in parietal regions. Evidence for a task dependency of the subsequent memory effect has also been put forward by electrophysiological studies investigating ERPs (Otten and Rugg 2001b). To date, however, no study has yet been conducted investigating brain oscillations and addressing the question of whether the above-described effects, which were found in almost all frequency ranges, can be dissociated into semantic and nonsemantic subsequent memory effects.

The current study aims to address this question and sets out to investigate whether different frequency bands are related to successful memory encoding in different encoding tasks. Comparable with several other incidental subsequent memory studies, 2 encoding conditions were employed, a deep and a shallow encoding task, with the former task requiring semantic processing (living/nonliving judgments) and the latter task requiring alphabetical processing of the study material. Thus, semantic processes should be involved mainly in the deep study condition, whereas nonsemantic processes should contribute to subsequent memory mainly in the shallow study condition. We searched for the oscillatory correlates of such semantic and nonsemantic encoding processes.

Materials and Methods

Subjects

Forty subjects participated in the study, half of them were assigned to the deep study group and the other half to the shallow study group. Seven subjects had to be excluded from analysis because their EEG was heavily contaminated by artifacts. Eight other subjects were excluded because they had too few responses (<15) in one of the 3 response categories (high confident, low confident, miss). Thus, 25 subjects remained for data analysis (6 males; mean age: 22.08; range: 19–30) of whom 13 performed the deep encoding task and 12 the shallow encoding task. All subjects had normal or corrected to normal vision, and all had German as their native language. All except 3 subjects were right handed and no one reported a history of neurological disease. Prior to the experiment all participants gave written informed consent. Subjects were paid or received course credits for participation.

Procedure

Each participant was randomly assigned to one of the 2 study tasks (deep or shallow). In the deep encoding task, subjects had to judge whether the presented word was animate (or referred to the property of a living entity) or inanimate. In the shallow encoding task, the subjects had to judge whether the first and the last letter of the presented word were in alphabetical order or not. Such deep and shallow encoding instructions have been used in several other previous subsequent memory studies (e.g., Otten et al. 2001). All subjects gave their responses manually by pressing one of 2 response buttons (“yes” or “no”) with the middle and the index finger of their right hand. To control for motor activity, the assignment of the buttons was counterbalanced (half of the subjects were instructed to press “yes” with their index finger, the other half pressed the “no” button with their index finger). All subjects were naïve about the later memory test, and did not rehearse the presented items as revealed by a questionnaire which was conducted at the end of the experiment.

The stimuli consisted of 300 words which were selected from the CELEX database and were grouped into 2 lists (150 words each). List 1

contained 48 animate words and list 2 contained 42 animate words. These lists were further matched according to word frequency (10–117 per million), concreteness (252–593), imageability (452–638), and number of letters (3–8). The values for concreteness and imageability refer to rating norms (values ranging from 100 to 700) and were derived from the MRC psycholinguistic database (Coltheart 1981). During the study phase, the items of one of the 2 word lists were presented with a visual angle of approximately $0.45^\circ \times 1.37^\circ$ on a computer screen. The items from the other list served as new items for the recognition phase. Across subjects the 2 lists were counterbalanced. A trial in the study phase started with a fixation cross with variable duration (1500–2000 ms), thereafter a word was presented for 1500 ms, and then a blank screen was shown for 2000 ms. Subjects were instructed not to react during item presentation but to give their response after appearance of the blank screen. After the study phase, a distracter task was performed during which 50 pictures of famous actors were shown, and the subjects’ task was to rate the publicity of the actors by using a 6-point rating scale. This was done in order to bar the participants from rehearsing the item material and to make the subjects familiar with the handling of the 6 response buttons, which were used in the subsequent recognition phase.

In the recognition phase, the 150 old items were presented together with 150 new items. The sequence of the 300 items was randomized and the subjects’ task was to rate their confidence of an item being old or new using the same 6-point rating scale they had used before in the distracter task (ranging from *C1: very sure old* to *C6: very sure new*). Participants were instructed to use the whole range of the confidence rating scale. Subjects gave their response with the index, middle, and ring fingers of their left and right hands on a computer keyboard. Again, the assignments of the buttons were counterbalanced across subjects (half responded with their left hand for the buttons *C1, C2, C3—ring, middle, and index finger, respectively*—and the other half used their right hand for the buttons *C1, C2, C3*). A trial during the recognition phase started with a fixation cross with variable duration (1500–2000 ms). Thereafter a word was presented for 1500 ms and then a question mark was shown which disappeared when the subject gave his/her response.

EEG Recording

The EEG was recorded from 62 approximately equidistant Ag/AgCl scalp electrodes mounted in an elastic cap (BrainCap64, Easycap, Herrsching-Breitbrunn, Germany), arranged according to the extended 10–20 system. Vertical and horizontal eye movements were recorded from 2 additional channels. Electrode FCz served as common reference. Signals were digitized with a sampling rate of 500 Hz and amplified between 0.3 and 70 Hz with a Notch-filter at 50 Hz (BrainAmpMR plus, Brain Products, Gilching, Germany). EEG recordings were off-line re-referenced against average reference. The EEG data were corrected for eye movements using calibration data to generate individual artifact coefficients and the algorithm implemented in the software package BESA (MEGIS Software BESA v5.1.8; see Ille et al. 2002; for details). Remaining artifacts were excluded from analysis by careful visual inspection.

Behavioral Data Analysis

For behavioral data analysis, a modeling approach was used in order to classify the responses into 3 categories: *High Confident Hit (HC)*, *Low Confident Hit (LC)*, and *Misses (M)*. For each subject, an unequal-variance signal detection model (Macmillan and Creelman 2005; Mickes et al. 2008) was fitted to the rating data (for technical details, see Spitzer and Bäuml 2007), yielding estimates of the individual response criteria associated with each of the 6 rating categories. Such modeling circumvents problems which may arise by just pooling the different response categories across subjects. For example, one subject may use only the response buttons *C1* and *C2* to indicate a recognized old item, whereas another subject may use the buttons *C1–C5* to indicate old responses. By using receiver operating characteristics (ROCs), signal detection theory allows to objectively quantify such individual response biases and to correct for tendencies to use the single buttons of the rating scale differently. On the basis of the estimated individual response criteria, target items associated with a more conservative than

neutral response criterion (i.e., *true old* responses) were classified as *hits*, and target items associated with a more liberal than neutral response criterion (i.e., *true new* response) were classified as *misses*. Hits were further subdivided into *High Confidence Hits (HC)* and *Low Confidence Hits (LC)*, according to whether they were given with maximal confidence (“*very sure old*”) or with lower confidence.

An example of this procedure is illustrated in Figure 1. Figure 1*a* shows the ROC data of 2 representative subjects, with comparable memory performance but different response criteria. Subject A showed a quite liberal response behavior and appeared to have used the response button C3 to indicate a relatively weak degree of “true” memory strength, as indicated by a high false alarm rate for this response category (Fig. 1*a*, left). In contrast, subject B used the response button C3 quite conservatively as indicated by a lower false alarm rate (Fig. 1*a*, right). This example demonstrates that a modeling approach helps to separate “true old” from “true new” responses by grouping the individual responses according to their location relative to an objectively neutral response criterion, because the same response button (C3) may be used for “true” old responses by one subject and for “true” new responses by another subject (Fig. 1*b*). For 10 subjects (shallow: $n = 3$; deep: $n = 7$) the neutral response criterion was located between response C2 and C3 (as in the example of Fig. 1*a*, left); for 9 subjects (shallow: $n = 4$; deep: $n = 5$) the neutral response criterion was located between responses C3 and C4 (as in the example of Fig. 1*a*, right); for 4 subjects the neutral response criterion was located between C4 and C5 (shallow: $n = 3$; deep: $n = 1$); for 2 subjects in the shallow encoding group the neutral response criterion was located between responses C5 and C6. These results also indicate that subjects were indeed using the rating scale quite differently.

For statistical analysis of the behavioral data, nonparametric Wilcoxon sign-rank tests were used for within-subject comparisons. The relevant dependent variables for these comparisons were reaction time and accuracy rate during encoding for HC and M items. For between subject

comparisons (deep vs. shallow) nonparametric Mann-Whitney tests were carried out. The relevant dependent variables for these comparisons were memory performance (d'), in the recognition task, and accuracy rate and reaction time at encoding.

EEG Data Analysis

All analyses were carried out using the BESA software package and self-written MATLAB codes (The Mathworks, Inc., Munich, Germany). The EEG data were segmented into 2000-ms epochs (ranging from 500 ms preceding stimulus onset to 1500 ms after stimulus onset). Depending on the subjects' response in the recognition phase, the epochs were grouped into 2 categories: *high confidence hit (HC)* and *miss (M)*. After rejection of artifact contaminated epochs an average of 64 (HC) and 31 (M) epochs remained for the deep study group. For the shallow study group an average of 37 (HC) and 55 (M) epochs remained for data analysis. No subject had less than 15 trials in one of the 2 conditions. (In order to prove that a stable event-related desynchronization (ERD) pattern may already be obtained with a minimum of 15 trials, we carried out a simulation experiment, in which a given number of single trials was drawn randomly sampling with replacement for each subject. Thereafter, the mean ERD across these single trials was computed. After 50 permutation runs the variance across the mean ERD was calculated. These permutations were carried out using an increasing number of single trials, starting with 5 and ending with 30 single trials. The results of this analysis are plotted for 3 single subjects for the alpha ERD [8–12 Hz] in Supplementary Fig. 1*a-c*. To statistically determine how many single trials are needed to obtain a stable ERD estimate, the variance of each single trial bin [5, 6, 7, ... 29] was compared with the variance of the 30 single trial bin by means of variance homogeneity tests [Levene - Tests]. The results indicate

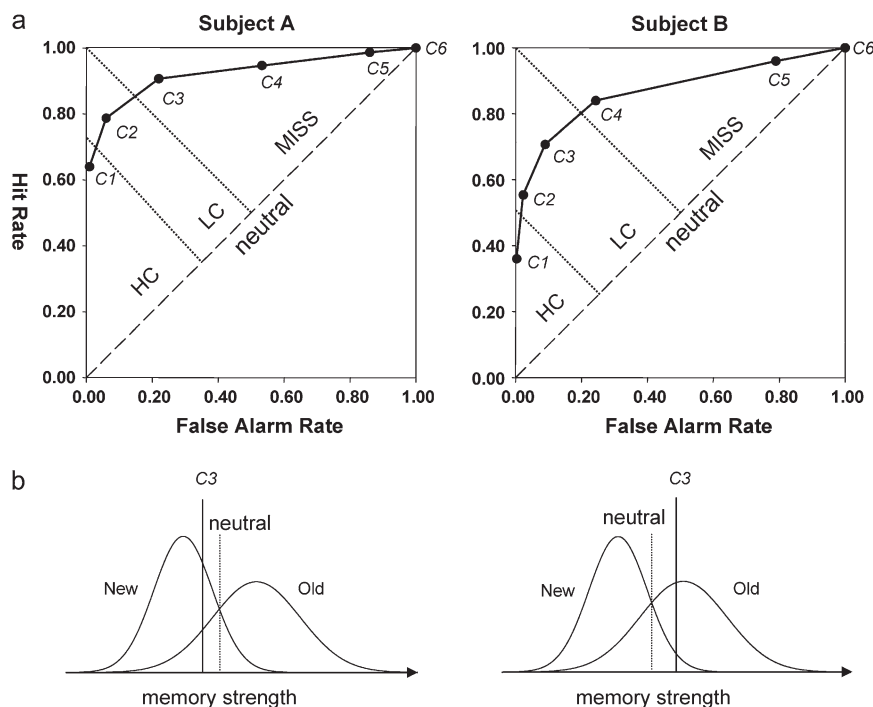


Figure 1. An example of how the 6 responses were grouped into high confidence hits (HC), low confidence hits (LC), and misses (M) is shown for 2 subjects (both performing the deep study condition). (*a*) The ROC for a subject with relatively liberal response criteria (left column) and for a subject with relatively conservative response criteria (right column) is shown. The cumulated hit rate is plotted on the y-axis, and the cumulated false alarm rate is plotted on the x-axis. C1–C6 refer to the 6 levels of response confidence (C1: very sure old and C6: very sure new). For subject A the neutral response criterion is located between C2 and C3, showing that this subject used the responses C3–C6 to indicate a new response. In contrast, for subject B the neutral response criterion is located between C3 and C4, which indicates that this subject used C4–C6 to indicate a new response. (*b*) A schematic illustration of the memory strength distribution of new and old items is shown for the 2 subjects. As it is assumed by the unequal-variance model, old items show more variance in memory strength than new items (Macmillan and Creelman 2005; Mickes et al. 2008). The neutral response criterion is always located at the crossover between old and new items. Note that subject A used the response C3 to indicate a relatively weak memory signal, whereas subject B used the same response to indicate a relatively strong memory signal.

that variance decreases markedly from 5 to around 15 single trials but stays quite stable thereafter).

For oscillatory power analysis (μV^2) the complex demodulation algorithm as implemented in BESA (MEGIS Software BESA v5.1.8) was used. For time-frequency analysis BESA uses an FIR filter with a Gaussian window. In order to get rid of filter artifacts at the edges of the epochs, BESA filters the data in a slightly bigger time interval than specified. The data were filtered in a frequency range of 4–70 Hz. For the lower frequency ranges (4–20 Hz) the time resolution was set to 78.8 ms (50% power drop) and the frequency resolution was set to 1.42 Hz (50% power drop). The time-frequency data were exported in bins of 50 ms and 1 Hz. For the higher frequency ranges (20–70 Hz) the time-frequency resolution was set to 15.8 ms and 7.08 Hz. The data for this frequency range were exported in bins of 10 ms and 5 Hz. This approach is comparable with a Morlet-Wavelet which also changes the time-frequency resolution for the different frequency bands in order to accommodate for the different frequency characteristics. To prevent smearing of the lower frequencies into the higher frequency ranges (due to a much lower frequency resolution for the 20–70 Hz range), the raw data were filtered with a 20-Hz high-pass filter (Butterworth, 48 db/oct) prior to time-frequency transformation. To calculate event-related power changes, the event-related desynchronization/event-related synchronization (ERD/ERS) method was used (Pfurtscheller and Aranibar 1977). This method examines stimulus induced power changes by calculating the percentage of power decrease (ERD) or power increase (ERS) in relation to a prestimulus baseline (set to 500–0 ms prior stimulus onset). For statistical analysis, ERD/ERS values were collapsed in order to obtain 6 frequency bands: Theta (4–7 Hz); Alpha (8–12 Hz); Beta1 (12–20 Hz); Beta2 (20–30 Hz); Gamma1 (30–45 Hz); Gamma2 (55–70 Hz), and 3 time windows: T1 (0–500 ms); T2 (500–1000 ms); T3 (1000–1500 ms).

For supplementary control analyses, we also analyzed the P300 component for animate and inanimate words. For this control analysis the mean amplitude in a time interval ranging from 550 to 700 ms was used. Baseline correction to the waveforms was applied using a prestimulus interval ranging from –200 to 0 ms. No significant differences between animate and inanimate words occurred during this baseline interval ($P_{\text{corr}} > 0.2$). The waveforms were low pass filtered at 15 Hz with a butterworth filter (12 db/oct; zero phase shift). Mean number of trials were 41 (range: 36–47) for the animate words and 96 (range: 89–104) for the inanimate words. For statistical comparisons, the same procedures were used as for the frequency analysis (see below).

Statistical Analysis of EEG Data

In order to minimize influences from outliers and to compensate for the small sample number only nonparametric statistical tests are used throughout the whole analysis. To examine differences between subsequently remembered and subsequently forgotten words, pair-wise contrasts between high confidence hits (HC) and misses (M) were calculated for each frequency band and time window. Contrasting high confidence hits with misses, and leaving low confidence hits is a procedure which has been used in several other subsequent memory studies (Brewer et al. 1998; Wagner et al. 1998; Otten et al. 2001). To account for multiple testing, a 2-stage randomization procedure was carried out. At first, Wilcoxon sign-rank tests were calculated in order to investigate which electrodes differ between the HC and M condition ($P < 0.05$; 2-tailed). Thereafter, a randomization test using 2000 permutation runs was conducted. In this randomization procedure the 2 conditions are interchanged randomly for each subject and each randomization run. The swapping of the conditions is done consistently across electrodes. For each randomization run Wilcoxon sign-rank tests are calculated, returning the number of electrodes showing a significant difference between the 2 conditions. After several permutation runs (e.g., 2000) a distribution of the number of electrodes which randomly show significant differences between 2 conditions can be generated. This distribution can then be used to determine the P -level of a given number of significant electrodes. If the P value (P_{corr}) of this randomization test is below 0.05, less than 5% of the permutation runs exhibited equal or more electrode sites with a significant difference between the 2 conditions. This method is based on the randomization procedure proposed by Blair and Karniski (1993) and was already used in

several prior studies from our lab in order to investigate time-frequency responses (Hanslmayr et al. 2007; Bäuml et al. 2008; Pastötter et al. 2008).

For the analysis in the gamma frequency range (30–70 Hz) this randomization procedure was restricted to a region of interest (ROI) consisting of 19 posterior electrode sites (P3, P4, O1, O2, P7, P8, Pz, Oz, P1, P2, PO3, PO4, P5, P6, TP7, TP8, PO7, PO8, and POz). This was done because in contrast to memory effects in the lower frequency range (<20 Hz), which have been found across various recording sites on the scalp, memory related effects in the gamma band are typically reported over posterior recording sites (Osipova et al. 2006; Spitzer et al. forthcoming). Moreover, a recent study (Yuval-Greenberg et al. 2008) has shown that, if an average reference is employed, gamma band power over anterior electrode sites can reflect miniature eye movement artifacts. Thus, by restricting the analysis of gamma subsequent memory effects (SMEs) to posterior recording sites, the risk of potential ocular artifact contamination in the gamma frequency band can be minimized.

In order to investigate whether the 2 groups differ with respect to their subsequent memory effects a similar randomization test was conducted. First, Mann-Whitney Tests between the deep and shallow encoding group were calculated for the differences of HC and M items for each electrode. Next, 2000 permutation runs were carried out, in which the subjects were randomly assigned to one of the 2 groups. Mann-Whitney tests were calculated after each permutation run, returning the number of significant electrodes. As before, a distribution of the number of electrodes which randomly show significant differences was generated, to determine the P -level (P_{corr}) of a given number of significant electrodes. This calculation was carried out only for those time windows and frequency bands, where subsequent memory effects were found in one of the 2 groups.

Results

Behavioral Results

Mean reaction time and mean accuracy rate in the deep encoding task was 561 ms and 84.4%, respectively. This indicates that the participants were attentively performing the semantic encoding task. No difference in reaction time was obtained between items which were later remembered at high confidence and items which were later missed (577 vs. 557 ms; $Z = 1.36$; $P > 0.15$). During encoding, a trend was observed that high confidently remembered items showed slightly lower accuracy rates than missed items (82.2 vs. 87.1%; $Z = 1.85$; $P = 0.07$). The ratio of animate words across the 3 response categories was significantly different (HC: 37%, LC: 30% and Miss: 20%; $\chi^2 = 7.41$; $P < 0.05$), indicating that animate words were more likely to be recognized than inanimate words. To exclude a possible target effect on animate words during encoding, due to the lower ratio of these stimuli (1/3 vs. 2/3) a control analysis was conducted, in which we compared the mean amplitude of the P300 component between animate and inanimate words. The results are depicted in Supplementary Figure 2 and show that the 2 categories elicited roughly the same P300 component ($P_{\text{corr}} > 0.5$), thus excluding an oddball like target effect on animate words.

For the alphabetical task mean reaction time and mean accuracy rate was 687 ms and 86.8%, respectively. At encoding, reaction times for high confidence hits were significantly faster than for misses (658 vs. 726 ms; $Z = 2.19$; $P < 0.05$). Similarly, accuracy was slightly higher for high confidence hits in contrast to misses (89.1 vs. 84.4%; $Z = 1.96$; $P = 0.05$). The 2 encoding groups did not differ with respect to mean reaction time or accuracy (both P s > 0.15), indicating that the 2 tasks were roughly the same with respect to task difficulty.

The overall recognition results are illustrated in Table 1. Measures of recognition performance (d') were derived from

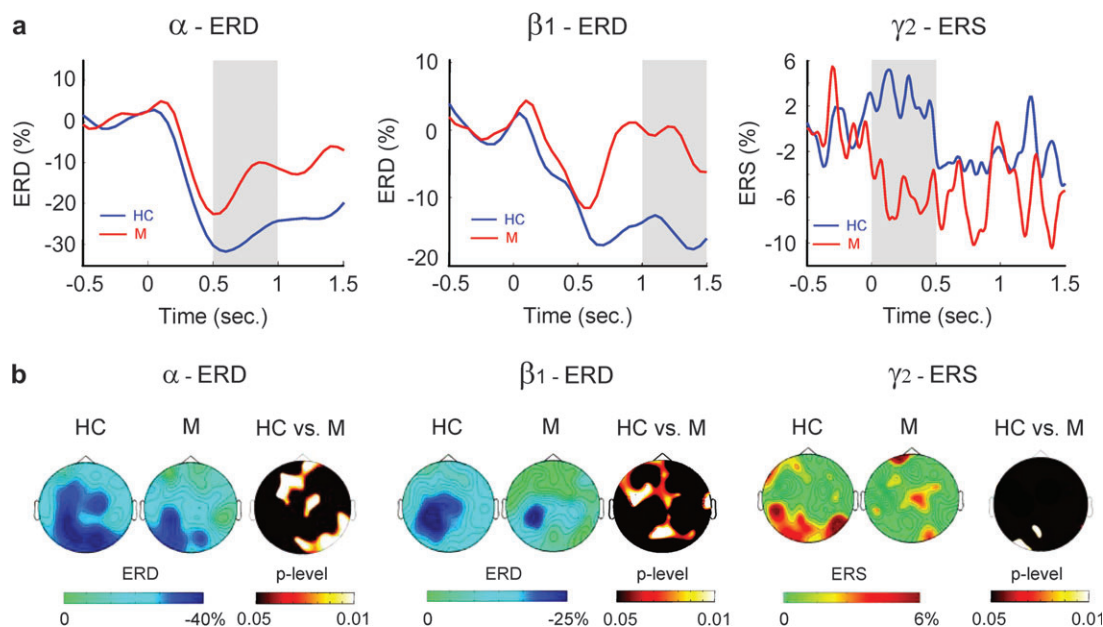


Figure 2. The results of the ERD/ERS analysis for the deep study group are plotted. (a) The time course of alpha (left plot), beta1 (middle plot), and gamma2 (right plot) ERD/ERS is shown. A power increase is denoted by positive values (ERS) and a power decrease is labeled with negative values (ERD). The averaged data is shown for those electrodes which exhibited significant differences between later high confidently remembered (HC) and later missed (M) items. In the alpha and beta1 frequency bands power decrease was stronger for HC-items versus M-items. The gray bars indicate the time windows which were used to plot the topography. The ERD/ERS curves were smoothed using a running average with a window size of 2 bins (100 ms) for lower frequency bands (alpha and beta1) and a window size of 5 bins (50 ms) for the gamma frequency band. (b) Topographical maps of ERD are plotted for the 3 conditions and each frequency band, with cold colors indicating power decrease (alpha and beta1) and warm colors indicating power increase (gamma2). The difference between the HC and M condition is expressed by topographical plotting of the P -levels obtained by nonparametric Wilcoxon sign-rank tests.

Table 1

Proportions of study items subsequently classified as high confidence hits (HC), low confidence hits (LC), and Misses for the deep and shallow encoding group, together with recognition accuracy (d')

	HC	LC	Miss	d'
Deep	52.1	23.2	24.7	2.17
Shallow	25.8	35.4	38.8	1.02

signal detection analysis of the individual subject data. In order to evaluate the goodness of fit to our data, we used a conventional χ^2 test. The signal detection model fit the data of all the subjects adequately as indicated by nonsignificant maximum likelihood test (all P s > 0.40). As expected, the deep study group performed better on the memory test than the shallow study group (d' : 2.17 vs. 1.02; $Z = 4.05$; $P < 0.001$). These results also show that the deep study group achieved more high confidence hits and fewer misses than the shallow study group. Note, that recognition performance is reported only for those subjects who entered the EEG analysis, and thus had a sufficient number of trials in each of the 2 response categories [HC and Miss]. In the deep encoding group several subjects had to be excluded because they showed too few miss trials. In contrast, several subjects in the shallow encoding group were excluded because they showed too few high confident hit trials. Therefore, recognition performance for the shallow encoding group is slightly overestimated, whereas the recognition performance for the deep encoding group is slightly underestimated in this selected sample of subjects.

Table 2

Number of electrodes showing significant differences (HC > M/HC < M) between later high confidently (HC) recognized items and misses (M) for the deep and shallow encoding group

	Deep			Shallow		
	T_1	T_2	T_3	T_1	T_2	T_3
Theta	—/4	1/1	—/4	2/—	14*/—	2/—
Alpha	—/6	—/20**	—/23**	1/1	1/—	—/11*
Beta1	—/—	—/8*	—/20**	2/2	—/—	1/—
Beta2	1/—	1/—	—/3	2/2	—/—	—/1
Gamma1	—/1	2/—	1/—	—/—	1/—	—/—
Gamma2	3*/—	1/—	—/—	—/—	1/—	—/1

Note: * $P_{\text{corr}} < 0.05$; ** $P_{\text{corr}} < 0.01$. The first digit indicates number of electrodes exhibiting significantly more power for HC versus M items. The second digit indicates number of electrodes exhibiting significantly less power for HC versus M items. P_{corr} refers to the P -level of the randomization test. T_1 (0–500 ms), T_2 (500–1000 ms), and T_3 (1000–1500 ms) indicate the 3 time windows over which ERD/ERS data was collapsed (see Methods).

EEG—Results

Deep Study Group

An overview of the ERD/ERS results for the deep and the shallow study group is shown in Table 2. Concerning the deep study group, statistical analysis revealed that items which were later remembered at high confidence (HC) differed from later missed items (M) in the alpha (8–12 Hz), the beta1 (12–20 Hz), and in the gamma2 (55–70 Hz) frequency bands. The subsequent memory effect in the alpha frequency band (8–12 Hz) started to emerge in the middle time window (500–1000 ms) and was also persistent during the later time window (1000–1500 ms). In the beta1 frequency band (12–20 Hz) significant effects were also found during the last 2 time windows, though

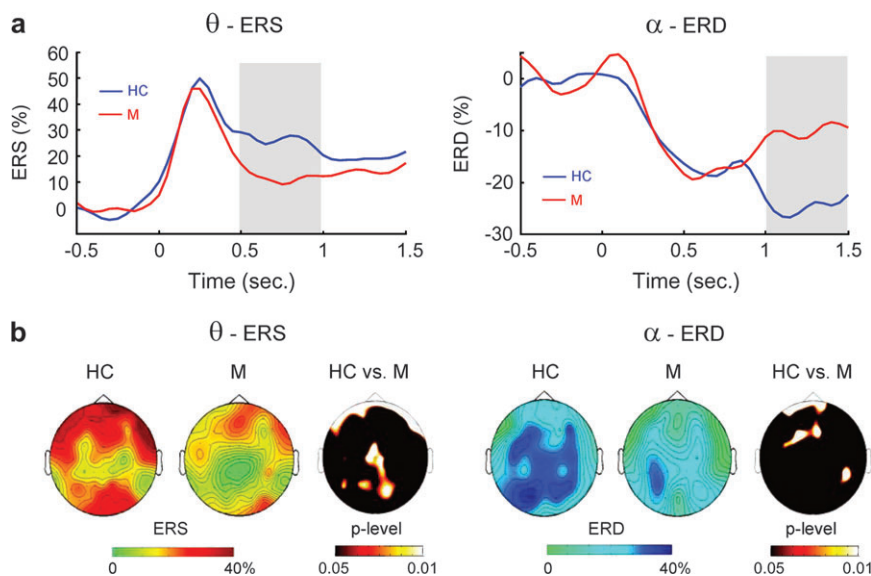


Figure 3. The results of ERD/ERS analysis for the shallow study group are plotted. (a) The averaged time course of theta ERS (left plot) and alpha ERD (right plot) is shown for those electrodes exhibiting a significant difference between the HC and M condition. For theta, stronger increase in power for HC-items was observed in contrast to M-items. According to alpha, stronger power decrease for the HC items was observed in contrast to M-items. The gray bars indicate the time windows used to plot the topography. The ERD/ERS curves were smoothed using a running average with a window size of 2 bins (100 ms). (b) Topographical maps of ERD/ERS are plotted for the 2 conditions and each frequency band, with warm colors indicating power increase (theta) and cold colors indicating power decrease (alpha). The difference between the HC and M condition is expressed by topographical plotting of the P -levels obtained by nonparametric Wilcoxon sign-rank tests.

being more pronounced in the later time window, 1000–1500 ms after stimulus onset. Regions of interest analysis (see Methods) in the gamma2 frequency band revealed a subsequent memory effect in an early time window, 0–500 ms after stimulus onset. Whereas the subsequent memory effects in the alpha and beta1 frequency ranges were due to less stimulus induced power for later remembered items versus later missed items, the effects in the gamma2 band showed more power for later remembered versus later missed items (Fig. 2*a*). Differences between HC and M items for alpha ERD were found over left frontal and right occipital electrode sites (Fig. 2*b*, left). SMEs in the beta1 frequency band were found over left frontal and parietal electrode sites (Fig. 2*b*, middle). The topography of the subsequent memory effect in the gamma2 frequency range is plotted in Figure 2*b* (right). No effects were found in the theta frequency band.

Shallow Study Group

The results of the ERD/ERS analysis for the shallow study group are summarized in Table 2. Differences between later remembered (HC) and later missed (M) items were found in the theta frequency band (4–7 Hz) during the middle time window (500–1000 ms). This effect was due to stronger theta ERS for items which were later remembered at high confidence than for items which were later missed (Fig. 3*a*, left). The power increase in the theta frequency band was mostly pronounced over frontal electrode sites in the HC condition (Fig. 3*b*, left). Differences between later remembered and later missed items (HC vs. M) emerged over frontal and parietal electrode sites (Fig. 3*b*, left). Subsequent memory effects were also found in the alpha frequency band with later remembered items showing a stronger alpha power decrease than later missed items in the time window from 1000 to 1500 ms (Fig. 3*b*, right). The topography of this subsequent memory effect shows that later high confidently remembered

items exhibited stronger ERD mostly over frontal electrode sites (Fig. 3*b*, right). No subsequent memory effects were found in higher frequency ranges (12–70 Hz) in this study group.

Comparison between Deep and Shallow Study Groups

The above results show that the deep study group exhibited SMEs in the alpha, beta1, and the gamma2 frequency band, whereas the shallow study group showed subsequent memory effects in the theta and alpha band. In order to investigate whether the SMEs dissociate between the deep and shallow study condition, we compared the SMEs (HC - M) between the 2 groups separately for each frequency band by means of nonparametric randomization tests (see Methods). This analysis was calculated for those time windows and frequency bands where a significant subsequent memory effect was obtained in one of the 2 groups. An overview of the results is plotted in Fig. 4*a*. The difference in theta ERS between later remembered and later missed items was significantly higher in the shallow than the deep study group (Fig. 4*a*). This effect was evident over frontal and parietal electrode sites (Fig. 4*b*). Concerning the alpha frequency band, the deep encoding group differed significantly from the shallow encoding group in the middle time window (500–1000 ms; Fig. 4*c*), but not during the later time window (1000–1500) where both groups showed roughly the same amount of alpha power difference between HC versus M items (Fig. 4*d*). In the beta1 frequency band, the deep study group showed significantly stronger SMEs than the shallow study group in the middle and late time window (500–1500 ms; Fig. 4*e* and *f*). No difference between the 2 encoding groups was obtained in the gamma frequency range ($P_{\text{corr}} > 0.2$).

Discussion

In this study, we addressed the question of whether brain oscillatory correlates of successful episodic memory encoding

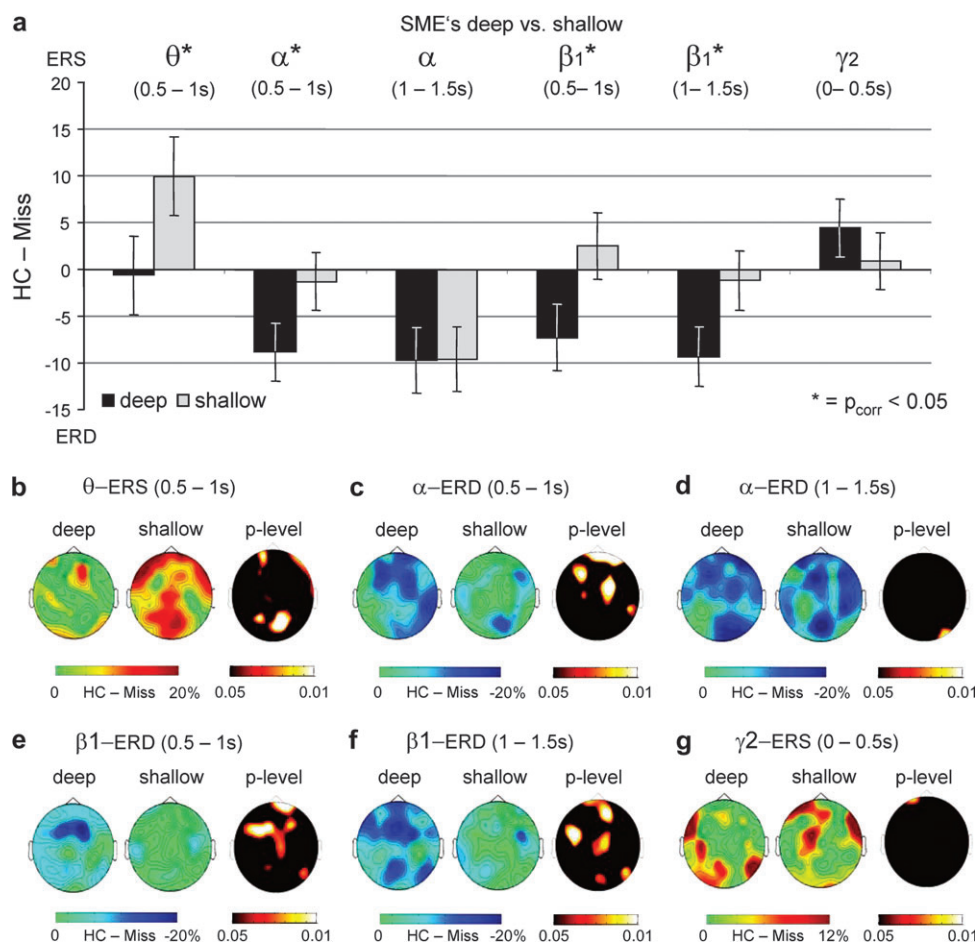


Figure 4. Comparison of the subsequent memory effects between the deep and the shallow study group. (a) The mean differences between HC and M items are shown for those frequency bands and time windows exhibiting subsequent memory effects in one of the 2 encoding groups. ERD/ERS differences (y -axis) were pooled across all 62 electrode sites, except for the gamma2 frequency band where the data was pooled across the 19 posterior electrode sites comprising the ROI (see Methods). The stars (*) refer to the P -level obtained by nonparametric randomization tests ($P_{\text{corr}} < 0.05$), the error bars indicate standard errors. (b-g) Topographical maps of the subsequent memory effects (HC - Miss) in the 2 encoding groups are plotted for the respective frequency bands and time windows. Warm colors indicate more power for HC in contrast to M items (ERS), cold colors indicate less power for HC versus M items (ERD). The differences between the 2 groups is expressed by topographical plotting of the P -levels obtained by nonparametric Mann-Whitney tests.

vary with encoding task. We used a between-subjects design in which one group performed a semantic (deep) and the other group an alphabetical (shallow) encoding task. Such encoding tasks are commonly used in incidental learning studies, and we replicated the typical result of superior memory performance in the semantic compared with the alphabetical study condition (e.g., Craik and Tulving 1975). The main result of this study is that different frequency bands predicted successful encoding in the 2 groups. Subsequent memory effects in the beta (12–20 Hz), alpha (8–12 Hz; 500–1000 ms), and gamma (55–70 Hz) frequency range were found only for the semantic study group, with a beta and alpha power decrease and a gamma power increase predicting later remembering. In contrast, theta power increases (4–7 Hz) for later remembered versus later forgotten words was found only in the shallow study group. In the alpha band (8–12 Hz), subsequent memory effects were found in both groups in the later time window (1000–1500 ms), during which an equal amount of power decrease predicted later remembering (cf. Fig. 4a). The results for each single frequency band will be discussed next.

Beta ERD and its Relation to Deep Encoding

The present results suggest that semantic encoding processes are reflected in the beta frequency range. This conclusion is supported by the fact that beta power was related to successful memory encoding in the semantic study group, whereas no such effect was observable in the shallow study group. Moreover, the difference between later remembered and later missed items at encoding was significantly higher for the deep than for the shallow group (Fig. 4). A relation between successful episodic memory encoding and beta power decrease was already reported in prior studies (Sederberg et al. 2003, 2007). However, using intentional rather than incidental learning, these studies also reported effects in the theta, alpha, and gamma frequency bands. Here we provide first evidence that the power decrease in the beta frequency range might be specifically related to processing of the items' semantic features. Inspection of the beta ERD waveforms shows that a pronounced beta power decrease occurred for later recognized as well as for later missed items. For high confident hits, however, beta power was decreased over a longer period of

time than for misses (cf. Fig. 2). This pattern suggests that the beta power decrease could reflect semantic processing per se, being stronger for hits than for misses.

Although not many studies investigated the role of beta oscillations for semantic processes, at least 3 prior studies suggest a role of this frequency band for the processing of word meaning. For instance, Weiss and Rappelsberger (1996) reported that beta band coherence differed between processing of concrete and abstract nouns. Bastiaansen et al. (2005) reported, amongst findings in theta and alpha frequency bands, a stronger beta power decrease for open class words (such as nouns, verbs, and adjectives) in contrast to closed class words (such as determiners, prepositions, and conjunctions). Similarly, Klimesch et al. (2001) showed a stronger beta power decrease over left frontal and left parietal sites for meaningful in contrast to pseudowords. Thus, our results are in line with previous work and extend these findings by showing that beta power changes play a specific role in the semantic encoding of episodic memories.

In several prior studies a decrease in the beta frequency band has been related to motor processes (see Neuper et al. 2006, for a review). However, the assumption that the effect in beta power, as it was observed here reflects mere motor rather than memory processes seems quite unlikely, because no motor responses were required during item presentation. Also, the fact that the beta power decrease was related to memory performance in the deep study group only speaks against such an interpretation, as responses were given in the same manner in the shallow study group as well.

Theta ERS and its Relation to Shallow Encoding

The present findings suggest that nonsemantic encoding processes are mainly reflected in the theta frequency band. This conclusion is supported by the fact that subsequent memory effects in the theta frequency band were observed in the shallow study group only, who performed a nonsemantic study task. Moreover, the theta power increase for later remembered words was significantly higher for the shallow than the deep encoding group (Fig. 4). A number of previous studies, mostly employing intentional learning, have reported subsequent memory effects for the theta frequency band (Sederberg et al. 2003; Summerfield and Mangels 2005, 2006; Osipova et al. 2006). Theta oscillations have been linked to different cognitive processes, such as central executive demands and working memory (Sarnthein et al. 1998; Tesche and Karhu 2000; Hanslmayr et al. 2008). That our results reflect stronger central executive demands to later remembered items, however, seems quite unlikely, because no difference in theta ERS was found between trials with slow and fast reaction times during the alphabetical encoding task ($P_{\text{corr}} > 0.5$).

Rather, the subsequent memory effects in this frequency band are consistent with the findings of other studies which have highlighted the role of theta oscillations in item-context binding (Summerfield and Mangels 2005). In animal studies theta oscillations have been intensively investigated in the hippocampus and their relation to the encoding and retrieval of contextual information has been demonstrated (Hasselmo 2005). Physiological studies have shown that neural activity in the prefrontal cortex shows a strong phase relationship to hippocampal theta oscillations (Hyman et al. 2005). Thus, larger theta power over frontal electrode sites (cf. Fig. 3b)

during encoding could reflect successful binding of an item to a context cue, increasing the chance of correct recognition on a later test. This interpretation would be in line with behavioral studies reporting larger context-dependent memory effects for non-associative (shallow) than associative (deep) processing of study material, which is taken as evidence that shallow encoding leads to strong encoding of contextual information, whereas deep encoding favors item-specific encoding (see Smith and Vela 2001). Therefore we prefer the view that the subsequent memory effect in the theta frequency band reflects stronger binding of an item to its context. Arguably, such an interpretation may conflict with previous work showing that, at test, deep encoding leads to stronger recollection of specific details from the study episode (Rugg et al. 1998). Obviously, further work is needed to examine to what extent the present strategy-dependent effects during encoding are related to specific memory processes operating during the final recognition test.

The fact that no subsequent memory effect in the theta frequency range was evident in the deep study group seems to be contradictory to the study by Klimesch et al. (1996a), who also employed an incidental deep learning task (animacy/inanimacy judgments). There are several differences between the present and this prior study which could be responsible for the difference in results. For example Klimesch et al. (1996a) used a free recall test, whereas in our study a recognition test was conducted. Another difference is that the subjects in our study performed a distracter task between encoding and test, whereas no distracter task was carried out in the Klimesch et al. study. Thus, a possible explanation of the Klimesch et al. findings might be that subjects recalled the words which were shown last in the learning phase and which were still active in working memory particularly well (recency effect; see Anderson 1995). This could lead to increased theta power for recalled words, because theta power increases with increasing word position in a list (Sederberg et al. 2006).

Alpha ERD and its Relation to Deep and Shallow Encoding

Concerning the results in the alpha frequency band, a mixed picture arises. In the middle time window (500–1000 ms) a clear dissociation between the 2 encoding groups was evident, where a SME was found in the deep study group only. This result suggests that semantic encoding processes are not only reflected in the beta frequency band, but are also reflected in the alpha frequency band. Such an interpretation would be compatible with the findings by Klimesch (1999) who related alpha power decreases to semantic memory processes.

In contrast, in the later time window (1000–1500 ms), a SME in the alpha frequency band was also evident in the shallow study group, which first of all speaks against a relation between alpha power decrease and semantic encoding. In the shallow encoding task, the subjects were instructed to judge whether a word's first and last letters were in alphabetical order. In some occasions, the subjects may have finished this task well before 1500 ms and may have focused on processing of the word meaning thereafter. Thus, the late SME in the alpha frequency band could reflect some delayed engagement of semantic encoding processes in the shallow study group (i.e., after execution of the alphabetical task).

Notice, however, that such delayed semantic processing was not found in the beta frequency band, suggesting that semantic

processing in the alpha and beta frequency band are not perfectly identical.

Gamma ERS

Consistent with other prior studies later remembered items showed higher gamma power than later missed items (Sederberg et al. 2003, 2007; Gruber et al. 2004; Osipova et al. 2006). This subsequent memory effect, observed over posterior electrode sites, was evident in the higher frequency ranges (>55 Hz) which is in line with the findings by Sederberg et al. (2007) and Osipova et al. (2006). A SME in the gamma frequency range was obtained for the deep encoding group only, which complements the findings by Gruber et al. (2004) who also employed a semantic encoding task. Another parallel to the Gruber et al. (2004) study is the early time window in which the SME in the gamma band was evident (~250 ms). Increased gamma activity in visual processing areas has been implicated to be a critical mechanism subserving the binding of several visual features into a unique object presentation (Tallon-Baudry and Bertrand 1999). Thus, the increased gamma activity could reflect the stronger activation of sensory networks during encoding which would increase the chance of an item being later remembered. However, no significant difference in gamma SME was found between the deep and the shallow encoding group, showing that the gamma SME did not clearly dissociate between the 2 encoding instructions (Fig. 4g).

This null result suggests 2 possible interpretations. Either, the deep study group indeed showed a stronger gamma SME than the shallow study group, whereby the difference did not emerge due to a lack of statistical power; or a gamma SME effect was present in the shallow encoding group as well, but did not cross the statistical threshold. Further work is needed to clarify this issue.

Conclusions

Several prior studies investigated the oscillatory correlates of the subsequent memory effect, with most of them using intentional learning. Thereby, nearly every frequency band between 4 and 70 Hz has been shown to indicate successful episodic memory encoding. By manipulating encoding strategy in an incidental learning task, this study provides first evidence that the subsequent memory effects in these frequency bands can be dissociated into semantic and nonsemantic effects. Whereas the semantic subsequent memory effects were specifically related to a power decrease in the beta frequency band, the nonsemantic subsequent memory effects were specifically related to a power increase in the theta frequency band. In the alpha frequency band, a power decrease in the middle time window (500–1000 ms), but not in the later time window (1000–1500 ms), was specifically related to semantic encoding. Thus, power differences mainly in the theta and beta frequency band, and partly within the alpha frequency band, distinguish between semantic and nonsemantic encoding of episodic material.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

Notes

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References

- Anderson JR. 1995. Learning and memory. New York: John Wiley.
- Bastiaansen MCM, van der Linden M, ter Keurs M, Dijkstra T, Hagoort P. 2005. Theta responses are involved in lexical-semantic retrieval during language processing. *J Cogn Neurosci*. 17:530–541.
- Bäuml KH, Hanslmayr S, Pastötter B, Klimesch W. 2008. Oscillatory correlates of intentional updating in episodic memory. *Neuroimage*. 41:596–604.
- Blair RC, Karniski W. 1993. An alternative method for significance testing of waveform difference potentials. *Psychophysiology*. 30:518–524.
- Brewer JB, Zhao Z, Desmond JE, Glover GH, Gabrieli JDE. 1998. Making memories: brain activity that predicts how well visual experience will be remembered. *Science*. 281:1185–1187.
- Caplan JB, Glaholt MG. 2007. The roles of EEG oscillations in learning relational information. *Neuroimage*. 38:604–616.
- Coltheart M. 1981. The MRC psycholinguistic database. *Q J Exp Psychol*. 33A:497–505.
- Craik FIM, Lockhart RS. 1972. Levels of processing: a framework of memory research. *J Verb Learn Behav*. 11:671–684.
- Craik FIM, Tulving E. 1975. Depth of processing and the retention of words in episodic memory. *J Exp Psychol Gen*. 104:268–294.
- Fries P. 2005. A mechanism for cognitive dynamics: neural communication through neuronal coherence. *Trends Cogn Sci*. 9:474–480.
- Gruber T, Tsivilis D, Montaldi D, Müller M. 2004. Induced gamma band responses: an early marker of memory encoding and retrieval. *Neuroreport*. 15:1837–1841.
- Hanslmayr S, Aslan A, Staudigl T, Klimesch W, Herrmann CS, Bäuml KH. 2007. Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage*. 37:1465–1473.
- Hanslmayr S, Pastötter B, Bäuml KH, Gruber S, Wimber M, Klimesch W. 2008. The electrophysiological dynamics of interference during the Stroop task. *J Cogn Neurosci*. 20:215–225.
- Hasselmo ME. 2005. What is the function of hippocampal theta rhythm?—Linking behavioral data to phasic properties of field potential and unit recording data. *Hippocampus*. 15:936–949.
- Hyman JM, Zilli EA, Amanda MP, Hasselmo ME. 2005. Medial prefrontal cortex cells show dynamic modulation with the hippocampal theta rhythm dependent on behavior. *Hippocampus*. 15:739–749.
- Ille N, Berg P, Scherg M. 2002. Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *J Clin Neurophysiol*. 19:113–124.
- Klimesch W. 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res Rev*. 29:169–195.
- Klimesch W, Doppelmayr M, Russegger H, Pachinger T. 1996. Theta band power in the human scalp EEG and the encoding of new information. *Neuroreport*. 7:1235–1240.
- Klimesch W, Doppelmayr M, Wimmer H, Gruber W, Röhm D, Schwaiger J, Hutzler F. 2001. Alpha and beta band power changes in normal and dyslexic children. *Clin Neurophysiol*. 112:1186–1195.
- Klimesch W, Schimke H, Doppelmayr M, Ripper B, Schwaiger J, Pfurtscheller G. 1996. Event-related desynchronization (ERD) and the DM effect: does alpha desynchronization during encoding predict later recall performance? *Int J Psychophysiol*. 24:47–60.
- Macmillan NA, Creelman CD. 2005. Detection theory: a user's guide. Mahwah (NJ): Erlbaum.
- Mickes L, Wixted JT, Wais PE. 2008. A direct test of the unequal variance signal detection model of recognition memory. *Psychon B Rev*. 14:858–865.

- Neuper C, Wörtz M, Pfurtscheller G. 2006. ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Prog Brain Res.* 159: 211-222.
- Osipova D, Takashima A, Oostenveld R, Fernandez G, Mariy E, Jensen O. 2006. Theta and gamma oscillations predict encoding and retrieval of declarative memory. *J Neurosci.* 26:7523-7531.
- Otten LJ, Henson RNA, Rugg MD. 2001. Depth of processing effects on neural correlates of memory encoding. *Brain.* 124:399-412.
- Otten LJ, Rugg MD. 2001a. Task-dependency of the neural correlates of episodic encoding as measured by fMRI. *Cereb Cortex.* 11: 1150-1160.
- Otten LJ, Rugg MD. 2001b. Electrophysiological correlates of memory encoding are task-dependent. *Cogn Brain Res.* 12:11-18.
- Paller KA, Kutas M, Mayes AR. 1987. Neural correlates of encoding in an incidental learning paradigm. *Electroencephalogr Clin Neurophysiol.* 67:360-371.
- Paller KA, Wagner AD. 2002. Observing the transformation of experience into memory. *Trends Cogn Sci.* 6:93-102.
- Pastötter B, Bäuml KH, Hanslmayr S. 2008. Oscillatory brain activity before and after an internal context change—evidence for a reset of encoding processes. *Neuroimage.* 43:173-181.
- Pfurtscheller G, Aranibar A. 1977. Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalogr Clin Neurophysiol.* 44:307-316.
- Rugg MD, Mark RE, Walla P, Schloerscheidt AM, Birch CS, Allan K. 1998. Dissociation of the neural correlates of implicit and explicit memory. *Nature.* 392:595-598.
- Sanquist TF, Rohrbaugh JW, Syndulko K, Lindsley DB. 1980. Electro-cortical signs of levels of processing: perceptual analysis and recognition memory. *Psychophysiology.* 17:568-576.
- Sarnthein J, Petsche H, Rappelsberger P, Shaw GL, von Stein A. 1998. Synchronization between prefrontal and posterior association cortex during human working memory. *Proc Natl Acad Sci USA.* 95:7092-7096.
- Sederberg PB, Gauthier LV, Terushkin V, Miller JF, Barnathan JA, Kahana MJ. 2006. Oscillatory correlates of the primacy effect in episodic memories. *Neuroimage.* 32:1422-1431.
- Sederberg RB, Kahana MJ, Howard MW, Donner EJ, Madsen JR. 2003. Theta and gamma oscillations during encoding predict subsequent recall. *J Neurosci.* 23:10809-10814.
- Sederberg PB, Schulze-Bonhage A, Madsen JR, Bromfield EB, McCarthy DC, Brandt A, Tully MS, Kahana MJ. 2007. Hippocampal and neocortical gamma oscillations predict memory formation in humans. *Cereb Cortex.* 17:1190-1196.
- Smith SM, Vela E. 2001. Environmental context-dependent memory: a review and meta-analysis. *Psychon B Rev.* 8:203-220.
- Spitzer B, Bäuml KH. 2007. Retrieval-induced forgetting in item recognition: evidence for a reduction in a general memory strength. *J Exp Psychol Learn.* 33:863-875.
- Spitzer B, Hanslmayr S, Opitz B, Mecklinger A, Bäuml KH. Forthcoming. Oscillatory correlates of retrieval-induced forgetting in recognition memory. *J Cogn Neurosci.*
- Summerfield C, Mangels JA. 2005. Coherent theta-band activity predicts item-context binding during encoding. *Neuroimage.* 24: 692-703.
- Summerfield C, Mangels JA. 2006. Dissociable neural mechanisms for encoding predictable and unpredictable events. *J Cogn Neurosci.* 18:1120-1132.
- Tallon-Baudry C, Bertrand O. 1999. Oscillatory gamma activity in humans and its role in object representation. *Trends Cogn Sci.* 3: 151-162.
- Tesche C, Karhu J. 2000. Theta oscillations index human hippocampal activation during a working memory task. *Proc Natl Acad Sci USA.* 97:919-924.
- Wagner AD, Schacter DL, Rotte M, Koutstaal W, Maril A, Dale AM, Rosen BR, Buckner R. 1998. Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. *Science.* 281:1188-1191.
- Weiss S, Rappelsberger P. 1996. EEG coherence within the 13-18 Hz band as a correlate of a distinct lexical organization of concrete and abstract nouns in humans. *Neurosci Lett.* 209:17-20.
- Weiss S, Rappelsberger P. 2000. Long-range EEG synchronization during word encoding correlates with successful memory performance. *Cogn Brain Res.* 9:299-312.
- Werkle-Bergner M, Müller V, Li SC, Lindenberger U. 2006. Cortical EEG correlates of successful memory encoding: implications for lifespan comparisons. *Neurosci Biobehav Rev.* 30:839-854.
- Yuval-Greenberg S, Tomer O, Keren AS, Nelken I, Deouell LY. 2008. Transient induced gamma-band response in EEG as a manifestation of miniature saccades. *Neuron.* 58:429-441.