Cerebral Cortex Advance Access published July 10, 2006

Cerebral Cortex
doi:10.1093/cercor/bhl030

Hippocampal and Neocortical Gamma Oscillations Predict Memory Formation in Humans

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Functional magnetic resonance imaging (fMRI) of the human brain has shown that the hippocampus and the left temporal and frontal cortices play a key role in the formation of new verbal memories. We recorded electrical activity from 2349 surgically implanted intracranial electrodes in epilepsy patients while they studied and later recalled lists of common words. Using these recordings, we demonstrate that gamma oscillations (44–64 Hz) in the hippocampus and the left temporal and frontal cortices predict successful encoding of new verbal memories. This increase in gamma oscillations was not seen in other frequency bands, whose activity generally decreased during successful memory formation. These findings identify a role for gamma oscillations in verbal memory formation with the hippocampus and the left temporal and frontal cortices, the same regions implicated using noninvasive fMRI recording methods.

Keywords: epilepsy, fMRI, free recall, gamma, iEEG, subsequent memory effect

Introduction

Human and animal lesion studies have demonstrated that the medial temporal lobe, and especially the hippocampus, is essential for episodic memory formation (Squire 1992; Eichenbaum 2000). Functional magnetic resonance imaging (fMRI), which can provide a noninvasive measure of blood flow within specific brain regions, has also yielded a wealth of knowledge concerning those brain regions that exhibit stronger activity during successful memory formation. fMRI studies have specifically implicated the hippocampus and 2 cortical regions, the left lateral and medial temporal cortices and the left inferior prefrontal cortex (LIPC), in the formation of new verbal memories. These regions exhibit increased blood flow during the encoding of words that are later recalled as compared with words that are not later recalled (Fernandez and others 1998; Wagner and others 1998; Kirchhoff and others 2000; Davachi and others 2001; Reber and others 2002; Strange and others 2002; Zubicaray and others 2005).

Although fMRI studies can effectively localize the regions that increase in activity during a particular cognitive process, they cannot characterize the underlying electrical activity generated by the neural networks in those regions. Multielectrode recordings, which are widely used in animal studies, can measure the electrical activity within small brain regions and thereby characterize how the neural assemblies in those regions react to changes in the animal's behavioral or cognitive state. Furthermore, implanted electrodes provide the only means to record electrical activity with high spatial and temporal specificity from deep structures, such as the hippocampus, which are not discernible by means of magnetoencephalogram or scalp electroencephalogram (EEG).

In humans, one can record intracranial electroencephalographic (iEEG) activity from arrays of surgically implanted electrodes in patients undergoing treatment for drug-resistant epilepsy. Previous analyses of iEEG recordings have revealed high-amplitude oscillations in human cortex at various frequencies and during a number of different behavioral states (Kahana and others 1999; Sederberg and others 2003; Tallon-Baudry and others 2005). In particular, gamma oscillations (28–64 Hz) have been theorized to play a crucial role in timing neural signals (Buzsàki and Draguhn 2004) and have been shown to be involved in both perceptual and memory processes (Rodriguez and others 1999; Fell and others 2001; Fries and others 2001; Sederberg and others 2003; Tallon-Baudry and others 2005).

Our goal was to characterize the electrophysiological activity of successful episodic memory formation and to relate human intracranial recordings to the noninvasive blood oxygen level–dependent (BOLD) signal measured using fMRI. We tested 39 patients with drug-resistant epilepsy who had arrays of subdural and/or depth electrodes surgically implanted for 1–2 weeks to localize the site or sites of seizure onset.

Subjects first studied lists of common nouns. Then, after solving arithmetic problems for ~18 s, subjects attempted to recall the nouns in any order (see Materials and Methods). To assess differences in brain oscillations between successful and unsuccessful memory formation, we compared oscillatory power during each word presentation for those words that were, and were not, subsequently recalled. This comparison was made separately at a series of logarithmically spaced frequencies between 2 and 64 Hz and at each of the 2349 electrodes recorded. A significant oscillatory "subsequent memory effect" (SME) (Paller and Wagner 2002) is said to occur when the comparison at a given frequency and for a given electrode exceeds a statistical criterion. This criterion was determined by using a permutation test to control for multiple comparisons while maintaining a fixed Type I error rate (see Materials and Methods). A positive SME indicates greater oscillatory power during the encoding of subsequently recalled words than during the encoding of nonrecalled words; a negative SME indicates lower oscillatory power during the encoding of subsequently recalled words.

Materials and Methods

Participants

We tested 39 patients (aged 8–53, 20 females) with drug-resistant epilepsy who had arrays of subdural and/or depth electrodes surgically

implanted for 1–2 weeks to localize the site or sites of seizure onset (See the Table of patient demographics in the Supplementary information). The clinical team determined the placement of these electrodes with the goal of localizing suspected epileptogenic foci and identifying functional regions to be avoided in surgery.

We excluded 4 patients because record review showed evidence of possible right or mixed language dominance (2 identified left-handed patients, 2 right language dominance on Wada), leaving us with 35 subjects contributing a total of 2349 electrodes (Table 1).

Behavioral Methods

Subjects studied lists of words for a delayed free-recall task. Lists were composed of 15 or 20 common nouns, chosen at random and without replacement from a pool of either English or German high-frequency nouns (http://memory.psych.upenn.edu/wordpools.php), depending on the subject's native language. Twenty-one subjects received 20-item lists, whereas the remaining 14 subjects received 15-item lists. Over the course of 1–4 sessions, subjects received between 9 and 60 study-test lists (the number of trials completed depended on the patient's interest and availability for testing). A computer controlled the stimulus presentations and recorded subjects' responses. At the start of each trial, a plus sign appeared at the center of the screen to alert subjects to the upcoming word presentation and to encourage them to fixate on the center of the screen. The plus sign appeared for 1600 ms, followed by an 800–1200 ms blank interstimulus interval (ISI). The computer then displayed each list item in capital letters for 1600 ms, followed by an 800–1200 ms blank ISI. This temporal jitter served to decorrelate the physiological responses from successive word presentations. To ensure that each word was attended to, we asked subjects to read each word aloud as soon as it appeared.

Immediately after each list presentation, subjects were given a series of simple arithmetic problems. Each problem took the form of $A + B + C = ?$, where A, B, and C were randomly chosen positive integers from the set 1–9. Subjects were asked to respond vocally as soon as they knew the answer, and the experimenter typed their answer into the keyboard. After subjects solved arithmetic problems for ~18 s, a row of asterisks, accompanied by a tone, signaled the start of the recall period. Subjects were given 45 s to recall list items in any order. Vocal responses, digitally recorded during the trial, were scored for analysis following each session (Sederberg and others 2003).

The iEEG Recordings

The iEEG signal was recorded from either subdural grids or depth electrodes. The signal was recorded by means of a Bio-Logic, XLTek, Neurofile, or Nicolet EEG system. Depending on the amplifier, the signals were sampled at 200, 256, 500, 512, or 1024 Hz and band-pass filtered between 0.3 and 70 Hz or between 0.1 and 100 Hz. Data were subsequently notch filtered with a Butterworth filter with zero phase distortion at 50 or 60 Hz to eliminate electrical line and equipment noise. Individual word presentation events were scanned for artifacts (e.g., spikes) and were discarded if the kurtosis of the amplitude distribution of the signal exceeded a threshold of 5 (Delorme and others 2006). Applying this method, we discarded 7.1 ± 0.6% of each subject's total word presentation events.

To synchronize the electrophysiological recordings with behavioral events, the experimental computer sent pulses through the parallel port via an optical isolator into an unused recording channel or digital input on the amplifier. The time stamps associated with these pulses aligned the experimental computer's clock with the iEEG clock to a precision well under the sampling interval of the iEEG recording (<4 ms). For all subjects, the locations of the electrodes were determined by means of coregistered postoperative computed tomography scans and preoperative magnetic resonance images (MRIs), or from postoperative MRIs, by an indirect stereotactic technique and converted into Talairach coordinates.

Our research protocol was approved by the appropriate institutional review boards at the University Clinic in Freiburg, Germany, Children's Hospital Boston, and Brigham and Women's Hospital in Boston. Informed consent was obtained from the subjects and their guardians.

Table 1
Total electrodes and number of subjects by hemisphere and lobe

	Left		Right	
	Number of electrodes	Number of subjects	Number of electrodes	Number of subjects
Hippocampal	91	15	60	12
Frontal	398	18	429	19
Temporal	548	25	492	23
Parietal	112	12	141	11
Occipital	28	8	50	7

Data Analysis

We used the Morlet wavelet transform (with wave number of 6) to compute the spectral power as a function of time for all our iEEG signals. Frequencies were sampled logarithmically at 41 intervals between 2 and 64 Hz. The wavelet power was calculated from –500 to 2000 ms around the onset of each presentation event, with an additional 1-s window on either side to avoid edge artifacts. The power was then Z-transformed with the mean and standard deviation of the signal during the orienting stimuli before all the lists as a baseline. A Wilcoxon rank sum test was then used to compare recalled items with items that were not recalled based on the mean of the Z-transformed wavelet power during either the early (0–1000 ms after presentation onset) or the late portion of the encoding period (1000–2000 ms after presentation onset). This comparison was made separately for each electrode and at each frequency.

We used a permutation procedure to generate an unbiased empirical estimate of the Type I error rate (Efron 1979; Sederberg and others 2003). First, we generated 1000 random samples of the experimental data by randomly swapping items designated as recalled and not recalled for each subject. Next, we performed the Wilcoxon rank sum test on the 1000 random shuffles of data.

To calculate the significance of the oscillatory SMEs aggregated across subjects for specific regions, we performed region of interest (ROI) analyses that combined the significance values for all electrodes in a region (Gibbons and Shanken 1987). First, cortical electrodes were categorized into Brodmann areas (BAs) by means of the Talairach Daemon (Lancaster and others 2000). For a region to exhibit an aggregate effect across subjects, we required that at least 5 subjects contribute electrodes to that region. We next applied the inverse normal transformation (Z-score) to both the P values obtained by comparing recalled and not-recalled items and the distribution of the P values from the permutation test. This was done at each frequency and for each electrode in a region. To ensure that each subject contributed equally to the aggregate significance value, we calculated the mean of the within-subject Z-scores and then summed the mean Z-scores across subjects, thus producing a summed Z-score and an empirically determined random distribution of summed Z-scores of what would have been expected by chance in that region. The point at which the summed Z-score for a particular region and frequency fell in the distribution of random summed Z-scores determined the P value for the probability of there being a significant oscillatory SME across subjects. To visualize the results of the ROI analysis, we overlaid the BAs defined by the Talairach Daemon on the standard Montreal Neurological Institute brain by using information in the WFU PickAtlas toolbox (Maldjian and others 2003).

We calculated time–frequency significance spectrograms for all electrodes in a given region according to the methods described above, with the following exceptions. All data were first down sampled to 128 Hz, and 100 random permutations were performed at each time point and frequency from 0 to 2000 ms poststimulus. Thus, we could aggregate across all electrodes in a specific region, calculating a P value at each point in time and each frequency for the significance and direction of the power difference between recalled and not-recalled items.

Results

Subjects who received 15-item lists recalled an average of 28.80%(standard error [SE] = 3.23) of the words per list, whereas those receiving 20-item lists recalled 19.85%(SE = 1.40) in each list. Both groups exhibited a small primacy effect, whereas the end-of-list distractor served to reduce any recency effects (see

Supplementary information). Results from both groups were combined for all subsequent analyses.

Across all 2349 electrodes and both the early and late time bins, recordings from 833 electrodes exhibited positive SMEs, whereas recordings from 1226 electrodes exhibited negative SMEs ($P < 0.05$, see Materials and Methods). Of the positive SMEs, 320 appeared in the gamma frequency band (see Fig. 1*A*,*C*,*E*), whereas negative SMEs often appeared as broadband effects at a range of frequencies, sometimes in conjunction with a positive gamma SME (Fig. 1*B*,*D*,*F*).

Because the large sample of electrodes provided widespread coverage of most brain regions (Table 1), we were able to aggregate data across both subjects and electrodes to determine if there was a statistically significant effect within a given brain region. Given the relatively small number of electrodes within the left and right hippocampus (151 from 18 subjects), we combined the electrodes from both the left and right hemispheres. We thus analyzed between-subject statistics on electrodes recording from brain regions defined by BAs for the cortical regions or from the hippocampal area as determined by the clinical team (see Materials and Methods) for 5 distinct frequency bands: 4–8 Hz (theta), 10–14 Hz (alpha), 16–26 Hz (beta), 28–42 Hz (low gamma), and 44–64 Hz (high gamma).

These analyses revealed similar patterns of oscillatory SMEs for the early and late encoding intervals (Table 2 and Fig. 2, left and right). In the 0 to 1-s encoding interval, we found positive gamma SMEs in the hippocampus, LIPC (BA47), left inferior temporal lobe (BA20), and right occipital lobe (BA19). In addition to the high-frequency positive SMEs, we found a positive theta/alpha SME in the left superior frontal lobe (BA8). The positive gamma SMEs in the hippocampus and LIPC remained during the 1 to 2-s encoding intervals, whereas

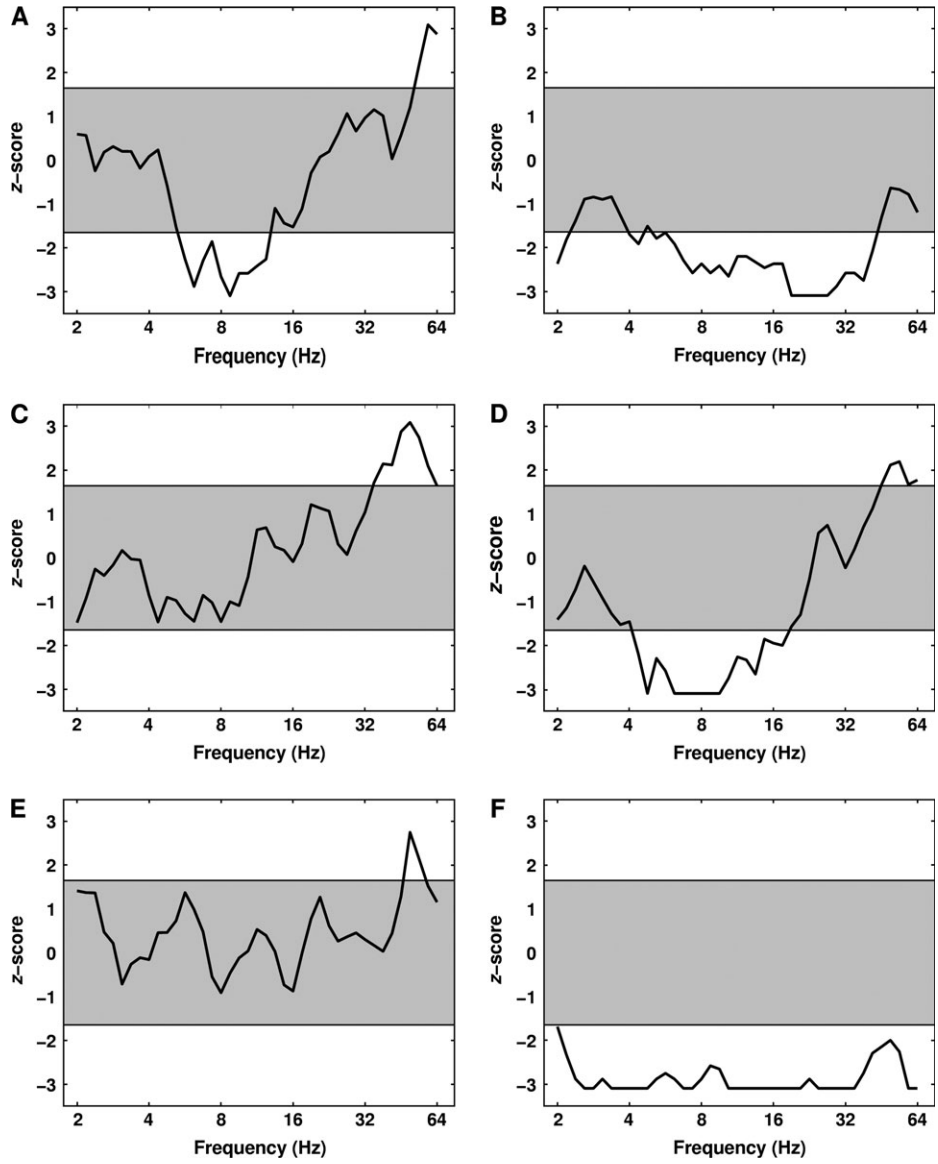

Figure 1. Example electrodes exhibiting oscillatory SMEs. Each panel shows the *Z*-transformed significance value of the difference in power between recalled and not-recalled words across frequencies from 2 to 64 Hz for the 1 to 2-s time bin. The sign indicates the direction of the effect, and the gray area indicates the $P > 0.05$ significance threshold. (*A*, *C*, and *E*) Data from electrodes in the hippocampus, LIPC (BA47), and the left temporal lobe (BA21), respectively, exhibiting significant positive gamma SMEs. (*B*, *D*, and *F*) Results from hippocampal, LIPC, and left temporal lobe electrodes illustrating broadband negative SMEs. Electrodes are from 5 different patients (Talairach coordinates: [23,–27,–9], [–27,–27,10], [–42,41,–5], [–47,18,–1], [–50,–25,0], [–59,–13,–6]).

positive gamma SMEs emerged in the left lateral temporal lobe (BA21), and the left occipital lobe (BA19). We also observed late positive SMEs in the beta and high-gamma bands in the right inferior frontal lobe (BA11). Our findings of positive gamma SMEs during the 2 encoding intervals contrasts with the broadband negative SME observed across frequencies in the theta, alpha, and beta frequency bands in the hippocampus and the left and right lateral temporal lobes. We also observed negative oscillatory SMEs in frontal theta frequency bands (BAs 9, 10, 45, 46).

One can further harness the temporal precision of iEEG to characterize the time course of the SMEs revealed by the region analysis. With the exception of the left frontal lobe (BA8), SMEs from all regions showed increased gamma oscillations coupled with an overall decrease in broadband oscillatory power for successfully as opposed to unsuccessfully encoded words (Fig. 3). Hippocampal gamma appeared to increase for successfully encoded words both between 500 and 1000 ms following stimulus presentation and, later in encoding, between 1500 and 2000 ms following stimulus presentation (Fig. 3*A*). Gamma activity appeared to increase throughout the encoding interval in the LIPC (Fig. 3*B*) and late in encoding in the left lateral temporal lobe (BA21, Fig. 3*C*) for subsequently recalled words relative to unsuccessfully recalled words. Unlike the other regions exhibiting SMEs, the left frontal lobe exhibited increased theta and alpha oscillations that began just after stimulus onset and remained significant until 1000 ms for successfully encoded words (BA8, Fig. 3*D*). Because a relatively small number of our subjects had electrodes simultaneously recording from the hippocampus, LIPC, and left temporal lobe,

Table 2
Frequency bands exhibiting significant increases or decreases in hippocampal oscillations that predicted successful memory formation

	0–1 s		1–2 s	
	Positive SME	Negative SME	Positive SME	Negative SME
4–8 Hz	—	0.001	—	0.001
10–14 Hz	—	0.001	—	0.001
16–26 Hz	—	0.001	—	0.001
28–42 Hz	—	0.003	—	0.049
44–64 Hz	0.006	—	0.001	—

Note: Table cells contain the *P* value for each significant comparison.

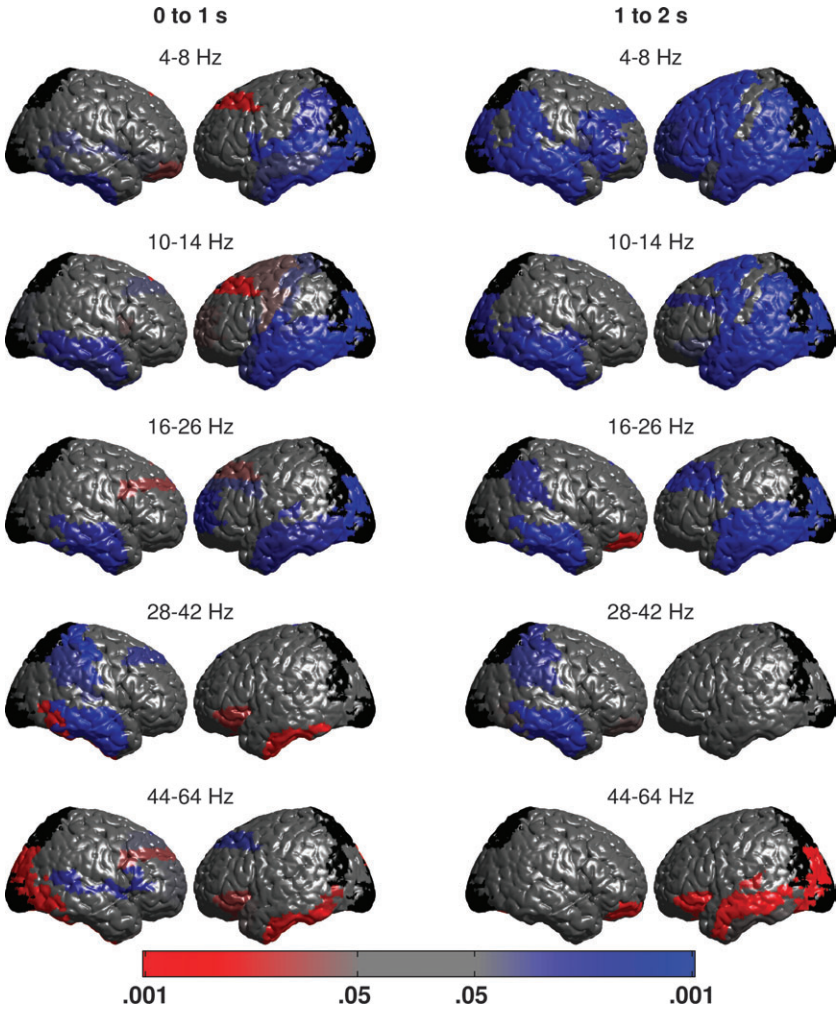

Figure 2. Cortical regions defined by BAs exhibiting across-subject differences between successful and unsuccessful encoding for the 0 to 1-s (left) and the 1 to 2-s (right) time bins. The color indicates the direction of the effect (red = positive, blue = negative), and the intensity of the color indicates the significance from $P < 0.05$ to $P < 0.001$. Gray areas denote regions that did not exhibit a significant effect across subjects. Regions containing electrodes from fewer than 5 subjects are shown in black. Each row corresponds to a different frequency band: 4–8 Hz (theta), 10–14 Hz (alpha), 16–26 Hz (beta), 28–42 Hz (low gamma), and 44–64 Hz (high gamma).

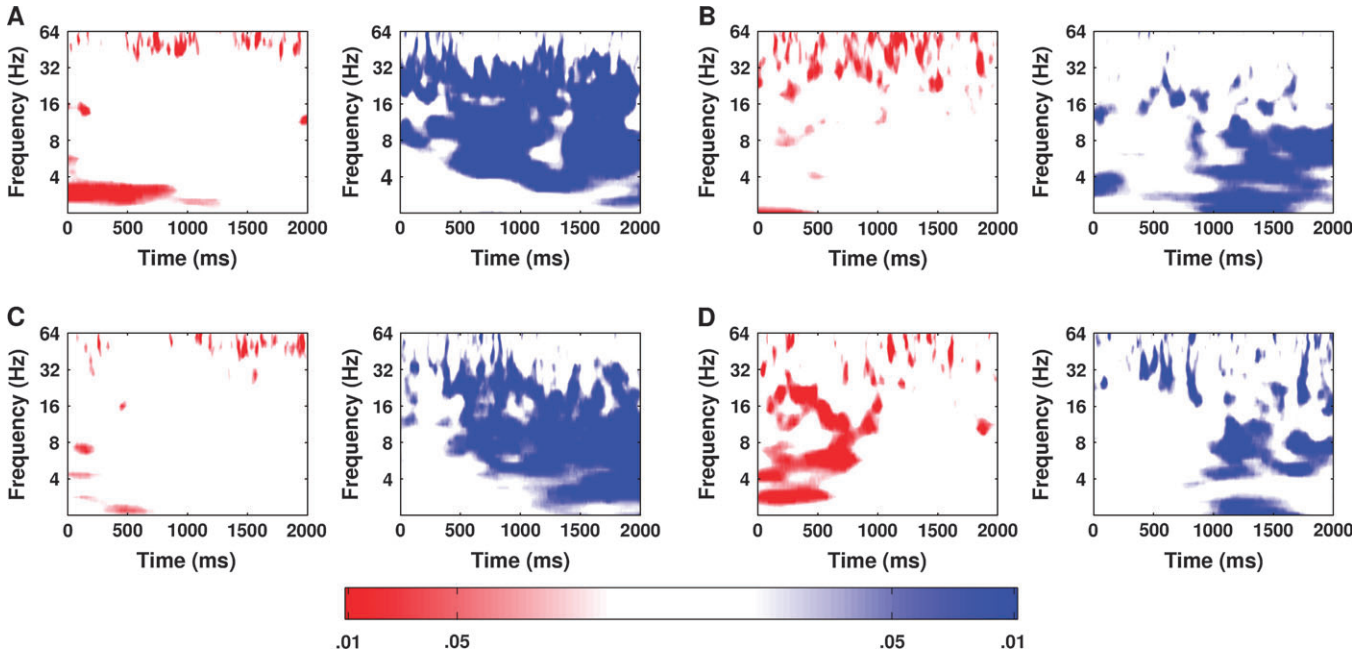

Figure 3. Time course of significant oscillatory activity for the hippocampus, LIPC, and the left temporal lobe. Each time course shows the significant increases (left column) or decreases (right column) in power for successful when compared with unsuccessful encoding at times ranging from 0 to 2000 ms and frequencies ranging from 2 to 64 Hz. The color indicates the direction of the effect (red = positive, blue = negative), and the intensity of the color indicates the significance. In the hippocampus, gamma oscillations increase early and late, whereas broadband power decreases during successful versus unsuccessful encoding (*A*). (*B*) The LIPC (BA47) exhibits heightened gamma oscillations throughout the encoding period and decreased broadband oscillatory power late in encoding of subsequently recalled items as compared with nonrecalled items. (*C*) Gamma oscillations in the left temporal lobe (BA21) ramp up late, whereas broadband power decreases, during encoding of subsequently recalled items. (*D*) Theta and alpha oscillations in the left frontal eye fields (BA8) increase for subsequently recalled relative to not-recalled items.

it is difficult to statistically quantify the differences between the timing profiles in these regions.

Discussion

Recording from 2349 electrodes across widespread cortical and hippocampal sites, we demonstrated that gamma oscillations in the hippocampus, left temporal lobe, and the LIPC increased during the encoding of words that were subsequently recalled.

The anatomical localization of the principal positive gamma SMEs to the hippocampus, LIPC, and left lateral temporal regions mirrors the anatomical localization of the strongest positive SMEs observed in fMRI studies (Fernandez and others 1998; Wagner and others 1998; Kirchhoff and others 2000; Davachi and others 2001; Otten and others 2001; Reber and others 2002; Strange and others 2002; Zubicaray and others 2005). This correspondence between gamma and the fMRI BOLD response during a complex behavioral task in humans builds on recent findings of a strong correlation between gamma oscillations in cortical local field potentials and fMRI BOLD signals recorded during visual perception in monkeys (Logothetis and others 2001) and cats (Niessing and others 2005) and auditory perception in humans (Mukamel and others 2005). Whereas an increase in gamma may be interpreted as an increase in synchronous activity (representing either functional connectivity between other regions and the recorded region or activity within the region [Logothetis and others 2001]), one possible interpretation of an increase in power that encompasses a wide range of frequencies is that it indicates asynchronous activity and thus inactivation or the nonparticipation of that region.

The increased gamma oscillations during successful encoding could be expected to accompany a relative increase in BOLD signal; and the broadband increase in power during unsuccessful encoding, centering in the alpha band, could be expected to accompany a decreased BOLD signal (Daselaar and others 2004; Mukamel and others 2005). Increases in alpha power, in particular, have been correlated with decreases in simultaneously recorded fMRI BOLD signals in widespread brain regions (Goldman and others 2002; Laufs and others 2003) and with decreased memory performance (Klimesch and others 1997; Klimesch 1999). Consequently, our finding of heightened gamma activity in the LIPC throughout the encoding interval for subsequently recalled words (Fig. 3*B*) suggests why fMRI studies have found such strong SMEs in this region (Wagner and others 1998; Reber and others 2002).

The overlap with previous fMRI results and the distinct time courses of the gamma SMEs suggest 2 different psychological mechanisms underlying successful memory formation. In a subsequent memory paradigm with directed forgetting, Reber and others (2002) found increased BOLD activity in the LIPC that correlated with the intention to encode, whereas they found that increased activity in the medial temporal lobe correlated with actual encoding success. Consequently, increased gamma activity in the LIPC, which began at stimulus onset and lasted throughout the encoding interval, may be related to increased attention (Tallon-Baudry and others 2005), whereas increased gamma in the hippocampus may be more directly related to episodic encoding processes. The significant increases in hippocampal gamma that differentiated successful from unsuccessful encoding began 500 ms following stimulus onset, further supporting the idea that the hippocampal activity relates to encoding processes that are distinct from the initial sensory processing of an item (Fig. 3*A*). Consistent with the hypothesized recruitment of left lateral temporal regions during

semantic processing of words (Kirchhoff and others 2000), which would be expected to occur following the initial sensory processing and vocalization of each word presentation, left temporal gamma ramped up in the latter half of the encoding interval for subsequently recalled words (Fig. 3*C*). This semantic processing may drive further encoding, which is reflected by the increase in hippocampal gamma oscillations 1500 ms after the word presentation (Fig. 3*A*). Thus, the first mechanism reflects the modulation of general attention throughout the encoding period, wherein heightened gamma activity indicates enhanced attentional processing (Reber and others 2002; Tallon-Baudry and others 2005). The second mechanism is related to associative encoding and occurs after the initial processing of an item. This associative mechanism that underlies episodic encoding links attributes of the just-presented item with attributes of neighboring and semantically similar list items (Kahana 1996; Howard and Kahana 2002).

The present study distinguishes itself from previous studies of intracranial oscillations and memory formation in a number of ways. Although Fell and others (2001) reported a negative gamma SME in the hippocampus, they restricted their analyses to oscillations below 48 Hz, defining gamma as the 32–48 Hz range. Consistent with their report, we also found a negative gamma SME in the hippocampus for the 28–42 Hz lower gamma range and only found a positive SME in the high-gamma range from 44 to 64 Hz (see Table 2).

In a previous study including 10 of the 35 subjects reported here, we examined encoding-related iEEG activity at individual electrodes and found electrodes exhibiting both theta and gamma positive SMEs (Sederberg and others 2003). As in the current manuscript, there were also a large number of electrodes exhibiting broadband negative SMEs. Given the extensive electrode coverage afforded by 35 subjects, the analysis method employed in the current manuscript sought to reveal the oscillatory correlates of successful memory formation across subjects, instead of reporting individual electrodes. Consequently, in any given region and frequency band, only the dominant effect across subjects emerged. At lower frequencies (theta and alpha bands), we tended to see negative SMEs. The one region that exhibited a positive low-frequency SME was the left frontal eye fields (BA8, Fig. 3*D*), which may indicate directed attention to the just-presented word (Kanwisher and Wojciulik 2000). At higher frequencies, significant SMEs tended to be positive, most notably in the gamma band.

Consistent with functional magnetic resonance imaging (fMRI) studies that implicate the hippocampus and the left temporal and frontal cortices in successful memory formation (Fernandez and others 1998; Wagner and others 1998; Kirchhoff and others 2000; Davachi and others 2001; Reber and others 2002; Strange and others 2002; Zubicaray and others 2005), we showed that gamma activity increased during encoding of later recalled words in these regions. These findings demonstrate a role for gamma oscillations in memory formation and provide a critical link between the hemodynamic response, measured using fMRI, and electrophysiological signals measured directly in the human brain.

Supplementary Material

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

Notes

We thank E. Dolan and R. Aschenbrenner-Scheibe for data collection, as well as P. Johnsen, M. Van Vugt, J. Jacobs, S. Polyn, R. Epstein, and M. Howard for helpful comments on the manuscript. This research was supported by grants from the Swartz Foundation, the National Institutes of Health (MH061975, MH062196, and MH072138), and the National Science Foundation (SBE0354378). *Conflict of Interest*: None declared.

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