Rhinal-Hippocampal Information Flow Reverses Between Memory Encoding and Retrieval

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Abstract. The medial temporal lobe is crucial for the encoding and retrieval of episodic long-term memories. It is widely assumed that memory encoding is associated with information transfer from sensory regions via the rhinal cortex into the hippocampus. Retrieval of information should then be associated with transfer in the reverse direction. However, experimental evidence for this mechanism is still lacking. Here, we show in human intracranial EEG data during two independent recognition memory paradigms that rhinal-hippocampal information flow significantly changes its directionality from encoding to retrieval. Using a novel phase-based method to analyze directional coupling of oscillations, coupling values were more positive (i.e., from rhinal cortex to the hippocampus) during encoding as compared to retrieval. These effects were observed in the delta (1–3 Hz) range where rhinal-hippocampal post-stimulus phase synchronization increased most robustly across both experiments.

Keywords: Directional coupling · Long-term memory · Intracranial EEG · Medial temporal lobe · Hippocampus · Rhinal cortex

1 Introduction

Processes within the human medial temporal lobe are crucial for episodic long-term memory [1–3]. It is assumed that encoding of new events depends on information flow from sensory cortices via peri- and entorhinal cortex (here together referred to as rhinal cortex, RC) to the hippocampus (HC), which supports the rapid formation of novel memory traces. Retrieval of these events after a short time period should be associated with information flow in the reverse direction [4, 5]. To our knowledge, no previous study has tested this prediction, possibly due to methodological challenges: First, recording neural activity from medial temporal brain structures is difficult in humans and ideally requires intracranial EEG electrodes, which are only implanted in specific populations of pharmacorefractory epilepsy patients. Second, EEG activity is characterized by oscillatory networks [6, 7], but investigating directional interactions between oscillators is a methodologically complex issue [8].

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Here, we report results from two intracranial EEG experiments in which time-resolved analyses of directional coupling were performed in order to characterize the flow of information between RC and HC during memory encoding and retrieval. EEG was recorded via medial temporal depth electrodes in epilepsy patients undergoing presurgical evaluation. In both experiments, a large number of trial-unique pictures either with complex landscapes and houses (experiment 1; n = 11 patients), or with cut-out depictions of faces and houses (experiment 2; n = 7 patients), was presented for encoding and had to be recognized again among a smaller number of lures during retrieval (Fig. 1). To investigate directional information flow, we first identified the frequency band which in both experiments and during both, encoding and retrieval, consistently showed task-related changes in RC-HC phase synchronization (i.e., increases in phase synchronization after a stimulus is presented as compared to baseline). Then, we estimated directional RC-HC coupling within this frequency band with a phase-based method particularly well suited to capture oscillatory EEG dynamics [9, 10]. Finally, directional coupling values for the encoding and the retrieval phase were compared with non-parametric label permutation tests [11]. Because RC-HC

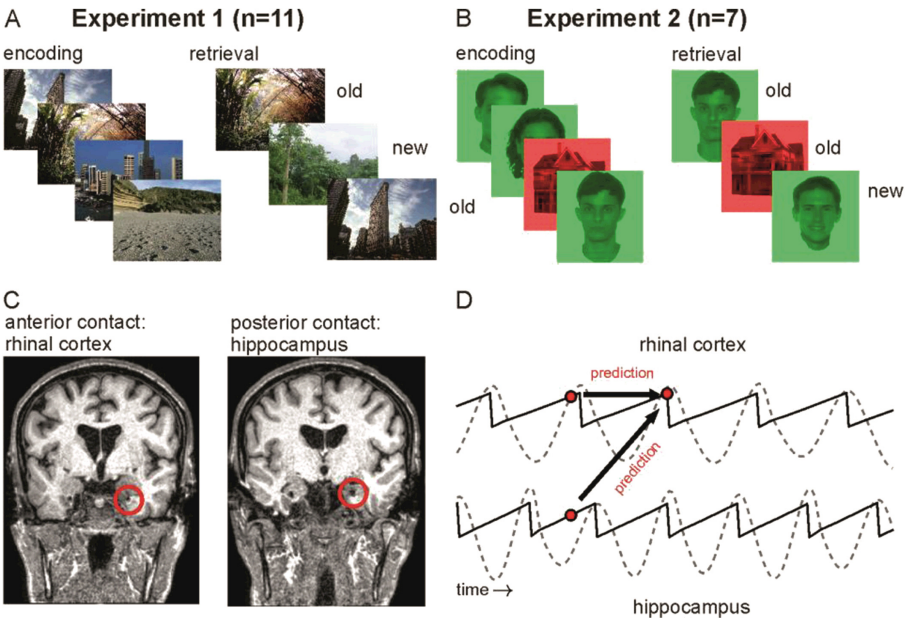

Fig. 1. Analysis of directional coupling during memory encoding and retrieval. (A) In the first experiment (n = 11), recognition memory was tested for complex landscapes and buildings. **(B)** In the second experiment (n = 7), participants encoded pictures of faces and houses, and memory was afterwards inquired in a recognition test. **(C)** Post-implantation MRI from one patient showing one intracranial EEG electrode contact in the rhinal cortex (left) and in the hippocampus (right). **(D)** Directional coupling between rhinal cortex and hippocampus was analyzed based on phase dynamics of delta (1–3 Hz) oscillations in the two regions. In principle, the influence of activity in one region on activity in the other region was quantified by the improvement of prediction of activity in region *A* at time *t* by knowledge of activity in region *B* at time $t\text{-}\tau$.

information transfer is thought to depend on the output of early rhinal memory operations [12], we furthermore evaluated the temporal dependency between directional coupling effects and the rhinal N400 component.

2 Methods

2.1 Participants and Experimental Design

Both experiments were performed by patients with pharmaco-refractory temporal lobe epilepsy undergoing invasive presurgical investigation. The first experiment (involving memory encoding and recognition of landscapes and buildings) was conducted by 11 patients (39.4 ± 10.1 years), the second experiment (involving encoding and recognition of houses and faces) by 7 patients (35.3 ± 13.2 years). Previous analyses of these experiments have been published before (first experiment: [13]; second experiment: [14]), and details about the paradigms can be found in these papers.

In brief, in the first experiment (Fig. 1A), we presented complex pictures of landscapes and buildings in four separate learning sessions, which took place on two different days (two on each day). In each learning session, 80 pictures were presented (presentation time 1200 ms, inter-trial interval 1800 ± 200 ms), and subjects had to indicate whether they were presented a landscape (half of the items) or a building. On one day, the first learning session was followed by an afternoon "nap" of around 60 min duration, while subjects did not take a nap on the other day. The second learning session followed 15 min after the nap (or around 90 min after the first learning session on the day without nap) and contained 80 new pictures on each day. During the subsequent retrieval phase, which followed the second learning session after an interval of 15 min, subjects were shown the 160 items presented before on that day, randomly intermixed with 80 new items, and were asked to indicate via button-press whether they remembered each item or not (presentation time 1200 ms, inter-trial interval 2000 ms ± 200 ms).

The second experiment (Fig. 1B) consisted of several (between 2 and 8, depending on the participant's availability) consecutive blocks, each of which contained a familiarization phase, an encoding phase, and a retrieval phase. During the familiarization phase, four stimuli which afterwards served as "repeats" (see below) were presented four times each in random order. These data were not analyzed here. During the encoding phase, 112 pictures from three different classes were presented (presentation time 2500 ms, inter-trial interval 1500 ms), and subjects had to rate their pleasantness by either pressing the left mouse button or the right mouse button. Items from class one (80/112 items, "expected") consisted of trial-unique pictures of a house or a face, presented on a green or a red background. In each block, all expected items showed either faces or houses, and had either red or a green background, and this changed throughout the blocks. Items from class two (16/112 items, "unexpected") showed trial-unique pictures from the other category and with the other background color. Finally, items from class three (16/112 items, "repeats") consisted of the four pictures shown during the familiarization phase, which had the same category and background color as the expected items (but were not trial-unique). During retrieval, we presented 72 test items (presentation time 5000 ms, inter-trial interval 1500 ms). Thirty-two of them were

old items shown on "expected" trials, 16 were new items from the same category and background color as in the expected trials, 16 were old items shown on "unexpected" trials, and 8 were novel items from the same category and background color as the unexpected trials. On each trial, subjects indicated on a four-point scale whether they believed an item had been presented before ("sure old", "unsure old", "unsure new", "sure new"). Notably, in our previous paper [14], we compared EEG activity during presentation of expected and unexpected items in the encoding phase; in the current analysis, we focused on "expected" items during both encoding and retrieval.

2.2 Recordings

The location of electrode contacts was ascertained by MRI in each patient (see Fig. 1C for a typical example). Electrodes (AD-Tech, Racine, WI, USA) had 10 cylindrical platinum-iridium contacts and a diameter of 1.3 mm. All recordings were performed using a Schwarzer recording system (Schwarzer GmbH, Munich, Germany). The EEG data were referenced to linked mastoids, recorded at a sampling rate of 1000 Hz, and band-pass filtered (0.01 Hz [6 dB/octave] to 300 Hz [12 dB/octave]). EEG trials were visually inspected for artifacts (e.g., epileptiform spikes), and trials with artifacts were excluded from further analysis. Group statistical analyses were performed by analyzing data from one rhinal and one hippocampal contact in each patient. All recordings were taken from the nonepileptic hemisphere (i.e., contralateral to the epileptogenic focus), to minimize the possibility of artifact contamination. In each patient, we selected one rhinal and one hippocampal contact based on the following criteria: (1) anatomical localization in post-implantation MRI scans; (2) low contamination by electrical and epileptiform artifacts; (3) high overall t-value within the analyzed epochs (averaged across all conditions and then compared to baseline), indicating relatively consistent responses across trials. Recordings were performed at the Department of Epileptology, University of Bonn, Germany. The studies were approved by the local ethics committee, and all patients gave written informed consent.

2.3 Analysis of Phase Synchronization

Phase synchronization was quantified based on calculating circular variance [15]. To avoid edge effects, data were demeaned before phase estimation and the borders of the time windows were cut off afterwards (keeping the central 1200 out of 4096 data points). For the analysis of synchronization strength, we used wavelet transformation (Morlet wavelet) to derive phases for 23 different center frequencies (logarithmically scaled). The synchronization values were averaged across a baseline interval from −200 ms to 0 ms, as well as across a poststimulus interval from 0 to 1000 ms.

2.4 Analysis of Directional Coupling

The time-resolved measure used here is an extended variant of the directional coupling measure proposed by Rosenblum and Pikovsky [9], which is based on the concept of phase synchronization. This time-resolved directional coupling measure has been

described in detail previously ([10]; see Fig. 1D). Phase values were estimated using a combination of a band-pass filter (1st order forward/backward Butterworth filter) and a subsequent Hilbert transformation. It was shown that this transformation is equivalent to the usage of the wavelet transformation applied above [16]. In the following, the phases of two systems (1,2) – in our case: EEG recordings from rhinal cortex and hippocampus – are denoted as $\Phi_{1,2}(t_j^r)$. With j = 1,…,n as a time index related to an arbitrary time point (e.g. an external cue) of an ensemble of realizations r = 1,…,m. We modeled the slope of the phase of one system as a function of the phases of both systems. For example, the phase dynamics of system 1 were quantified by the phase slope of system 1 between two time points with a time delay τ,

$$\Delta\phi_1(t_j^r) = \phi_1(t_{j+\tau}^r) - \phi_1(t_j^r)$$

These phase dynamics were modeled by two-dimensional Fourier series

$$\Delta\phi_1 \approx \sum_{k,l} a_j^{k,l} \exp(i[k\phi_1(t_j^r) + l\phi_2(t_j^r)])$$

with k, l denoting the order of the Fourier terms, by approximating the Fourier coefficients $a^{k,l}_j$ in a least-square sense over the m realizations. In this model, the phase dynamic of system 1 depends on previous phase states of system 1 and system 2. Following Rosenblum and Pikovsky [9], we used fixed combinations of orders k, l and a fixed value of τ, corresponding to the average length of one oscillatory cycle. The influence from system 2 onto system 1 was calculated via

$$c_j^2(1|2) = 1/(a_j^{0,0})^2 \sum_{k,l} (a_j^{k,l})^2$$

With $l \neq 0$, as described previously [17]. With the analogously calculated influence of system 1 onto system 2, the time-resolved directional interaction follows as

$$D_j(1,2) = c_j(2|1) - c_j(1|2)$$

Therefore $D_j > 0$ reflects a predominant influence of system 1 onto system 2, $D_j < 0$ a predominant influence of system 2 onto 1, while $D_j \approx 0$ corresponds to a bidirectional or no influence between the systems.

The calculation of directional coupling requires large numbers of trials, which need to be equal across conditions [10]. Therefore, we cumulated all encoding trials from the two subsequent days in experiment 1, and compared these to an equal number of randomly drawn retrieval trials. In experiment 2, the minority of trials which differed in terms of background color and picture category (“unexpected items”) were excluded from further analysis, and again an equal number of encoding and retrieval trials was selected. All statistical results were corrected on the cluster level for multiple comparisons using a nonparametric permutation-based approach [11]. This procedure effectively corrects the alpha level for multiple comparisons on an assumption-free basis regarding the sampling distribution under the null hypothesis. We first calculated for

each time point whether coupling directions differed significantly (using a paired-samples t-test with an uncorrected threshold of $p < .05$). Then, we added the t-values for contiguous significant time points, resulting in one sum t-value for each cluster. Next, we shuffled the data across trials within each condition (encoding and retrieval) and for each patient, thereby randomly re-assigning rhinal cortex activity from trial i to hippocampal activity from trial j, and again extracted clusters as in the empirical data. For each permutation, only the largest surrogate cluster was taken into account. Finally, corrected p values were obtained as the rank of each empirical data cluster within the sorted distribution of surrogate data.

2.5 Results

First, we investigated the strength of stimulus-related phase synchronization in different frequency bands during encoding and retrieval. We calculated a four-way ANOVA with "band" (delta: 1–3 Hz, theta: 4–8 Hz, alpha: 9–12 Hz, beta: 13–25 Hz, gamma: 26–45 Hz), "encoding vs. retrieval" and "poststimulus vs. baseline" as repeated measures and "study" as between-subject factor. We found an interaction of "poststimulus vs. baseline" with "band" ($F_{4,64} = 4.428$; $p = 0.003$), indicating that both experiments were associated with significantly different task-related changes of phase synchronization in the different frequency bands. Importantly, there were no main effects of, or interactions with, the factors "study" or "encoding vs. retrieval", indicating similar stimulus-related effects across encoding and retrieval and in both studies.

Given the "poststimulus vs. baseline" × "band" interaction, we next calculated separate three-way ANOVAs in all bands with the factors "encoding vs. retrieval" and "poststimulus vs. baseline" as repeated measures and "study" as between-subject factor. In the delta frequency range, there was a significant main effect of "poststimulus vs. baseline" ($F_{1,16} = 7.941$; $p = 0.012$), reflecting a significant enhancement of rhinal-hippocampal delta synchronization during memory processing in both paradigms. For the beta band, there were significant interactions for "poststimulus vs. baseline" × "encoding vs. retrieval" ($F_{1,16} = 6.959$; $p = 0.018$) and "poststimulus vs. baseline" × "encoding vs. retrieval" × "study" ($F_{1,16} = 4.627$; $p = 0.047$). In the beta range, we thus compared phase synchronization during the experiment as compared to the baseline phase separately during encoding and retrieval using T-tests. However, none of these tests became significant. There were no main effects of, or interactions with, the factor "poststimulus vs. baseline" in the theta, alpha, or gamma frequency range. As poststimulus (task-related) increases in RC-HC phase synchronization were exclusively evident in the delta (1–3 Hz) frequency range across the two experiments, further analyses of directional coupling focused on rhinal and hippocampal phase dynamics in this frequency band.

Next, we compared the direction of information flow during encoding and retrieval. As described in detail in the Methods section, we used a surrogate-based non-parametric statistical approach to search for significant clusters of differences between these two experimental conditions [11]. In the first experiment, we found that the direction of information flow significantly differed between encoding and retrieval from 244 to 247 ms and from 251 to 295 ms after stimulus presentation, with an increased RC➔HC

coupling during encoding as compared to retrieval ($p_{corr} < .05$; Fig. 2A). Similar results were obtained for the second experiment: Here, the direction of information flow reversed between 113 and 161 ms, again with a significantly increased RC➔HC coupling during encoding as compared to retrieval (Fig. 2B).

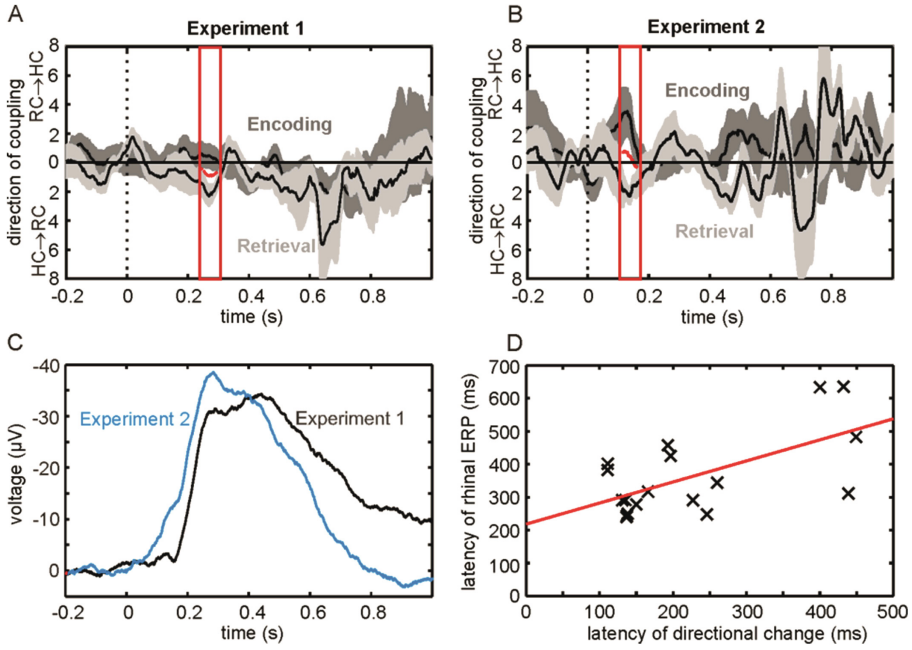

Fig. 2. Direction of rhinal-hippocampal coupling changes between memory encoding and retrieval. (A, B) In two separate recognition memory experiments, we found that during memory encoding, directional coupling values from RC to HC are more positive than during retrieval (average values across patients and standard errors of the mean are shown; difference values are depicted by red lines where significant). These effects occurred slightly earlier in the second as compared to the first paradigm. **(C)** These latency differences were paralleled by a numerically earlier peak of the average encoding-related rhinal event-related potential (N400 component) in the second as compared to the first experiment. **(D)** There was a significant inter-individual correlation between the peak latencies of the rhinal N400 components during encoding and the latencies of directional coupling effects ($R = 0.62$; $p = 0.006$).

Finally, we investigated the functional relevance of these effects in greater detail. Hippocampal memory processes are thought to depend on the output of rhinal memory operations evaluating, for instance, stimulus novelty [18]. Since early rhinal memory operations are considered to be reflected by the N400 component [12], we tested whether latencies of the rhinal N400 component predicted inter-individual differences in the latencies of directional RC-HC coupling effects (Fig. 2C). Corresponding to the earlier directional coupling effect in experiment 2 compared to experiment 1, the average N400 peak during encoding occurred numerically earlier in experiment 2 (see Fig. 2C; individual peak latencies did not significantly differ in both experiments). More importantly,

directional coupling latencies across both experiments correlated significantly with the peak latencies of the N400 component during encoding ($R = 0.62$; $p = 0.006$; Fig. 2D), and a similar trend was evident during retrieval ($R = 0.41$; $p = 0.09$). Hereby, maximal directional coupling differences occurred at times corresponding to the pre-peak slope of the rhinal N400 component.

2.6 Discussion

Our data show that the direction of information flow between RC and HC changes significantly between memory encoding as compared to retrieval, with a stronger RC➔HC coupling during encoding and stronger HC➔RC coupling during retrieval. The timing of directional coupling differences fits well with single-cell and intracranial EEG data indicating that earliest hippocampal responses to visual stimuli occur around 200 ms [14, 19], i.e. in close temporal proximity to the observed increase of RC➔HC information transfer during encoding.

An electrophysiological marker of early rhinal memory operations, which are thought to precede and provide a necessary basis for hippocampal processes, is the rhinal N400 component [12]. This component has been found to be related, for instance, to semantic preprocessing and evaluation of stimulus novelty [18, 20, 21]. Thus, we hypothesized that rhinal N400 peak latencies and the latencies of directional coupling effects may be interindividually correlated. Indeed, we observed such an interrelation. Generally, the peak of an event-related potential rather corresponds to the endpoint than to the initiation of a neural process. Together with the finding that maximal directional coupling differences occurred at times corresponding to the pre-peak slope of the rhinal N400 component, this suggests that RC-HC information transfer crucially depends on the output of early rhinal memory operations.

Furthermore, our results are in line with findings showing that phase synchronization of oscillations across RC and HC is highly relevant for memory operations [7, 22]. During both encoding and retrieval, we consistently detected prominent stimulus-related synchronization enhancements in the delta frequency range. Based on this initial finding, we demonstrated a reversal of directional RC-HC coupling of delta oscillations during encoding compared to retrieval. Our results are in accordance with recent intracranial EEG data indicating a prominent role of human medial temporal delta oscillations for memory encoding and retrieval [23–27]. In this sense, our findings moreover support the idea that rodent medial temporal theta oscillations, which are an essential element in models of hippocampal encoding and retrieval operations [4, 28], may be functionally most closely paralleled by human delta oscillations [24–27, 29].

As a methodological remark, the applied method for estimating directional coupling, although particularly well suited to capture oscillatory dynamics, requires large amounts of data to provide robust estimates [9, 10]. Therefore, we used as many trials as possible and were unable to analyze relevant subconditions, for instance, encoding trials with subsequently remembered versus forgotten items or retrieval trials with correct versus incorrect responses. Still, the interindividual variance of the directional coupling values appears to be quite large, in particular, during the second 500 ms after stimulus presentation (Fig. 2A and B). Hence, application of the described method to more extended

encoding and retrieval data is needed to validate our findings. Furthermore, an improved method for the quantification of directional oscillatory coupling being less reliant on large amounts of data would be desirable.

To summarize, our data show that the direction of oscillatory coupling within the human medial temporal lobe reverses between memory encoding and retrieval. Further studies, including analysis of larger EEG data sets and recordings of action potentials in animal experiments, will be required to validate our findings and to elucidate the cellular mechanisms underlying this effect.

References

1. Scoville, W.B., Milner, B.: Loss of recent memory after bilateral hippocampal lesions. J. Neurol. Neurosurg. Psychiatry **20**, 11–21 (1957)
2. Squire, L.R., Stark, C.E., Clark, R.E.: The medial temporal lobe. Ann. Rev. Neurosci. **27**, 279–306 (2004)
3. Eichenbaum, H., Yonelinas, A.P., Ranganath, C.: The medial temporal lobe and recognition memory. Ann. Rev. Neurosci. **30**, 123–152 (2007)
4. Hasselmo, M.E.: 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 (2005)
5. Carr, M.F., Frank, L.M.: A single microcircuit with multiple functions: state dependent information processing in the hippocampus. Curr. Opin. Neurobiol. **22**, 704–708 (2012)
6. Buzsáki, G., Draguhn, A.: Neuronal oscillations in cortical networks. Science **304**, 1926–1929 (2004)
7. Fell, J., Axmacher, N.: The role of phase synchronization in memory processes. Nat. Rev. Neurosci. **12**, 105–118 (2011)
8. Osterhage, H., Mormann, F., Wagner, T., Lehnertz, K.: Detecting directional coupling in the human epileptic brain: limitations and potential pitfalls. Phys. Rev. E **77**, 011914 (2008)
9. Rosenblum, M.G., Pikovsky, A.S.: Detecting direction of coupling in interacting oscillators. Phys. Rev. E **64**, 045202 (2001)
10. Wagner, T., Fell, J., Lehnertz, K.: Detection of transient directional couplings based on phase synchronization. New J. Phys. **12**, 053031 (2010)
11. Maris, E., Oostenveld, R.: Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods **164**, 177–190 (2007)
12. Fernández, G., Effern, A., Grunwald, T., Pezer, N., Lehnertz, K., Dümpelmann, M., Van Roost, D., Elger, C.E.: Real-time tracking of memory formation in the human rhinal cortex and hippocampus. Science **285**, 1582–1585 (1999)
13. Axmacher, N., Haupt, S., Fernández, G., Elger, C.E., Fell, J.: The role of sleep in declarative memory consolidation - direct evidence by intracranial EEG. Cereb. Cortex **18**, 500–507 (2008)
14. Axmacher, N., Cohen, M.X., Fell, J., Haupt, S., Dümpelmann, M., Elger, C.E., Schlaepfer, T.E., Lenartz, D., Sturm, V., Ranganath, C.: Intracranial EEG correlates of expectancy and memory formation in the human hippocampus and nucleus accumbens. Neuron **65**, 541–549 (2010)
15. Lachaux, J.P., Rodriguez, E., Martinerie, J., Varela, F.J.: Measuring phase synchrony in brain signals. Hum. Brain Mapp. **8**, 194–208 (1999)
16. Bruns, A.: Fourier-, Hilbert- and wavelet-based signal analysis: are they really different approaches? J. Neurosci. Methods **137**, 321–332 (2004)

17. Kralemann, B., Cimponeriu, L., Rosenblum, M.G., Pikovsky, A.S., Mrowka, R.: Phase dynamics of coupled oscillators reconstructed from data. Phys. Rev. E **77**, 066205 (2008)
18. Staresina, B.P., Fell, J., Do Lam, A.T., Axmacher, N., Henson, R.N.: Memory signals are temporally dissociated in and across human hippocampus and perirhinal cortex. Nat. Neurosci. **15**, 1167–1173 (2012)
19. Mormann, F., Kornblith, S., Quiroga, R.Q., Kraskov, A., Cerf, M., Fried, I., Koch, C.: Latency and selectivity of single neurons indicate hierarchical processing in the human medial temporal lobe. J. Neurosci. **28**, 8865–8872 (2008)
20. Nobre, A.C., McCarthy, G.: Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. J. Neurosci. **15**, 1090–1098 (1995)
21. Grunwald, T., Beck, H., Lehnertz, K., Blümcke, I., Pezer, N., Kurthen, M., Fernández, G., Van Roost, D., Heinze, H.J., Kutas, M., Elger, C.E.: Evidence relating human verbal memory to hippocampal N-methyl-D-asparate receptors. Proc. Natl. Acad. Sci. U.S.A. **96**, 12085–12089 (1999)
22. Jutras, M.J., Buffalo, E.A.: Synchronous neural activity and memory formation. Curr. Opin. Neurobiol. **20**, 150–155 (2010)
23. Fell, J., Ludowig, E., Rosburg, T., Axmacher, N., Elger, C.E.: Phase-locking within human mediotemporal lobe predicts memory formation. Neuroimage **43**, 410–419 (2008)
24. Lega, B.C., Jacobs, J., Kahana, M.: Human hippocampal theta oscillations and the formation of episodic memories. Hippocampus **22**, 748–761 (2011)
25. Clemens, Z., Borbély, C., Weiss, B., Eröss, L., Szücs, A., Kelemen, A., Fabó, D., Rásonyi, G., Janszky, J., Halász, P.: Increased mesiotemporal delta activity characterizes virtual navigation in humans. Neurosci. Res. **76**, 67–75 (2013)
26. Watrous, A.J., Tandon, N., Conner, C.R., Pieters, T., Ekstrom, A.D.: Frequency-specific network connectivity increases underlie accurate spatiotemporal memory retrieval. Nat. Neurosci. **16**, 349–356 (2013)
27. Watrous, A.J., Lee, D.J., Izadi, A., Gurkoff, G.G., Shahlaie, K., Ekstrom, A.D.: A comparative study of human and rat hippocampal low-frequency oscillations during spatial navigation. Hippocampus **23**, 656–661 (2013)
28. Hanslmayr, S., Staudigl, T.: How brain oscillations form memories - a processing based perspective on oscillatory subsequent memory effects. Neuroimage **85**, 648–655 (2014)
29. Buzsáki, G., Logothetis, N., Singer, W.: Scaling brain size, keeping timing, evolutionary preservation of brain rhythms. Neuron **80**, 751–764 (2013)