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Dissecting out conscious and unconscious memory (sub)processes within the human medial temporal lobe

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Abstract

The human medial temporal lobe (MTL) system mediates memories that can be consciously recollected. However, the specific natures of the individual contributions of its various subregions to conscious memory processes remain equivocal. Here we show a functional dissociation between the hippocampus proper and the parahippocampal region in conscious and unconscious memory as revealed by invasive recordings of limbic event-related brain potentials recorded during explicit and implicit word recognition: Only hippocampal and not parahippocampal neural activity exhibits a sensitivity to the implicit versus explicit nature of the recognition memory task. Moreover, only within the hippocampus proper do the neural responses to repeated words differ not only from those to new words but also from each other as a function of recognition success. By contrast parahippocampal (rhinal) responses are sensitive to repetition independent of conscious recognition. These findings thus demonstrate that it is the hippocampus proper among the MTL structures that is specifically engaged during *conscious* memory processes.

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Introduction

Two important structures within the medial temporal lobe (MTL) memory system are the hippocampus proper and anterior parahippocampal region including the entorhinal and perirhinal cortices. Studies in human patients and monkeys have shown that hippocampal and parahippocampal structures are crucial for memory formation and retrieval (e.g., Zola-Morgan et al., 1986; Squire and Zola, 1996; Meunier et al., 1996; Rempel-Clower et al., 1996). Although the precise anatomical and functional organizations of human memory are still matters of debate, there is a common consensus that an intact MTL system is necessary for declarative and episodic memory (Squire and Knowlton, 1995; Gabrieli, 1998; Tulving and Markowitsch,

1998). Memory deficits brought about by damage to the hippocampal formation have in common the feature that they affect memories that are accessible to conscious recollection, leading to the hypothesis that the MTL specifically mediates conscious recollection (Moskovitch, 1995). However, the hippocampus proper and the anterior parahippocampal region may well make different (Eichenbaum et al., 1996) or perhaps even independent (Young et al., 1997) contributions to recollection. Converging evidence from studies in human and nonhuman animals indicates that both structures may subservise two different aspects of recognition memory: While parahippocampal neural activity seems to contribute especially to the discrimination of repeating stimuli on the basis of their “familiarity” and “recency,” the hippocampus proper seems to be more involved in “remembering” a prior occurrence of a stimulus (for a review see Brown and Aggleton, 2001).

To assess the individual roles of the parahippocampal (rhinal) cortex and the hippocampus proper in conscious

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memory processes we recorded limbic event-related potentials (ERPs) from bilateral depth electrodes implanted via the longitudinal axis of the hippocampus. Rostral contacts of these electrodes were situated anterior to the hippocampal head within the parahippocampal gyrus, which is covered by rhinal cortex. Within this anterior MTL region, visually presented words normally elicit marked negative field potentials peaking around 400 ms (AMTL-N400), which are linked to memory formation (Fernández et al., 1999) and are reduced in amplitude with stimulus repetition (e.g., Smith et al., 1986; Halgren et al., 1994; McCarthy et al., 1995). Posterior electrode contacts were situated within the hippocampus proper where word repetitions are known to elicit a prominent late negative component (LNC), which normally peaks around 750–800 ms (Grunwald et al., 1995, 1999). We examined limbic event-related potentials elicited in both regions in an indirect test of recognition memory and a direct test of recognition memory (Richardson-Klavehn and Bjork, 1988). In the indirect test, patients were asked to identify letter strings that were nonsense words among a list of successively presented real German words, 50% of which were repeated once during the course of the experiment. Immediately thereafter the patients took part in a direct task of recognition memory in which they were asked to indicate which of a series of words was being presented for the first time in the experiment (“new”) and which was being repeated (“old”); there were no nonwords in this experiment. We recorded parahippocampal (rhinal) and hippocampal responses with the aim of determining the extent to which one or both of these MTL regions exhibit a sensitivity to the indirect versus direct nature of our recognition memory task. Moreover, we asked whether neural responses to repeated words within one or both of these regions differ from each other as a function of recognition success.

Materials and methods

Multicontact depth electrodes were implanted bilaterally via an occipital approach along the longitudinal axis of each hippocampus during presurgical evaluation for epilepsy surgery (Van Roost et al., 1998) because the zone of seizure onset and/or the functional integrity of the contralateral hippocampus could not be determined unequivocally by noninvasive investigations. Each contact had a cylindrical surface area of 10 mm² and a sensitivity that is maximal for field potentials generated within the adjacent brain tissue and decays with the inverse square of the distance (Morris and Lüders, 1985). Thus, earlier studies have been able to show that depth potentials recorded in the parahippocampal gyrus or in the hippocampus proper are locally generated within these areas (for a review see Grunwald et al., 2000). The placement of electrode contacts within the hippocampus and the anterior parahippocampal gyrus was ascertained by magnetic resonance images in each patient.

Seventeen temporal lobe epilepsy patients (12 women; 9 left, 8 right; age 34 ± 9 years) participated in the study. All gave written informed consent, and the study was approved by the local medical ethics committee. In the indirect test patients were asked to press a button in response to nonsense words and refrain from responding to real words. A total of 320 stimuli were presented (duration 600 ms, interstimulus interval 2300 ± 700 ms): 80 nonsense words and 160 frequent German nouns, 80 of which were repeated once after 3 to 6 intervening words. In the direct test of recognition memory patients were asked to indicate whether an item was new or old by pressing one of two buttons. Three hundred nouns (duration 200 ms) were presented sequentially on a computer monitor every 1800 ± 400 ms; half of these were repeated, 75 with a lag of 3 ± 1 intervening items and 75 with a delay of 14 ± 4 intervening stimuli. In an earlier study we found no significant effect of different spans between first presentations and repetitions (Grunwald et al., 1998). This direct test of recognition memory is part of our routine presurgical workup in patients with depth electrodes within the medial temporal lobes because its results can help to predict postoperative seizure control and memory performance (Grunwald et al., 2000).

Depth-ERP recordings (sampling rate 173 Hz per channel, epoch length 1200 ms, prestimulus baseline 200 ms) were referenced to two linked electrodes placed on both mastoid processes (bandpass filter setting 0.03 to 85 Hz, 12 dB/oct). Because limbic ERPs may be reduced in amplitude near the epileptogenic focus, we used recordings from the nonepileptic temporal lobe only. Recordings from the contact exhibiting the largest amplitude within the parahippocampal region and from the contact with the largest responses within the hippocampus proper were chosen for the grand averages and statistical analyses. ERPs were quantified with respect to the prestimulus baseline as mean amplitudes within the time window from 300 to 600 ms for parahippocampal responses and within the 300–600 and 600–900 ms latency ranges for the hippocampus proper. ERP measurements were subjected to repeated-measures ANOVA (*F* test with Greenhouse–Geisser corrections where appropriate). In the case of significant main effects, subsidiary ANOVAs were conducted to assess repetition effects under the different conditions. When significant effects were found, post hoc *t* tests for paired samples were applied. Post-hoc nonparametric Wilcoxon tests for paired samples were employed to test differences between hippocampal and parahippocampal new-minus-old recognition effects.

Results

Within the anterior parahippocampal region words elicited AMTL-N400 potentials peaking around 420 ms. Here we found a significant effect of repetition ($F_{1,16} = 32.06$; $p < 0.0005$) that did not interact with task effects: Com-

pared to “new” words, mean AMTL-N400 amplitudes were significantly reduced by repetition in both the indirect (new vs old words: -40 vs -27 μV , $p < 0.005$) and the direct recognition memory tasks (new vs old words: -52 vs -40 μV , $p < 0.0005$)—i.e., whether or not the participants were explicitly trying to recognize repeated words (see Fig. 1). The magnitudes of AMTL-N400 repetition effects in both tasks were not significantly different. These repetition effects then suggest that the anterior parahippocampal (rhinal) region contributes to memory processes whether they are incidentally or intentionally engaged.

Grand averages of hippocampal recordings proper show an early positive response. However, this component was not reliably present in all patients, and ANOVA did not show significant effects of repetition or task in this earlier time window. By contrast, repetition effects on the LNC peaking around 730 ms within the hippocampus proper ($F_{1,16} = 21.39$; $p < 0.0005$) did interact with task effects ($F_{1,16} = 5.31$; $p < 0.05$) and were more pronounced in the direct test (new vs old words: -12 vs -43 μV ; $p < 0.005$) relative to the indirect test of recognition memory (new vs old words: -7 vs -18 μV ; $p < 0.005$). Here both memory effects were significantly different ($p < 0.05$). Moreover, it was only in the direct (and not the indirect) test that words elicited a significantly larger positive hippocampal potential, peaking between 300 and 600 ms (see Fig. 1). Hippocampal ERPs between 300 and 600 ms were affected by repetition ($F_{1,16} = 10.22$; $p < 0.01$) and task ($F_{1,16} = 16.43$; $p < 0.005$). These factors interacted ($F_{1,16} = 4.54$; $p < 0.05$). Repetition effects were absent in the indirect ($F_{1,16} = 0.05$; ns) but present in the direct task ($F_{1,16} = 7.89$; $p < 0.05$), in which initial presentations elicited smaller responses (new vs old words: 20 vs 31 μV ; $p < 0.05$).

This finding raises the distinct possibility that conscious recognition is mediated by the hippocampus proper rather than by the entire MTL system. Prior investigations into the brain electrical activity specifically associated with conscious recollection have contrasted the scalp-recorded ERPs elicited by correctly recognized repetitions versus unrecognized repetitions (Van Petten and Senkfor, 1996; Rugg et al., 1998; Senkfor and Van Petten, 1998). Following this same logic we sought evidence of conscious recollection processes within the MTL system by comparing the limbic ERPs elicited in the direct task by old words that were correctly recognized versus those that were erroneously judged as new. Ten of the patients produced enough (more than 16) misclassifications of old words to allow a reliable analysis of limbic ERP responses for this comparison. Here again we found different patterns of sensitivity to this comparison for structures within the MTL consistent with the hypothesis that it is the hippocampus proper that is involved in conscious recollective memory processes: within the hippocampus proper, significant LNC repetition effects were evident only for old words that were correctly recognized as such. ANOVA (for “new” vs “recognized old” vs “unrec-

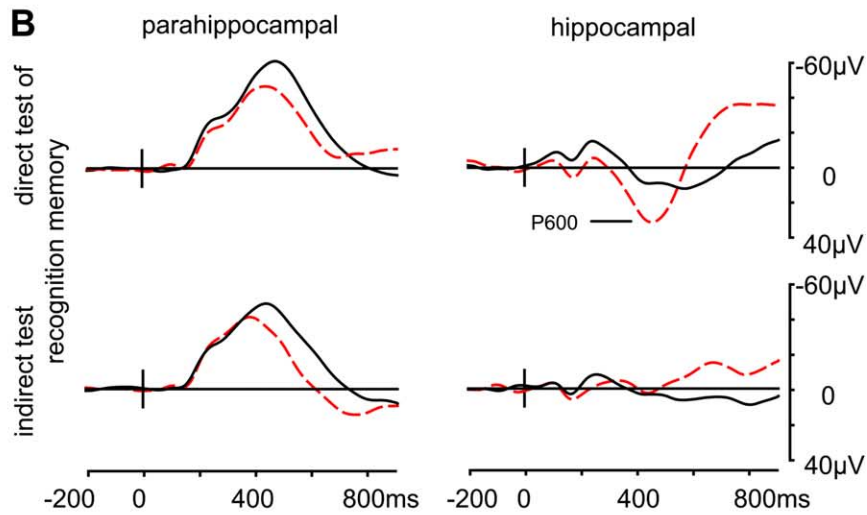
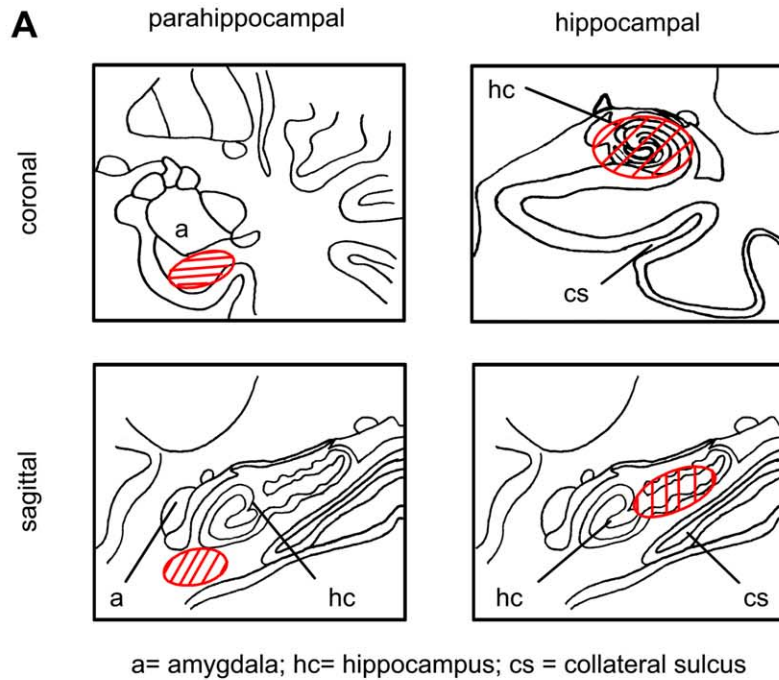
ognized old” words) showed a significant main effect ($F_{2,8} = 11.63$; $p < 0.005$) for hippocampal LNCs. Repetition effects were significant only for recognized ($F_{1,9} = 14.92$; $p < 0.005$) and not for unrecognized old words ($F_{1,9} = 0.20$; ns). Mean amplitudes of hippocampal LNCs to recognized repetitions were larger than those to new words ($p < 0.005$) while those to new and to unrecognized words did not differ ($p = 0.59$). Accordingly, both memory effects were significantly different ($p < 0.01$).

At the same time rhinal AMTL-N400s were reduced by repetition regardless of recognition success (see Figs. 2 and 3): They exhibited a significant main effect ($F_{2,8} = 9.24$; $p < 0.01$), and subsidiary ANOVAs demonstrated that repetition effects were significant for both recognized ($F_{1,9} = 12.20$; $p < 0.01$) and unrecognized repetitions ($F_{1,9} = 26.85$; $p < 0.005$). Mean amplitudes of rhinal AMTL-N400s were larger to new than to recognized ($p < 0.01$) and unrecognized old words ($p < 0.005$) while the latter two and the associated new-minus-old differences did not differ.

Discussion

Previous studies have implicated the MTL system as a whole in various memory processes whether they were (Martin et al., 1997) or were not (Rugg et al., 1997) intentionally engaged. Our data go beyond merely confirming the undifferentiated involvement of the MTL system in recognition memory, by revealing distinct patterns of participation of the different MTL structures: Specifically, we find that the anterior parahippocampal region participates similarly in both indirect and direct memory tasks, while the hippocampus proper is especially activated by direct recognition tasks: Parahippocampal AMTL-N400 repetition effects were similar in indirect and direct tasks, while the positive hippocampal potential peaking between 300 and 600 ms exhibited sensitivity to repetition only in direct and not in indirect tasks. Repetition effects of hippocampal LNCs are reduced but still present in the indirect task. However, it is difficult to interpret LNC modulations in an indirect memory test because our second experiment shows that LNCs are elicited only by consciously recognized repetitions, and recognition cannot be controlled in an indirect task.

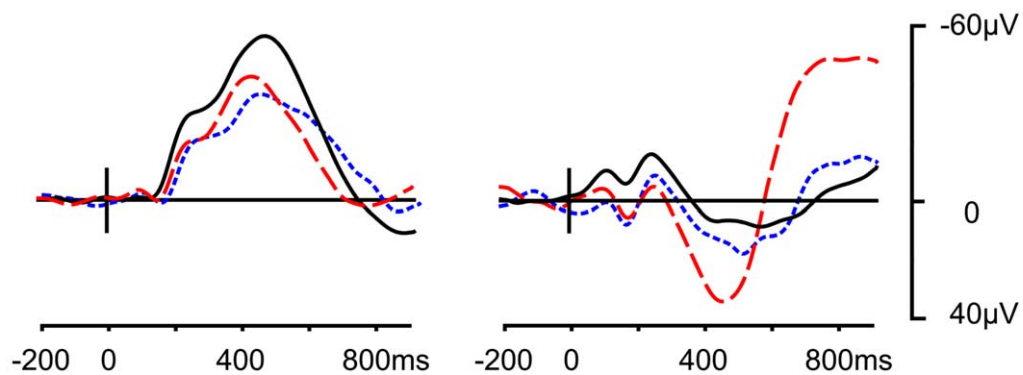
Although the underlying theoretical principles are not identical, indirect recognition memory tests tap aspects of implicit memory (Graf and Schacter, 1985). Thus, our findings may also suggest that while the hippocampus proper contributes especially to explicit memory, the parahippocampal (rhinal) cortex participates in both explicit and implicit memory processes. However, the fact that the amnesic patients H.M. (Gabrieli, 1990) and E.P. (Stefanacci, 2000) show intact implicit memory despite the lesions of their rhinal cortices indicates that this participation is not prerequisite for implicit memory. Nevertheless, the parahippocampal region may be sensitive to implicit memory tasks



1 — new words -- old words

parahippocampal region

hippocampus proper



2 — new words - - - recognized old words - · - · unrecognized old words

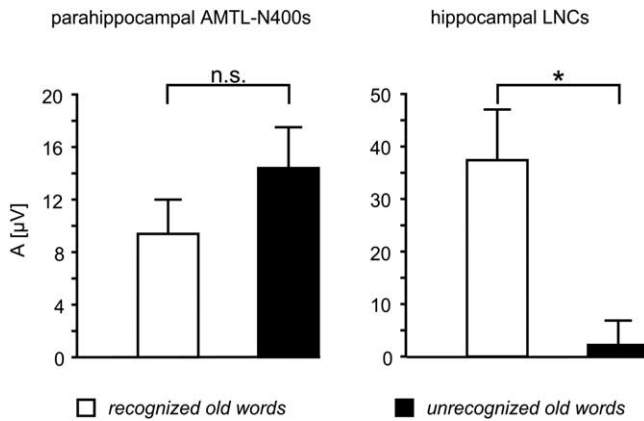


Fig. 3. Magnitudes of ERP memory effects: mean new-minus-old differences (+SEM) of the parahippocampal 300–600 ms and hippocampal 600–900 ms latency regions. Mean amplitudes of parahippocampal AMTL-N400s were larger to new than to recognized ($p < 0.01$) or unrecognized old words ($p < 0.005$) while the latter two and the associated new-minus-old differences did not differ. Mean amplitudes of hippocampal LNCs to recognized repetitions were larger than those to new words ($p < 0.005$) while those to new and to unrecognized words did not differ ($p = 0.59$). Accordingly, both memory effects were significantly different ($p < 0.01$). * $p < 0.01$.

that have been shown to activate various neocortical regions (e.g., Uecker et al., 1997; Wagner et al., 2000).

The patent importance of the MTL system for consciously accessible memories raises the long-standing question of the nature of the relationship between this brain region and consciousness itself. For instance, it has been proposed that the MTL might encode and store only information that has been consciously perceived (Moskovitch, 1995). Alternatively, it has been suggested that the hippocampus makes conscious recollection possible by encoding the consciousness of the experience as part of the memory engram (Moskovitch, 1996) or that the hippocampus contributes to the conscious experience itself as a prerequisite for memory encoding (Clark and Squire, 1998). However, at least one study indicates that the hippocampal formation also may mediate *implicit*—and thus unconscious—learning of complex contextual information (Chun and Phelbs, 1999), although a follow-up study could not replicate this finding (Manns and Squire, 2001). Our findings may help to resolve the apparent contradiction by demonstrating that the hippocampus and the rhinal cortex contribute differentially to memory-related processes. Both are sensitive to repetition; however, the rhinal cortex, unlike the hippocampus proper, responds independently of whether repetitions are consciously recognized as such.

The distinct effects of repetition on parahippocampal AMTL-N400s and hippocampal LNCs are especially noteworthy in light of recent findings distinguishing repetition-sensitive subcomponents of event-related potentials recorded at the scalp: A late positive component which has been hypothesized to reflect conscious recollection in brain-intact individuals (e.g., Rugg et al., 1998; Rubin et al., 1999) was observed to behave abnormally to word repetition in amnesic patients at the same time that repetition effects on an earlier N400 component were preserved (Olichney et al., 2000; Düzel et al., 2001). The sensitivity of the surface N400 to repetition has been taken to reflect priming at a “conceptual” level. Speculatively, we point to a possible relationship between the parahippocampal AMTL-N400 in the present study and the (surface) N400 repetition effect on the one hand and between the hippocampal LNC and the surface positivity linked to recollection on the other.

Functional imaging studies have shown that parahippocampal neural activity decreases with increasing stimulus familiarity (Gabrieli et al., 1997; Cho et al., 2000). Our finding that old words elicited equivalent AMTL-N400 responses relative to new words whether or not they were recognized is evidence of repetition activity in the absence of recognition in the anterior parahippocampal area. Ultimately, this may help to explain why lesions limited to an individual’s hippocampus proper can selectively impair their episodic memory without necessarily impeding that same individual’s ability to acquire knowledge of facts (“semantic memory”; Vargha-Khadem et al., 1997) as well as why more extensive damage to the MTL system also can vitiate implicit contextual learning (Chun and Phelbs, 1999). We thus propose that the anterior parahippocampal (rhinal) area contributes to the acquisition of knowledge independent of the conscious recollection of its acquisition.

Conversely, our finding that within the hippocampus proper neural responses to old words do distinguish those recognized from those that are not is consistent with the results of several studies demonstrating that the hippocampal formation is activated during conscious recollection (Schacter et al., 1995; Badgaiyan and Posner, 1997). Consistent with results of a functional imaging study demonstrating increased activity of the hippocampus proper during conscious recollection (Eldridge et al., 2000), our electrophysiological data strongly suggest that the hippocampus *proper* is the cardinal (and perhaps the only) MTL structure contributing specifically to conscious recollection. Of course, hippocampal and parahippocampal functions are not wholly independent, and the hippocampus proper has been

Fig. 1. (A) Electrode positions and (B) ERPs averaged across participants in both recognition memory tasks. (A) Hatched areas indicate the regions in which maximal parahippocampal AMTL-N400 and hippocampal LNC potentials were recorded in all patients. (B) Parahippocampal AMTL-N400s to repetitions were smaller than those to initial presentations in the explicit and implicit tasks. Hippocampal repetition effects between 300 and 600 ms were absent in the implicit but present in the explicit task.

Fig. 2. Parahippocampal and hippocampal ERPs to new, recognized, and unrecognized old words averaged across 10 participants. Parahippocampal AMTL-N400 repetition effects were significant for both recognized and unrecognized repetitions. Hippocampal LNC repetition effects were significant only for recognized and not for unrecognized old words.

found to be involved in the generation of AMTL-N400s, at least in part (Grunwald et al., 1998). Recently it has also been shown that successful as opposed to unsuccessful memory formation is accompanied by an initial rhinal-hippocampal γ -band phase coupling followed by a later decoupling (Fell et al., 2001). However, the finding that hippocampal LNC repetition effects are limited to old words that are recognized indicates that the hippocampus proper is not sensitive to repetition priming or unconscious familiarity per se. We take it to imply that the human hippocampus proper preferentially partakes in explicit (and not implicit) memory processes.

In sum, we found that the various structures within the MTL system contribute differentially to human memory: The anterior parahippocampal region, including the rhinal cortex, participates in memory-related processes independent of a person's intention to remember or awareness of an event's history; the hippocampus proper seems instead to become involved especially during conscious recollection.

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