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RAPID COMMUNICATION

Field Potentials in the Human Hippocampus During the Encoding and Recognition of Visual Stimuli

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ABSTRACT: Intracranial field potentials were recorded from electrodes implanted in the hippocampus in 12 epileptic patients. Potentials were elicited by stimuli presented during a delayed matching-to-sample test. Each trial began with a sample stimulus composed of a 3 × 3 grid of rectangular color patches. The sample was followed by a sequence of similar but task-irrelevant stimuli and the sequential presentation of two test stimuli, one of which was identical to the sample. Patients indicated their recognition of the test stimulus that matched the sample with a button press. High-amplitude negative potentials were consistently elicited by sample and test stimuli. Peak amplitudes occurred 300–500 ms after stimulus onset and were larger for the sample in all cases. The patterns of potential gradients observed between adjacent hippocampal contacts and the locations of maximal amplitudes, as verified by magnetic resonance imaging in seven patients, suggest that these potentials were produced by neuronal activity in posterior hippocampus. These field potentials appear to index a memory storage function engaged in response to events that will later be remembered. The hippocampal contribution to storing declarative memories can thus begin, in some circumstances, within the first half-second after the presentation of a to-be-remembered stimulus. *Hippocampus 2002;12:415–420.* © 2002 Wiley-Liss, Inc.

KEY WORDS: memory; matching-to-sample test; event-related potentials; intracranial electrodes; hippocampal potentials

INTRODUCTION

A comprehensive understanding of the role of the hippocampus in human memory must be based on patterns of memory breakdown after hippocampal damage as well as on neurophysiological analyses of normal hippocampal function. Selective memory deficits in patients with amnesia have been attributed to bilateral hippocampal dysfunction (Scoville and Milner, 1957; Zola-Morgan et al., 1986). The primary deficits are in declarative memory–recalling and recognizing facts and episodes. Many contemporary memory theories postulate that declarative memories are stored in neocortical networks and that this memory storage is contingent on the confluence of medial temporal, diencephalic, and neocortical processing (Mayes and Downes, 1997; Eichenbaum, 2000; Paller, 2002; Squire and Schacter, 2002). Hippocampal circuitry is thought to be engaged in conjunction with networks in adjacent medial temporal regions, but characterizing the specific contributions from each of these regions, as well as exactly when these contributions are made, remains controversial.

One way to gain further evidence concerning the hippocampal contribution to declarative memory is to monitor brain electrical activity during memory storage and retrieval. Toward this end, measures of neural activity generated during a memory test can be obtained in a variety of species. Some doubt often remains, however, about whether declarative memory functions studied in humans and in another species are indeed parallel. Given this uncertainty, the animal evidence may be most valuable when it can be evaluated in conjunction with comparable evidence from humans. And yet, there are very few opportunities to directly observe neural responses of the hippocampus in humans.

Electrical recordings from patients with implanted electrodes provide a rare opportunity to observe the human hippocampus in action. When activated synchronously, groups of neurons with appropriate geometry can generate extracellular electrical fields measurable as event-related potentials (ERPs) (Allison et al., 1986; Kutas and Dale, 1997). For example, potentials have previously been recorded from the hippocampus during cate-

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gorization tasks (Halgren et al., 1980; McCarthy et al., 1989). We hypothesized that potentials produced in the hippocampus would reflect its role in memory processing and thus provide vital evidence to help guide theories on the neural substrates of declarative memory.

In order to monitor brain activity associated with acquisition and recognition, we adapted a visual object recognition test that has been used to show declarative memory deficits in patients with amnesia and in monkeys with experimentally induced amnesia (Mishkin, 1978; Aggleton et al., 1988; Squire et al., 1988; Baxter and Murray, 2001). Each trial of this delayed matching-to-sample (DMS) test includes a unique, to-be-remembered stimulus known as the sample. After a delay, the subject indicates recognition by selecting the sample. A long retention delay and/or interfering events can undermine rehearsal so as to make performance contingent on declarative memory.

We recorded ERPs to visual stimuli presented sequentially in the DMS test (Fig 1). The sample was composed of nine rectangles, each of which could be either red, yellow, green, or blue. Each sample was unique across trials (given that sample repetition tends to confound recognition with recency discrimination). Patients were encouraged to remember the sample without relying on verbal strategies. Data were recorded during 60–100 trials. Cue stimuli lasted 1,000 ms, other stimuli 200 ms, and interstimulus intervals 900–1,000 ms. On each trial, one test stimulus (the match) was identical to the sample. Mismatch and all distractor stimuli were unique and were constructed to be highly similar to the sample, by randomly rearranging the nine rectangles used for the sample. Because both test stimuli and the distractors were composed of the same components, DMS performance was highly attention-demanding.

Recordings from 12 epileptic patients were made during a 5- to 8-day clinical evaluation in which electrodes were implanted to analyze the course of seizures for neurosurgical planning (Spencer et al., 1982). Nine patients were right-handed, five were men, and all suffered from complex partial seizure disorders not adequately controlled by anticonvulsant medication. The mean full-scale intelligence quotient (IQ) was 92.8 (range 73–117; SE = 3.9), mean age was 31.3 years (range 24–39; SE = 1.4).

Electroencephalographic (EEG) recordings were amplified with mastoid or earlobe reference (0.1–100-Hz bandpass, 4–6 ms/sample). Contact locations were determined using x-rays for platinum-iridium probes (n = 5) or magnetic resonance imaging (MRI) for nichrome probes (n = 7). Further methodological details have been described previously (McCarthy et al., 1989; Allison et al., 1999).

Figure 2a shows recordings from a platinum–iridium probe implanted in the right hemisphere of a patient who later underwent a partial left temporal lobectomy. Large negative ERPs were apparent at several contacts at 250–900 ms after stimulus onset. At contact RP11, the sample response reached a peak of −360 μV, roughly twice as large as the match response. In this study, and in subsequent analyses, the match response was computed using only trials in which the match occurred in the test-1 position (the results were similar for test-2, but match/mismatch status cannot be anticipated for test-1). The location of contact RP11 was estimated to be in the posterior hippocampus. At more posterior contacts RP6–RP9, positive potentials were elicited in the same latency range. At deeper contacts RP15–RP18, positive potentials were observed for the match. In this patient, and in general, recordings from other probes in temporal and frontal regions showed late responses that were relatively small and/or inconsistent compared with hippocampal responses.

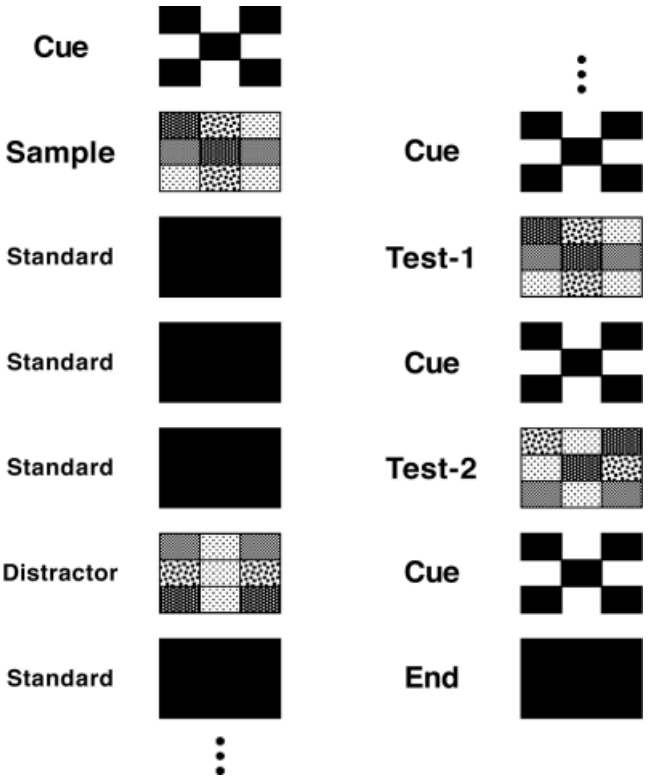

FIGURE 1. Schematic representation of a typical trial of the delayed matching-to-sample (DMS) test. Stimuli were composed of a 3-by-3 matrix of rectangles presented on a monitor. Color rectangles were used only for sample, distractor, and test stimuli (patterns shown here represent colors). Each stimulus subtended a visual angle of 4.2° × 3.1° and appeared on a rectangular white background (7.2° by 5.2° visual angle). Trials included an acquisition/delay sequence (cue, sample, standards, and distractors) followed immediately by a test sequence (cue, test-1, cue, test-2, cue, end). A button press was used to initiate each trial, with a 1-s delay, and to register the recognition choice. Recognition responses were counted as correct only if they occurred during the cue presentation that followed the test stimulus that was identical to the sample (test-1 in the trial depicted). The number of standards and distractors delivered during the retention interval was randomized from 10 to 20, yielding an average delay from sample to test-1 of about 16 s. The first three stimuli and the last three stimuli in the retention interval were standards, whereas the intervening stimuli were randomly either standards (80%) or distractors (20%).

Figure 2b shows recordings from a nichrome probe implanted in the right hemisphere of another patient. MRI findings from this patient, as shown in Figure 2c, indicated that contacts RP5–RP9 intersected the hippocampus. Large negative ERPs were elicited by the sample from these contacts. ERP patterns changed abruptly between adjacent contacts RP4/RP5 and RP9/RP10. Although the MRI magnetic inhomogeneity artifacts produced by the contacts were insufficient for substructural localization, it is likely that con-

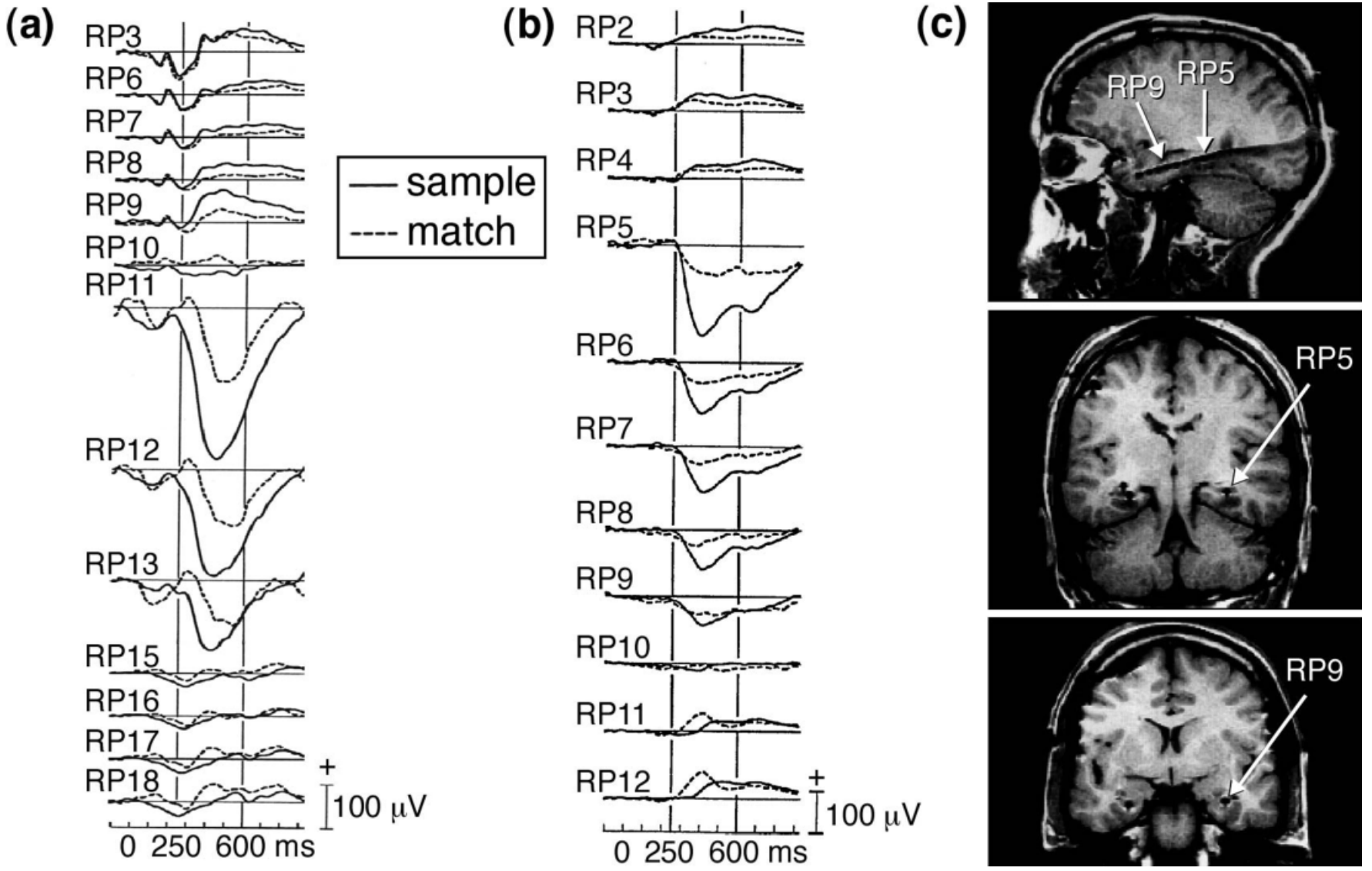

FIGURE 2. **Intracranial results from two patients. a: Large negative potentials were elicited by the sample from contacts RP11 to RP13. These contacts appeared to be located in posterior hippocampus on the basis of an x-ray localization procedure (Darcey and Williamson, 1985). Similar potentials, but with smaller amplitudes, were elicited by the match. Potentials of opposite polarity were apparent at neighboring contacts. b: In another patient, large negative potentials were elicited by the sample from contacts RP5 to RP9, with smaller potentials for the match. Potentials of opposite polarity were again apparent at neighboring contacts. c: Sagittal and coronal MRIs from the patient represented in b show contact locations and demonstrate that contacts RP5 to RP9 were in or near the hippocampus. Reduced hippocampal volume is apparent in the left hemisphere.**

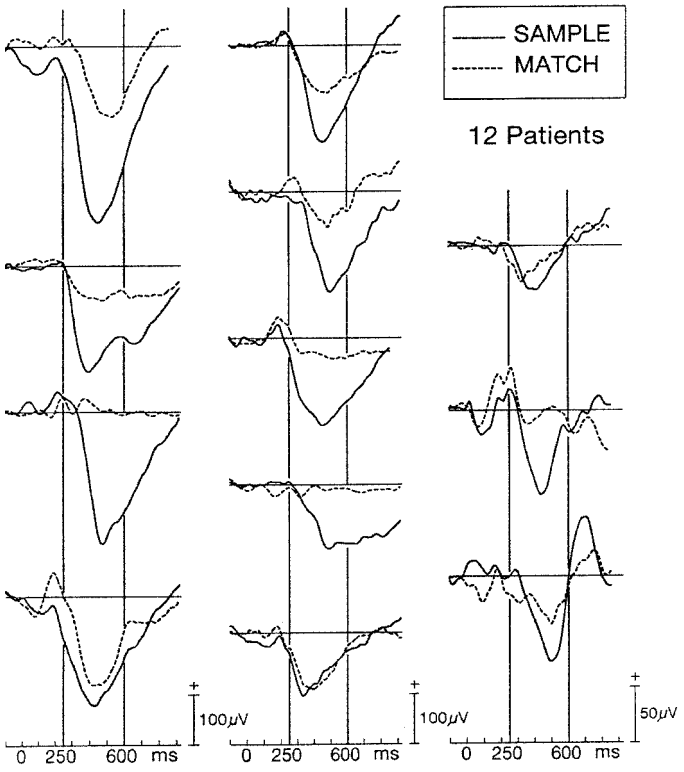

FIGURE 3. Event-related potentials (ERPs) from all 12 patients showing larger responses to the sample than to the match. Recordings shown were from the region of the posterior hippocampus and were selected on the basis of where the largest potentials were elicited. Note different scale for right column. Recordings were from the left hemisphere in six patients and from the right hemisphere in six patients, always on the side opposite to a hippocampal seizure focus.

tacts that recorded the negative potentials were within the hippocampus, whereas contacts that recorded positive potentials were outside the hippocampus. This pattern of potential gradients is highly suggestive of local generation within the hippocampus. We also observed these hippocampal potentials with similar topographic patterns in response to target events in discrimination tasks (as previously described by McCarthy et al., 1989), and they were likewise localized to posterior hippocampus. In this patient, simultaneous cortical surface recordings from regions inferior to the temporal lobe and anterior to the hippocampus yielded positive ERPs to sample and match, with larger amplitudes for the match. Simultaneous recordings from parietal scalp also yielded positive ERPs with larger amplitudes for the match. This pattern of scalp ERPs was also observed in a group of 12 healthy individuals performing the same DMS test. These robust positive ERPs to the match may reflect events of memory retrieval and correspond with ERP results from a wide variety of memory tests in which such ERPs have been associated with the recollection of declarative memories (Friedman and Johnson, 2000; Mecklinger, 2000; Paller, 2000).

Figure 3 shows sample and match responses from each of the 12 patients. The contact for each patient was selected on the basis of where these negative responses were largest, and all were in or near the region of the posterior hippocampus. These data highlight the consistency with which high-amplitude negative ERPs were elicited by the sample. The peak latency of these potentials ranged from ~300–500 ms. Variability in absolute peak amplitude may reflect nonspecific factors, including variability in electrode position relative to hippocampal cell layers, as observed in our previous studies of hippocampal potentials in categorization tasks (McCarthy et al., 1989; Paller et al., 1992). However, the peak amplitude elicited by the match was in all cases smaller than that to the sample. Match peak amplitude computed as a percentage of sample peak amplitude was 41% (range 3–88; SE = 9).

In comparisons across all stimulus types, the largest negative potentials were elicited by the sample, intermediate responses were elicited by the match, mismatch, distractor, and test cue, and smallest responses by the initial cue, response cue, and standard. Peak amplitude measurements from the individual patients ($\mu V \pm$ SE) averaged 176 ± 26 for the sample, 63 ± 16 for the match, 69 ± 9 for the mismatch, 66 ± 13 for the distractor, 92 ± 16 for the test cue, 54 ± 11 for the initial cue, 17 ± 6 for the response cue, and 11 ± 2 for the standard. Peaks differed significantly as a function of condition [$F(7,88) = 12.78$, $P < 0.001$] and the Fisher test verified that ERPs were (1) larger for the sample than for all other stimuli, (2) smaller for the standard than for all other stimuli except response cue, and (3) smaller for response cue than for all other stimuli except initial cue and standard. Match and mismatch ERP amplitudes were not significantly different.

To summarize the results, the sample and match in the DMS test were physically identical but elicited different ERPs due to differential cognitive processing at acquisition and retrieval. These potentials were elicited from locations distant from epileptic foci; recordings from other patients with hippocampal contacts only in regions of suspected pathology were excluded. Furthermore, findings of similar negative potentials from monkeys with no epileptic pathology (Paller et al., 1992) suggest that the present results reflect normal hippocampal function and not artifacts of recording from epileptic patients.

What is the neural basis of these potentials? McCarthy et al. (1989) observed similar field patterns in the medial temporal region and speculated that they were generated by the synchronous activation of spatially aligned hippocampal pyramidal cells. These field patterns were apparent both for the sample and for rare target events in simple categorization paradigms (Halgren et al., 1980; McCarthy et al., 1989). Moreover, when both the DMS test and categorization paradigms were administered to patients in the present group, the location of maximal response was generally the same, although amplitudes were larger in the DMS test. The proposal that hippocampal neurons generate these potentials is also supported by negative correlations between hippocampal pathology and hippocampal ERP amplitudes (Squires et al., 1983; Puce et al., 1989). These potentials may reflect the arrival into the hippocampus of neocortical information, of modulatory input from diffusely projecting brain systems, or of recurrent inhibition from hippocampal pyramidal cells. Recurrent inhibition could coincide with synchronous hippocampal output to entorhinal cortex thought to act to strengthen new connections (Buzsaki et al., 1990).

Given the hypothesized role of the hippocampus in consolidating declarative memories, a reasonable speculation is that hippocampal potentials reflect the integration of information that is projected into the hippocampus and that defines the context of the

learning episode plus high-level perceptual representations of to-be-remembered stimuli. Whereas consolidation is generally thought to take place during an extended time after the original episode, it may begin when the episode is first experienced. The present results raise the possibility that this hippocampal function begins within the first 300–900 ms after the onset of to-be-remembered stimuli, when relevant information may first be conveyed to the hippocampus.

Why did the sample elicit the largest hippocampal responses? All stimuli in the DMS test could potentially be remembered, yet most emphasis is certainly placed on remembering the sample. The response was smaller for the match, which was identical to the sample, as well as for the mismatch and distractors. Novelty may be another factor that influences hippocampal responses (Tulving et al., 1994; Dolan and Fletcher, 1997), and the sample was arguably a relatively novel stimulus in the DMS test. Whereas novel events may attract encoding resources, perhaps hippocampal activity can also be regulated on the basis of current goals to remember particular events.

Test stimuli presumably instigated retrieval and decision processes involving neocortical processing. Hippocampal negativity and concurrent scalp positivity during DMS may reflect these separate encoding and retrieval processes, respectively, given that scalp responses were larger for the match whereas hippocampal potentials were larger for the sample. Accordingly, the scalp activity should not be considered a reflection of the concurrent hippocampal activity. Similarly, scalp-recorded P300 potentials and hippocampal negativities often co-occur, but lesion evidence suggests that scalp P300s are not distant reflections of hippocampal activity (Stapleton et al., 1987; Johnson, 1988; Paller et al., 1988).

Hippocampal responses recorded in other paradigms have also been associated with memory formation. For example, ERPs to words were found to differ after ~500 ms as a function of later recall performance (Fernández et al., in press). These differences, sometimes termed Dm (Paller and Wagner, 2002), were unaffected by word frequency. Similarly, greater EEG gamma-band phase synchronization between rhinal and hippocampal regions was observed after words that were subsequently remembered (Fell et al., 2001). Scalp-recorded EEG theta rhythms have also been associated with successful episodic encoding and have been attributed to corticohippocampal feedback loops (Klimesch, 1999).

By contrast, some analyses have failed to show relationships between hippocampal responses and memory storage. Puce et al. (1999) compared ERPs during learning and recognition phases of a face–name association task, a gender categorization task, and simple categorization tasks. The largest negative hippocampal responses were elicited in the categorization tasks, and there was no apparent association between hippocampal responses and face–name learning. This finding contrasts with the present results in which large hippocampal responses were elicited by the to-be-remembered stimulus in the DMS test. Accordingly, it is not possible at present to specify all possible factors that may be required in order for these hippocampal potentials to be observed. Several factors may have contributed to the association between encoding and hippocampal potentials in the present design: (1) people were not maintaining to-be-remembered information at the moment sample stimuli were presented; (2) the sample stimulus in each trial was relatively novel; and (3) sample stimuli required distinctive processing compared with what was required for most stimuli presented. The sample stimulus could have been categorized in a particularly meaningful way—as a stimulus that should be remembered.

Hippocampal activity measured indirectly using other methods also supports a role in forming declarative memories (Schacter and Wagner, 1999). Recently, for example, event-related fMRI demonstrated greater left hippocampal activation for words that were subsequently recognized (Fernández et al., 1998; Kirchhoff et al., 2000; Otten et al., 2001; Siwiec et al., 2001; Davachi et al., 2001). Similar effects were also observed bilaterally for visual scenes (Kirchhoff et al., 2000). Some single-unit recordings in epileptic patients may also reflect memory functions. In a DMS test, hippocampal responses were apparently related to the presentation of a stimulus or to the response demands, although cells also fired to stimuli or response demands apparently unrelated to memory (Halgren et al., 1978). During word-pair processing, firing rates of some neurons demonstrated a positive correlation and others a negative correlation with later recall (Cameron et al., 2001). This work can facilitate connections to unit studies in other species, including studies in which DMS tests were used (Wible et al., 1986; Coburn et al., 1990; Wilson et al., 1990; Salzmann et al., 1993). Multiple perspectives can thus be combined to further our understanding of the physiology of human memory.

The present results obtained using a nonverbal version of the DMS test, in conjunction with other findings discussed above, support the notion that synchronous input to spatially aligned hippocampal pyramidal cells contributes to the formation of declarative memories. By virtue of the high temporal resolution inherent in the ERP method, we have obtained indications that this contribution can begin within a few hundred milliseconds after to-be-remembered events. Current theories on the hippocampal contribution to declarative memory, mostly based on neuropsychological findings, suggest that enduring memory storage relies on interactions between neocortical and hippocampal processing (e.g., Paller, 1997, 2002; Squire and Schacter, 2002). The present findings indicate that hippocampal potentials index one of the earliest neurophysiological events that can ultimately lead to the lasting storage of a declarative memory.

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