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Conscious awareness, memory and the hippocampus

Howard Eichenbaum

Declarative memory, the conscious recollection of past experiences, is known to involve the hippocampus. Now a study of amnesic patients shows that hippocampus-dependent learning can occur in the absence of conscious awareness.

Memories exist in multiple forms mediated by different brain systems[1]. A distinction between memories accessible to conscious awareness and unconscious memories dates back at least to 1804, when the French philosopher Maine de Biran[2] distinguished between well-circumscribed, conscious 'ideas' and habitual actions or vague feelings that do not generate an idea. Despite the subsequent growth of experimental memory research, the issue lay dormant during most of this century, suppressed by efforts to provide a systematic accounting of learning without reference to covert mental events. However, it strongly re-emerged with the discovery that conscious and unconscious memory can be dissociated in brain-damaged patients. Lesions of the medial temporal lobe[3], including those that are restricted to the hippocampus[4,5], cause a selective loss of declarative or explicit memory—the capacity for conscious recollection of specific facts and events[6,7]. Conversely, damage to other specific brain areas selectively impairs unconscious forms of memory[8–10] but spares conscious memory. Do these findings indicate that hippocampus-dependent memory is equivalent to conscious memory? In this issue of *Nature Neuroscience*, a study of patients with hippocampal damage[11] indicates that the relationship is not so simple.

Because hippocampal damage causes amnesia without abolishing consciousness, this region cannot be necessary for awareness in general, but it could be a 'gateway' for awareness to enter into memory. Clark and Squire[12] recently argued that the study of memory processing in the hippocampus may lead to insights about consciousness. Their experiment was based on a puzzling finding on hippocampal damage and classical (Pavlovian) conditioning in animals. Hippocampal lesions do not prevent rabbits from learning to blink in response to a tone when they are trained on a conventional protocol in which the tone begins before and then slightly overlaps with an air puff to the eye. However, unlike intact animals, rabbits with hippocampal damage fail to learn on a variant of this protocol in which the tone and air puff are separated by a half-second 'trace' interval. (This gap is probably too brief for rabbits to forget the tone, judging by the short-term memory capacity retained by humans with similar damage.)

Clark and Squire[12] replicated this pattern of findings in amnesic people with hippocampal damage. During conditioning, subjects were shown a silent movie, which they were instructed to remember while ignoring distracting sounds and air puffs. Afterward, they were asked whether they had become aware that the tones predicted air puffs. In the conventional conditioning protocol, amnesics and normal controls both acquired the eyeblink response, and no relationship between performance and awareness was observed in normal subjects. In the trace conditioning protocol, however, amnesics failed to learn, whereas among normal subjects, success was limited to those who became aware of the relationship. Clark and Squire concluded that hippocampal mediation of conscious awareness is critical to trace conditioning, and they suggested that this form of learning provides "a means for studying awareness in nonhuman animals".

Now Chun and Phelps[11] challenge the conclusion that hippocampus-dependent learning necessarily involves awareness. This paper and another recent study (discussed below) are consistent with an alternative view of how the hippocampus processes information, namely that it subserves the networking of relevant relationships among items stored in memory[13]. Such a relational organization is promiscuous in the sense that information within the network can be accessed by many routes including, but not restricted to, conscious awareness. This focus on network organization and accessibility, rather than on consciousness *per se,* is emphasized in research on hippocampal function in animals. Across a broad range of experiments, the hippocampus is critical to learning and remembering relationships among items in memory, including relationships that characterize spatial layouts, items in the particular context in which they have been experienced, and other associative, sequential or logical relationships among experiences[13].

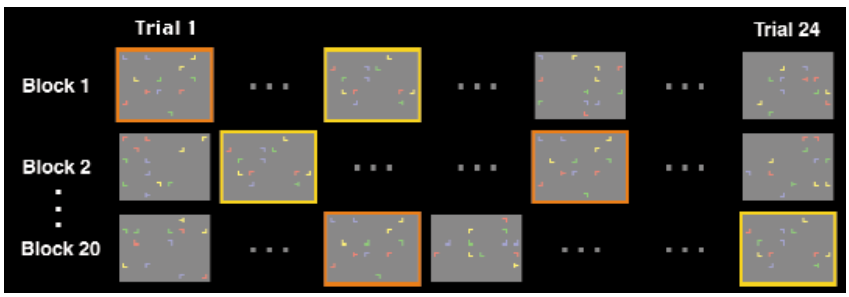

Fig. 1. Examples of screen presentations used in blocks of training trials. Each screen contains an arrangement of colored 'L's (background context) and a 'T' (target cue) in various orientations. Two repeating cue–context configurations are highlighted (orange or yellow outline); the remaining trials have novel cue–context configurations.

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Table 1. Summary of discussed observations on awareness, memory and hippocampal function.

	Conscious (explicit)	Unconscious (implicit)
Hippocampus-dependent	Recollection of facts & events Trace conditioning	Cue-in-context relations Object-in-scene relations
Hippocampus-independent		Habits/procedures Priming Emotional Delay conditioning

Guided by this perspective, Chun and Phelps[11] examined amnesic patients to determine whether learning of complex relationships depends on the hippocampus even without conscious awareness. The authors used a test of non-conscious (implicit) memory for the relationships between cues and the context in which they were presented[14]. Subjects were trained to locate a visual target stimulus (the letter 'T' in various orientations) among a background of many 'L' distractors. On some trials, the background was a new random configuration of distractors; on other trials, particular background configurations were repeated and consistently predicted the location of the target (**Fig. 1**). This protocol reveals two types of memory in normal subjects[14]. Search time decreases with practice on all trial types, presumably by procedural learning, which is known to be spared in amnesic patients. More importantly for the question at hand, search time is further decreased on trials with repeated configurations of target cues and contexts, showing memory for particular cue–context relationships; this performance advantage is unrelated to awareness that the context has been repeated.

Consistent with previous reports[14], Chun and Phelps[11] found that normal subjects could not discriminate novel from repeated backgrounds. Even subjects who were aware that repetitions had occurred could not identify the repeated contexts, nor did they show greater facilitation for repeated contexts than other subjects who were unaware. Thus this protocol assessed the capacity for learning cue–context relationships without conscious awareness. Amnesic subjects with hippocampal damage improved their response times with practice across novel configurations, in accordance with other findings that procedural learning is mediated by non-hippocampal systems[6]. However, they failed to show added facilitation due to experience with repeated contexts. (As expected, none of the amnesic subjects was aware of the repetition.) This pattern of spared learning of general task procedures and impaired learning of specific cue–context relations is consistent with many animal studies that have focused on relational organization without reference to awareness. More importantly, the results of this study support the notion that hippocampus-dependent memory is not fundamentally driven by awareness.

Another recent experiment points to the same conclusion. Using a formally similar design, Whitlow, Althoff and Cohen (*Soc. Neurosci. Abstr.* **21**, 303.5, 1995) examined the performance of amnesic patients using eye movement monitoring to measure nonconscious memory for spatial relations among objects within scenes. Subjects studied real-world scenes, then viewed either identical scenes or scenes in which some objects had been rearranged. In response to identical repeated scenes, normal subjects had fewer eye fixations and sampled fewer regions, indicating an overall facilitation or 'priming' in scanning familiar pictures (another type of memory spared in temporal lobe amnesia). When presented with rearranged scenes, normal subjects concentrated their scanning in the manipulated zones, and this effect did not depend on conscious awareness of the manipulation. Amnesic patients showed the same general facilitation when scanning familiar scenes, consistent with intact priming of perceptual processing for familiar items mediated by non-hippocampal systems. By contrast, they failed to show excessive scanning of manipulated zones in the rearranged scenes. These data show the same pattern of spared and impaired memory performances as the Chun and Phelps study, demonstrating generality of the selective deficit in implicit memory for stimulus relationships across two methods of testing.

These studies are consistent with Moscovitch's proposal[15] that conscious memory is special only because the conscious experience of the remembered event is stored along with other information about what occurred, and is therefore a part of the network organization. How can this view be reconciled with the link between conscious awareness and learning success that Clark and Squire reported in their human eyeblink conditioning experiments? It remains possible that awareness is not a prerequisite for learning; instead learning and awareness could be correlated because both are consequences of the way that the hippocampus processes information, as the networking hypothesis would suggest. According to this interpretation, the hippocampus mediates an organizational process that captures both the explicit predictive relationships of the conditioning protocol and the awareness of their occurrence. Taken together, these findings suggest that the hippocampus mediates the networking of memories with or without conscious awareness, but that one cannot have awareness of these memories without involvement of the hippocampal network (**Table 1**). Thus, awareness of a memory might best be seen as an emergent property of hippocampal processing, in that the networking of memories usually results in (or is usually accessible to) conscious awareness.

1. Schacter, D. L. & Tulving, E. in *Memory Systems 1994* (eds. Schacter, D. L. & Tulving, E.) 269–310 (MIT Press, Cambridge, Massachusetts, 1994).
2. de Biran, M. *The Influence of Habit on the Faculty of Thinking*, 1929 ed. (Williams & Wilkins, Baltimore, 1804).
3. Scoville, W. B. & Milner, B. *J. Neurol. Neurosurg. Psychiatry* **20**, 11–12 (1957).
4. Vargha-Khadem, F. *et al. Science* **277**, 376–380 (1996).
5. Zola-Morgan, S. M., Squire, L. R. & Amaral, D. G. *J. Neurosci.* **6**, 2950–2967 (1986).
6. Cohen, N. J. & Squire, L. R. *Science* **210**, 207–210 (1980).
7. Graf, P. & Schacter, D. L. *J. Exp. Psychol. Learn. Mem. Cogn.* **11**, 501–518 (1985).
8. Knowlton, B. J., Mangels, J. A. &, Squire, L. R. *Science,* **273**, 1399–1401 (1996).
9. Bechera, A. *et al. Science* **269**, 1115–1118 (1995).
10. Gabrieli, J. D., Fleischman, D. A., Keane, M. M., Reminger, S. L. & Morrell, F. *Psychol. Sci.* **6**, 76–82 (1995).
11. Chun, M. M. & Phelps, E. A. *Nat. Neurosci.* **2**, 844–847 (1999).
12. Clark, R. E. & Squire, L. R. *Science* **280**, 77–81 (1998).
13. Eichenbaum, H. *Annu. Rev. Psychol.* **48**, 547–572 (1997).
14. Chun, M. M. & Jiang, Y. *Cognit. Psychol.* **36**, 28–71 (1998).
15. Moscovitch, M. in *Memory Systems 1994* (eds. Schacter, D. L. & Tulving, E.) 269–310 (MIT Press, Cambridge, Massachusetts, 1994).

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