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Learning and Motivation 36 (2005) 190–207
Learning and Motivation
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Episodic recollection in animals: "If it walks like a duck and quacks like a duck…"

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Received 28 February 2005
Available online 8 April 2005

Abstract

In humans, episodic memory is most commonly defined as the subjective experience of recollection, presenting a major challenge to the identification of episodic memory in animals. Here we take the position that episodic memory also has several other distinctive qualities that can be assessed objectively in animals, as well as humans, and the examination of these properties provides insights into underlying mechanisms of episodic memory. We focus on recent evidence accumulated in this laboratory indicating that recognition in rats involves a threshold retrieval process, similar to that observed in human episodic recall. Also, rats can remember the temporal order of unique events, characteristic of the replay of vivid episodic memories in humans. Furthermore, rats combine elements of "when" and "where" events occur, as well as the flow of events within a memory, to distinguish memories that share overlapping features, also characteristic of human episodic memory. Finally, all of these capacities are dependent on the hippocampus, which also plays a critical role in human episodic memory. This combination of findings strongly suggests that animals have the same fundamental information processing functions that underlie episodic recall in humans.

Keywords: Episodic memory; Animal model; Recollection; Familiarity; Temporal order; What-where-when; Sequence disambiguation; Rat

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doi:10.1016/j.lmot.2005.02.006

The notion that animals experience episodic recollection has met stiff resistance from several sources over many years. Aristotle (350 BC) was among the earliest writers to scoff at animals' cognitive abilities. He contended that"… other animals (as well as human) have memory, but, of all that we are acquainted with, none, we venture to say, except human, shares in the faculty of recollection." By "memory," Aristotle referred to an elementary matching of current sensations to impressions from prior experience, and distinguished this process from a true recollective capacity. Tulving (2002), in his characterizations of episodic and semantic memory, acquiesced that animals had the capacity for semantic knowledge, but claimed that episodic recollection "…has evolved only once, and in only one species, although other species would benefit from it as much as do humans." Even poets have chimed in with a similar pessimistic tone. The Scottish poet laureate Robert Burns concluded his ode "To a mouse on turning up her nest with the plough" with the following stanza:

Still thou art blest, compar'd wi' me!
The present only toucheth thee:
But, och! I backward cast my e'e
On prospects drear!
An' forward, tho' I canna see,
I guess an' fear!

None of these appropriately celebrated great thinkers provided specific evidence in support of their contentions. With all due respect, whether or not animals have the capacity for episodic recollection cannot be resolved by mere assertion. Rather, a compelling resolution rests on experimental analysis. Here we will provide an overview of our initial steps in this direction.

Consider the following common experience. You are at an annual scientific meeting and, while walking down a corridor, see someone coming towards you who looks familiar. As he approaches, you are convinced you know this person, but cannot remember who he is or why you know him. He waves and stops to say hello, further raising your embarrassment at this predicament. Presumably you know him in your scientific life, and indeed you are sure you have interacted with him recently, but you just cannot recall the specific circumstances. A conversation ensues and much to your relief, he begins to talk about some specific results in his work and eventually offers a critical clue and reminder. Now a rich and complex memory comes flooding in. You had seen this person's poster just a few days ago at this very meeting and had had a long conversation about the experiment. You recall the person's name and institution, and you reconstruct the course of your previous discussion and the relationship between his results and other findings reported at this meeting. But wait—during this ensuing conversation, there is one more failure in your memory. You misattribute a result you heard later in the meeting to that person's poster. Having been politely corrected, you leave the interaction wondering about the possibility that age related memory loss has truly begun for you.

This anecdote reflects many of the features of episodic recollection in daily life. First, recollection of previous experiences is distinguished from a sense of familiarity,

even when that sense of familiarity can be quite strong and provide a clue about the recency of prior experience. When a true recollection comes, it arrives in a flood of information about the person and the circumstances of the prior encounter. Importantly, recollective experience is structured by a temporal organization, your memory of the flow of events in a unique experience. This recollective experience is not necessarily perfect, however, and indeed your reminiscence is challenged by interference from memories of other experiences that contain substantial common information. In this paper, we will consider these distinguishing features of episodic recollection, and ask whether they characterize the memory capacities of animals as they do humans. Thus, one of our approaches to the question of episodic memory in animals involves the identification of features of episodic recollection in humans that can be assessed in animals, and the subsequent exploration of these properties of episodic memory within animal memory performance.

In addition, we will employ functional anatomy to address the same question. In the field of human cognitive neuroscience, it is consensual that the hippocampus is critical to the capacity for episodic recollection (Eichenbaum & Cohen, 2001). Therefore, our experiments examine whether hippocampal function is necessary for features of episodic memory performance in animals. Our presumption is that functions for which the hippocampus is essential in animals likely constitute elements of cognitive processing that contribute to episodic memory in humans as well. The combination of findings from behavioral and neuropsychological studies provides strong evidence on the question of episodic recollection in animals.

Here we will consider three fundamental features of episodic memory that were illustrated in the anecdote above. First, episodic recollection is distinguished from a sense of familiarity by its threshold retrieval dynamic—recollection is qualitative whereas familiarity is gradual. Second, recollection is characterized by the temporal organization of experience—reminiscence replays the flow of events in unique episodes and not merely memory for the events themselves. Third, recollection can disambiguate experiences that share overlapping events—recollection allows us to distinguish one memory from other memories that contain similar information. Our efforts are aimed to develop animal models of each of these features of episodic memory, and to examine the role of the hippocampus in each.

Threshold retrieval dynamics: Distinguishing recollection from familiarity

> "What memory goes with is…a very complex representation, that of the fact to be recalled *plus* its associates…known in one integral pulse of consciousness…and demanding probably a vastly more intricate brain-process than that on which any simple sensorial image depends." William James (1890)

By "memory" James was clearly referring to what we call episodic recollection. James emphasized that episodic recollection involves a flood of rich associative information that comes when one passes some sort of threshold. James also suspected that recollection requires a special neural mechanism for processing the complexities of

episodic information, as compared with a simpler kind of sensory matching (similar to Aristotle as described above). Over the last 30 years, cognitive scientists have reexamined these distinctions and proposed dual-process theories for recognition memory (for review, see Yonelinas, 2002). These theories distinguish our capacity for recollection of prior experiences from a sense of familiarity of stimuli without recollection of the circumstances of prior experience.

Recollection and familiarity are distinguished by their cognitive mechanisms, by their retrieval dynamics, and by their putative brain substrates (Yonelinas, 2002). With regard to cognitive mechanisms, familiarity is determined by the strength of a perceptual match to prior exposure and, consequently, is susceptible to variations in superficial sensory qualities of the stimuli. By contrast, recollection allows one to recover the prior episode in which the stimulus was experienced, and emphasizes conceptual properties—the meaning of the object to be recognized—as well as associations of the object, including the spatial and temporal context in which it was experienced. With regard to the dynamics of retrieval, familiarity grows incrementally depending on the amount of prior exposure and degree of perceptual match. By contrast, recollection occurs at a threshold, before which no information is recovered and after which the object plus its associations and context are re-experienced, just as James describes. With regard to brain substrates, recent studies on amnesia and functional brain imaging in humans have suggested that the parahippocampal gyrus may mediate familiarity whereas the hippocampus may mediate recollection (Ranganath et al., 2004). These conclusions are, however, controversial because the anatomical resolution available in studies on amnesia and functional brain imaging does not allow unambiguous distinctions between the adjacent brain areas.

One of the most compelling methods for distinguishing recollection and familiarity is the analysis of receiver operating characteristics (ROC) functions of recognition (Yonelinas, 2001a). In a typical study, human subjects initially study a list of words and then are tested for their capacity to identify those words plus additional new words as "old" or "new." The resulting ROC analysis plots "hits," that is, correct identifications of old items, against "false alarms," incorrect identifications of new items as if they were old, across a range of confidence levels. ROC analysis of human verbal recognition typically reveals an asymmetric function characterized by an above-zero threshold of recognition at the most conservative criterion (zero false alarm rate) and thereafter a curvilinear performance function (Yonelinas, 2001a; Fig. 1A).

The positive *Y*-intercept is viewed as an index of recollection in the absence of measurable familiarity, whereas the degree of curvature reflects familiarity as typical of a signal-detection process (Macmillan & Creelman, 1991). With appropriate experimental manipulations (see Yonelinas, 2001a), the overall ROC curve can be decomposed into separate functions for recollection and familiarity. The recollection ROC curve contains the threshold component of recognition with performance thereafter characterized by a linear function (Fig. 1C), whereas the familiarity ROC curve is symmetrical and characterized by a curvilinear function (Fig. 1B).

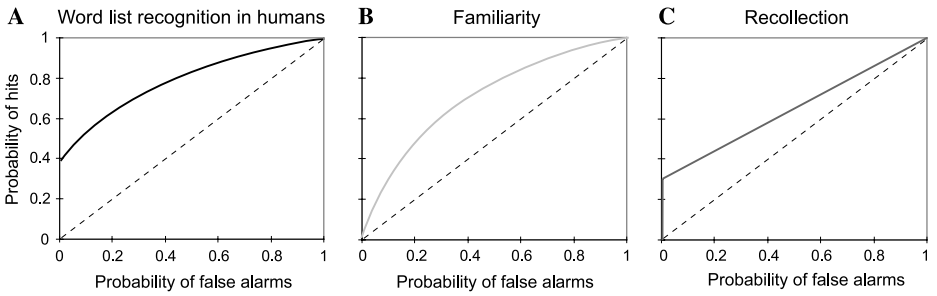

Fig. 1. Receiver operating characteristics (ROCs) for recognition performance in humans. (A–C) Performance of humans in verbal recognition memory.

To examine the retrieval dynamics of recognition memory in rats, we developed a recognition task that exploits rats' superb memory capacities with odors (Fortin, Wright, & Eichenbaum, 2004). On each daily test session, rats initially sampled 10 common household scents mixed in with playground sand in a plastic cup containing a cereal reward. When each sample was presented, the animal would dig for the reward and incidentally smell the odor of the sand. Following a 30 min memory delay, the same odors plus 10 additional odors were presented one at a time in random order. On each test, the animal followed a non-match to sample rule such that it could dig in the target odor to obtain a reward if the target was "new" (a non-match) or could refrain from digging at the target if the odor was "old" (a match) and instead obtain a reward in an empty cup on the opposite end of the test chamber (see Fig. 2). A different response criterion for each daily session was encouraged using a combination of variations in the height of the test cup, making it more or less difficult to respond to that cup, and manipulations of the reward magnitudes associated with correct responses to the test and the unscented cup. Notably, the use of a method for explicitly varying the animal's bias is different from the use of confidence judgments in experiments on recognition in humans (Yonelinas, 2001b, 2002); we conceive of both as merely methods for shifting the subject's criterion along the full range required to compute ROC curves.

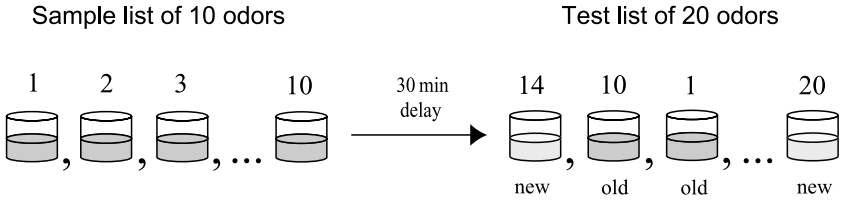

Fig. 2. Odor recognition task for ROC analyses in rats. In each session, rats initially dug for a 1/4 Cheerio reward in each of 10 cups filled with playground sand scented with a distinct odor, which were presented individually in the front of the home cage. For each of the subsequent 20 test odors, the animal could obtain an additional reward by digging in the test cup if the odor was 'new' (i.e., non-match) or by refraining from digging in the test cup and approaching an alternate empty cup at the back of the cage if the odor was 'old' (i.e., match). We recorded correct responses (hits) and incorrect responses (false alarms) at the alternate cup.

The ROC curve of intact rats was asymmetric (Fig. 3A), containing both a threshold component (above-zero *Y*-intercept) and a strong curvilinear component. This pattern is remarkably similar to the ROC of humans in verbal recognition performance (Fig. 1A), consistent with a combination of recollection-like and familiarity-based components of recognition in animals. Subjects were subsequently divided into two groups matched on both performance components and one group received selective lesions of the hippocampus whereas the other group received sham control operations. After recovery, we again tested recognition performance at each response criterion. The ROC of control rats continued to reflect both recollection-like and familiarity components, whereas the ROC of animals with selective hippocampal lesions was fully symmetrical and curvilinear (Fig. 3B), characteristic of familiarity-based recognition in humans (Fig. 1B). To describe these patterns quantitatively, we calculated indices of recollection and familiarity (Figs. 3A and B, insets). Whereas familiarity remains normal in rats with hippocampal lesions, recollection is severely impaired. Furthermore, if the recollective component is subtracted from the ROC of control animals, the resulting curve superimposes on the ROC of rats with hippocampal lesions (Fig. 3B), providing further evidence that recollection is selectively impaired in the hippocampal group.

The overall level of performance (averaged across biases) on the task is slightly worse in the hippocampal group (66%, compared to 73% in controls). Given that any performance deficit would be expected to result in an ROC closer to the diagonal (chance performance), it is possible that the alteration in their ROC pattern resulting from the hippocampal lesion reflects a generalized decline in memory. To compare their ROC with the pattern of forgetting in normal animals, we challenged the memory of control rats by increasing the memory delay to 75 min. This manipulation succeeded in reducing the overall level of performance of control animals to 64%, equivalent to that of the hippocampal rats. Yet, further testing of

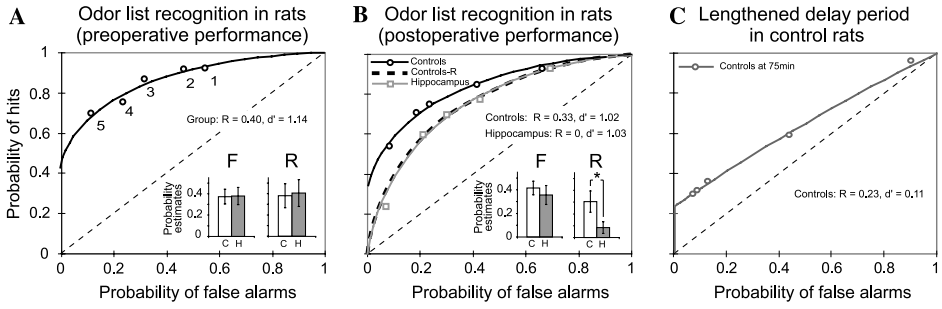

Fig. 3. Receiver operating characteristics (ROCs) for recognition performance in rats. (A) Normal rats tested at a 30-min memory delay. Insets show recollection estimates (R), which correspond to the *Y*-intercept obtained from the ROC of individual subjects, and familiarity estimates (F) which correspond to the degree of curvature (*d'*) of individual ROCs (transformed into a probability in order to facilitate comparisons with R). (B) Control rats and rats with selective hippocampal lesions at a 30-min delay; also shown is the ROC curve for Controls with the estimated recollection component (cf. Fig. 1C) algebraically removed (Controls-R). (C) Control rats tested at a 75-min memory delay.

the controls showed that their ROC continued to have an asymmetrical threshold component, as indicated by an above-zero *Y*-intercept (Fig. 3C—compare with Fig. 1C). Notably the controls' ROC was distinctly more linear than that of both the hippocampal rats and the controls when tested at the shorter memory delay. This pattern of performance suggests that, in normal rats, familiarity fades more quickly than recollection, similar to observations on humans (Yonelinas, 2002). Moreover, comparison of the ROC curve in normal rats at the 75 min delay vs that of rats with hippocampal damage at the 30 min delay emphasizes the distinction between these two groups in their differential emphasis on recollection and familiarity, respectively, even when the overall levels of recognition success are equivalent.

These findings strongly suggest that rats exhibit two distinct processes in recognition, one that is marked by a threshold retrieval dynamic characteristic of episodic recollection in humans, and another that follows a symmetrical and curvilinear processing function characteristic of familiarity in humans. These observations match recent findings that distinguish impaired recollection from intact familiarity in humans with putative damage to the hippocampus (Yonelinas et al., 2002).

Temporal organization of events in unique experiences

> "The organization of knowledge in the episodic system is temporal. One event precedes, co-occurs, or succeeds another in time." Tulving (1983)

> "Acts of recollection, as they occur in experience, are due to the fact that one thought has by nature another that succeeds it in regular order." Aristotle (350 BC)

These nearly identical characterizations emphasize that vivid episodic memories are constituted as sequences of events that unfold over time and space. Therefore, consideration of memory for the orderliness of events in unique experiences provides another potentially fruitful avenue for exploring the existence of episodic memory in animals.

To investigate the specific role of the hippocampus in remembering the order of events in unique experiences, we developed a behavioral protocol that assesses memory for episodes composed of a unique sequence of olfactory stimuli (Fortin, Agster, & Eichenbaum, 2002; see also Kesner, Gilbert, & Barua, 2002). In addition, our design allowed us to directly compare memory for the sequential order of odor events with recognition of the odors in the list (independent of memory for their order; Fig. 4). On each trial, rats were presented with a series of five odors, selected randomly from a large pool of common household scents. Memory for each series was subsequently probed using a choice test where the animal was reinforced for selecting the earlier of two of the odors that had appeared in the series. For example, the rat might be initially presented with odors A then B then C then D then E. Following the delay, two non-adjacent odors, e.g., B and D, were presented and the

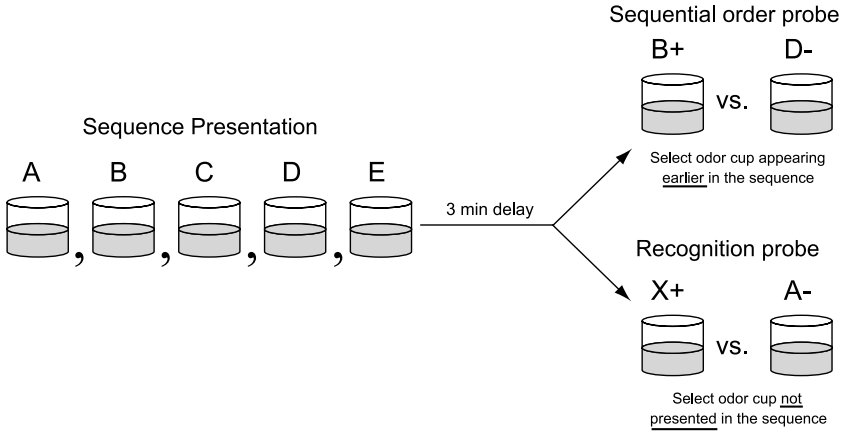

Fig. 4. Sequential order and recognition tasks. *Left*, presentation of sample sequence. Letters A–E designate the five randomly selected odors presented in a particular series. *Right*, examples of the sequential order and recognition probe for that series. +, reinforced odor; −, non-reinforced odor.

animal would be rewarded for selecting the odor that appeared earlier (in this case, B). Animals were tested with six different types of probes that assessed memory for different separations (lags) between odor presentations in the series. On each trial, any pair of non-adjacent odors might be presented as the probe, so the animal had to remember the entire sequence to perform well throughout the testing session.

Normal rats performed sequential order judgments across all lags, and performance on probes was dependent on the "lag," or number of intervening items, indicating that order judgments were easier for more widely separated items (Fig. 5A). Following assessment of the performance of normal rats, subjects were divided into two groups matched for performance; animals in one group were given selective

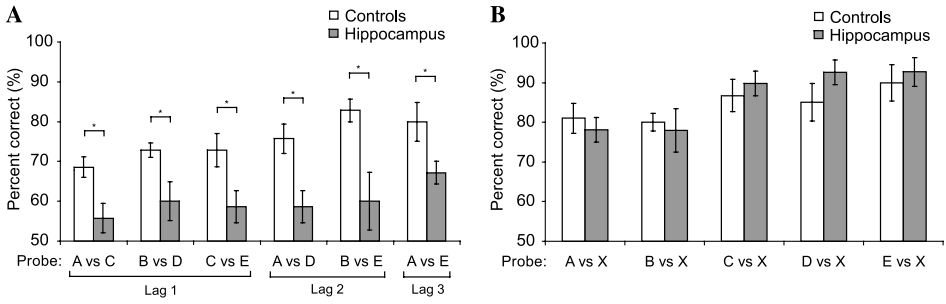

Fig. 5. Performance (mean percent correct ± *SEM*) of control rats and rats with hippocampal lesions on sequential order and recognition probes. (A) Performance on the sequential order probe types, grouped according to the lag (number of intervening elements) between items in the probe test. (B) Performance on the recognition probes. 'X' designates a randomly selected odor that was not presented in the series and used as the alternative choice. $*p < .05$.

hippocampal lesions whereas those in the other group received sham operations. After recovery, all animals were tested again on memory for the order of odors in unique odor sequences. Normal rats continued to perform well. By contrast, rats with hippocampal lesions judged the order of odors at near-chance levels and were impaired at all lags (Fig. 5A).

The same rats were then also tested on their ability to recognize the odors that were presented in the series (see Fig. 4). On each trial, a series of five odors was presented in a format identical to that used in the sequential order task. Then recognition was probed using a choice test in which the animal was presented with one of the odors from the series and another odor from the pool that was not in the series. Reinforcement was given for selecting the odor not presented in the series. For example, the rat was presented with the series A through E, and, then, following a delay, an odor selected randomly from those initially sampled and an odor not presented in the sequence, e.g., A and X, were presented. The rat was rewarded for choosing X. The five types of probes differed in the recency of the initially presented odor.

Both control rats and rats with selective hippocampal damage acquired the task rapidly, and there was no overall performance difference between the groups in acquisition rate. Subsequent analyses of the performance on the different types of probes showed that rats with hippocampal lesions performed as well as normal rats in recognition throughout the series (Fig. 5B). Furthermore, in both groups, recognition scores were consistently superior on probes involving odors that appeared later in the series, suggesting some forgetting of items that had to be remembered for a longer period and through more intervening items.

A potential confound in any study that employs time as a critical dimension in episodic memory is that memories obtained at different times are likely to differ in the strength of their memory traces, due to the inherent decremental nature of memory traces. To what extent could normal animals be using differences in the relative strengths of memory traces for the odors to judge their sequential order? The observation of a temporal gradient in recognition performance by normal animals suggests that memories were in fact stronger for the more recently presented items in each sequence (performance on E vs X is better than on A vs X; Fig. 5B). These differences in trace strength potentially provide sufficient signals for the animals to judge the order of their presentation. However, the observation of the same temporal gradient of recognition performance in rats with hippocampal damage indicated that they had normal access to the differences in trace strengths for the odors. Yet these intact trace-strength differences were not sufficient to support above chance discrimination on any sequential order probe (with the exception of deficient but above chance performance on the furthest separated items). These considerations strongly suggest that normal rats also could not utilize the relative strengths of memories for the recently experienced odors, and instead based their sequential order judgments directly on remembering the odor sequence. Our observations suggest that animals have the capacity to recollect the flow of events in unique experiences and that the hippocampus plays a critical role in this capacity.

"What–where–when" memory for unique experiences

In his original characterization of episodic memory, Tulving (1972) emphasized our ability to remember not only the flow of experiences but also where each event occurred. To explore these aspects of episodic memory, we developed a task that assesses memory for events from single episodes involving a combination of odors ("what") presented in unique places ("where") in a specific order ("when"; Ergorul & Eichenbaum, 2004). On each trial, rats sequentially sampled a unique series of four rewarded odor stimulus cups, each in a different place along the periphery of a large open field (Fig. 6). Then, memory for the order of those events was tested by presenting a choice between an arbitrarily selected pair of the odor cups in their original locations. We recorded both the stimulus of initial *approach* (defined as arriving at the edge of the cup) and the *choice* defined as the first cup in which the rat dug in the sand.

As measured by choices, normal rats performed this task well above chance (76.2% correct), indicating that they can remember the order of unique sequences of odors and places (Fig. 7A). Performance was above chance at all lags, and was superior at the largest lag to that at shorter lags. In addition, we found that rats first approached the correct stimulus at well above chance level (Fig. 7A), indicating they remembered the sequence of places where the cups were presented prior to perceiving information about the odor at that location; importantly, separate tests showed

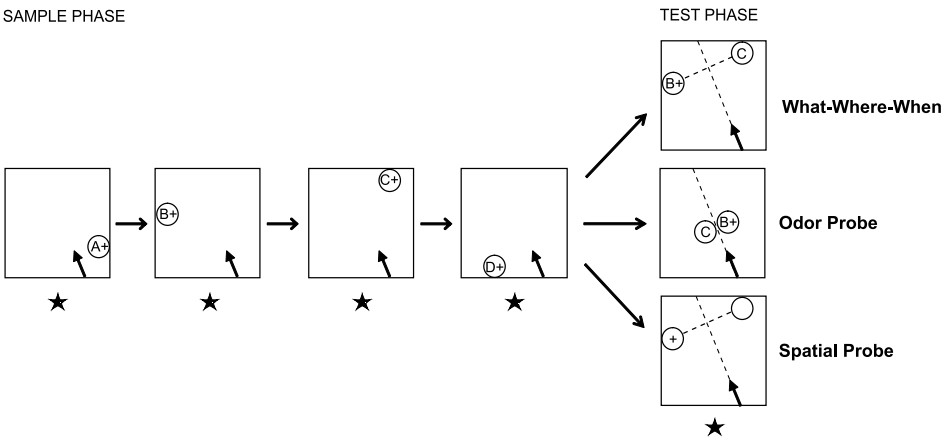

Fig. 6. An example (B vs C) trial for a what–where–when test and odor and spatial probes. In the *sample phase* of every trial, rats were presented with four odors in series (A+ → B+ → C+ → D+), each at a different location on a platform. In the following *test phase*, odors B and C were presented in their sample locations in the *what–where–when* choice test, or next to each other in the *odor probe*, or two non-odorous stimuli were presented in the sample locations of B and C in the *spatial probe*. +, reinforced stimulus; *arrow on the platform*: position of the rat at the starting-point (arrowhead corresponds to the rat's head); *star symbol*: the experimenter's fixed position throughout testing.

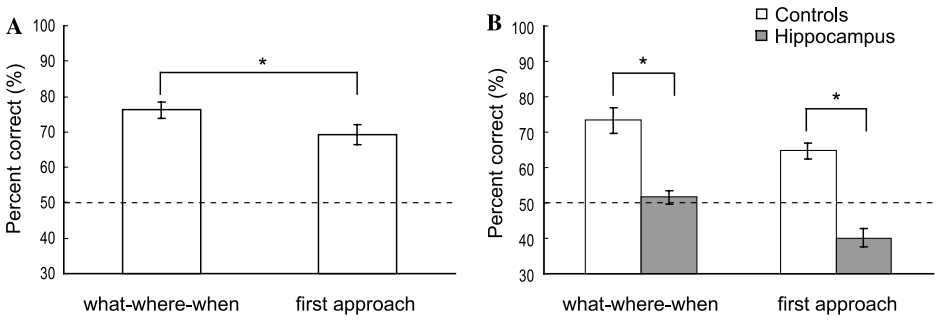

Fig. 7. Comparison of performance (mean ± *SEM*) vs percentage of correct first approaches on the what–where–when probe tests. (A) Pre-surgery performance of normal rats ($n = 14$). (B) Post-surgery performance of sham-control ($n = 7$) and hippocampal lesion ($n = 7$) groups. *Dashed line*: chance level. *$p < .05$.

that rats cannot accurately judge the odor in a cup until they arrive at the edge of the cup.

To examine the individual contributions of odor and spatial information that guided performance, we also presented probe tests where either the spatial information was eliminated (odor probe) or the odor information was removed (spatial probe; see Fig. 6). In these tests, the trial began with the usual presentation of a series of four odors. Then, in odor probes, two of the cups were presented side-by-side in the center of the open field. Rats chose well above chance, indicating they can remember the sequence of odor presentations, even without the normally accompanying spatial information. In spatial probes, two stimulus cups without odors were placed in their initial locations. Rats chose correctly no more often than predicted by chance. Poor performance on the spatial probes is surprising, because the same rats performed well on their initial approach to the odor cups on standard test trials. This combination of findings suggests that the removal of normally accompanying odor cues was disruptive to the choice on the spatial probe tests, indicating that normal rats use both the spatial and odor cues on standard trials.

As in the previous studies, animals were subsequently separated into matched groups and subjects in one group received selective hippocampal lesions. In post-surgical testing, intact rats continued to choose well on the standard "what–where–when" trials at all lags (Fig. 7B). By contrast, the performance of animals with hippocampal lesions was no better than chance at any lag. In addition, whereas intact rats continued to perform well on the initial approach, rats with hippocampal lesions approached the correct choice *less* often than expected by chance (Fig. 7B). Contrary to the strategy of normal rats and the reinforcement contingency of the test phase, rats with hippocampal damage were inclined to visit the *more recently* presented and rewarded place rather than the earlier visited locus. This observation indicates an intact spatial memory in rats with hippocampal damage that was employed despite its maladaptive consequences.

The full pattern of findings from this study indicates that normal rats employ both odor ("what") and spatial ("where") cues in composing their judgments about the

order ("when") of events in unique experiences, and that the hippocampus is critical for effectively combining these three qualities of each experience to compose the retrieved memory. Normal rats initially employ their memory of the places of presented cups and approach the location of the earlier experience. Then they confirm the presence of the correct odor in that location. Animals with hippocampal damage fail on both aspects of this task and, instead, their behavior is guided by other forms of memory. They can initially approach the most recently rewarded location based on spatial memory alone. Also, when the odors can be sampled concurrently, they can identify the more familiar of two odors. Even though they have some form of memory for both the spatial and olfactory cues, they cannot combine these cues effectively to judge the order of events that occur in particular places.

The findings from both of the above studies strongly support the notion that animals can remember the order of events in unique experiences and that the hippocampus makes an essential contribution to this kind of memory processing.

Disambiguation of episodic memories with overlapping elements

Another central feature of episodic memory is our capacity to distinguish one particular memory from other memories that share common elements. Extending the above characterization of vivid episodic memories as event sequences, Levy (1996) proposed that related memories can be viewed as event sequences that share elements. He argued that a fundamental function of the hippocampus is to disambiguate overlapping sequences so that behavior will be guided by the full series of events that compose a distinct episode.

To test whether sequence disambiguation is a fundamental feature of memory processing dependent on the hippocampus, we trained rats on a task designed after Levy's (1996) formal model that involved two fixed series of events that overlap in the middle items (Fig. 8; Agster, Fortin, & Eichenbaum, 2002). The two sequences were presented as a series of six pair-wise odor choices where, for each sequence, selection of the appropriate odor at each choice point was rewarded. The odor cups were covered by perforated lids, so that the rat could smell the odor without touching the lid, but had to push the lid aside to gain entry and dig for a reward. Each trial began with a forced choice between the two initial odors of each sequence. The choice was forced in that the lid over the incorrect choice was "locked," preventing access inside the cup, whereas the lid of the correct choice could be pushed aside and a food reward could be obtained within. Then the animals were given a forced choice between the second odors of each sequence. Next the animal was presented with two additional forced choices, but these choices were identical for both sequences (the overlapping elements); other never-rewarded odors were used as foils. Subsequently, the subject was allowed a *free* choice, and was rewarded for selecting the odor assigned to the ongoing sequence. Finally, the animal completed that sequence with one more forced choice. The critical feature of this task was the free choice. On that test, animals were required to remember their choices from the first two pairings of the current sequence during the ambiguous components of the

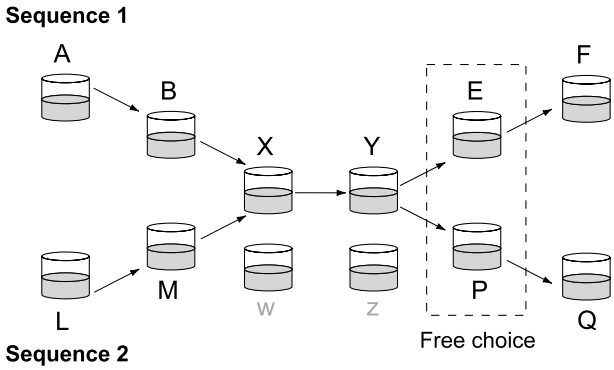

Fig. 8. The sequence disambiguation task. The two odor sequences are indicated by *letters*. In performing each sequence, the rat selected between vertically aligned odors in each sequence. Sequence 1 consisted of A-B-X-Y-E-F and Sequence 2 of L-M-X-Y-P-Q; note that in both sequences *X* was to be selected over *W*, and *Y* over *Z*. Choices were forced on the first four pairs (A vs L, B vs M, X vs w, and Y vs z) and on the last (F vs Q). However, on the fifth pair (E vs P) animals were allowed a free choice and were rewarded for selecting the odor assigned to the ongoing sequence. The spatial location where the odors were presented was randomly determined.

trial, and then use the earlier information to guide the correct odor selection for that episode.

In one variant of the task, rats were trained to alternate sequences of odor choices, with minimal delay between the alternations. Normal rats performed at a high level on the free choice, indicating the ability to disambiguate overlapping odor sequence memories (Fig. 9A). These rats were divided into two groups matched for performance, and one group received hippocampal lesions whereas the rats in the other group received sham control surgeries. The intact rats continued to perform well. By contrast, rats with damage to the hippocampus performed poorly on the free choice.

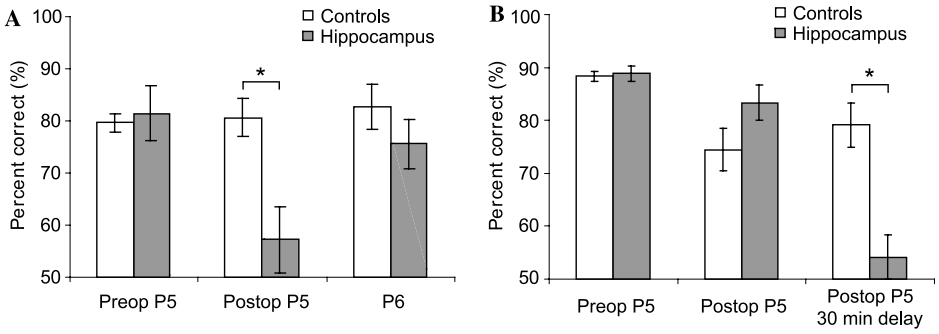

Fig. 9. Performance (mean percent correct ± *SEM*) of control rats and rats with hippocampal lesions in the sequence disambiguation task. (A) Alternation version: Performance of control rats and rats with hippocampal lesions on preoperative and postoperative pair five choices (E vs P), and on pair six choices (F vs Q). (B) Random-order version: Performance of control rats and rats with hippocampal lesions on pair five choices. Scores are shown under minimal delays during testing (preoperatively and postoperatively), and with a 30-min delay period immediately preceding the presentation of the free choice (P5). *$p < .025$.

Importantly, rats with hippocampal damage could correctly judge the final item in the sequence, which was unambiguously predicted by the preceding choice.

In another variant of the task, the sequences were presented in random order with a 15-min interval inserted between sequences to reduce interference. Normal animals again learned the task rapidly (Fig. 9B). Under this condition, rats with hippocampal lesions performed as well as normal rats when each trial involved uninterrupted presentation of the full sequence of odor choices. However, when we challenged their memory by introducing a substantial (30 min) delay before the free choice, hippocampal rats were severely impaired whereas intact rats performed well.

Comparison of the results from the two variants of the sequence disambiguation task offers clues about the cognitive demands of sequence memory that require hippocampal function. When the entire sequence was performed without interruption, rats with hippocampal damage were impaired on the alternation task but not on the random sequence task. Possibly this difference resulted from the fact that the alternation task involved a higher level of proactive interference because the sequences were repeated frequently. Nevertheless, even in the version of the task where animals with hippocampal lesions performed well (the random order task), when a 30-min delay was interposed prior to the critical free choice, their performance fell to chance. These findings suggest that some aspects of sequence memory can be accomplished outside of hippocampal function. Possibly, when memory demands are minimal, as in conditions of low proactive interference or no demand to hold information through ambiguous material, rats with hippocampal damage can succeed in creating unambiguous representations for learned sequences. This success may reflect an intact capacity of other brain systems, such as cortical–striatal pathways, to mediate habitual sequences under conditions where each segment of the sequence rapidly or unambiguously leads to the next. Conversely, when proactive interference is high, or a substantial delay is imposed, a representation mediated by the hippocampus is required to accomplish sequence disambiguation.

Conclusions

To the extent that the criterion for episodic memory relies upon measures of subjective experience, it seems very unlikely that the existence of this capacity can be determined in animals. However, one might be skeptical about whether subjective reports are adequate tests of the existence of an episodic memory even in humans, given that humans are prone to report subjective memory experiences for events that did not actually occur (e.g., Schacter, 2001). Therefore, the scientific analysis of episodic memory might most confidently proceed based on objective measures of memory performance, focusing on characteristics of episodic memory that can be measured across species.

Here we have identified three distinctive features of episodic memory that are common in characterizations of this kind of memory. Episodic memories involve a threshold retrieval dynamic, such that recollection occurs in an all-or-none fashion containing associative and contextual information as well as the object of recollec-

tion. Furthermore, episodic memories are characterized by a temporal organization of the flow of events in unique experiences and the places where they occur, as well as by the capacity to disambiguate experiences from one another when they contain common elements. We presented evidence that animals have each of these capacities. Furthermore, we found that the hippocampus is critical to each of these capacities, providing a common neural substrate for human episodic memory and features of memory in animal performance. We contend that the combination of these findings provides especially compelling evidence in favor of the view that animals indeed have the capacity for episodic recollection.

Other models of episodic memory in animals

Others have suggested additional properties that are characteristic of episodic memory. Perhaps most prominent among these is Clayton, Bussey, and Dickinson's (2003a) claim that episodic memory emphasizes information about the time at which different episodes occur and the flexible expression of this information. In a series of elegant experiments, they have shown that scrub jays can flexibly select or reject a preferred but degradable food that was previously cached, depending on whether a long or short time has passed since caching. This approach is appealing, in that it mirrors our capacity to declare "when" an episode happened. But any behavior that is dependent on large differences in the amount of time passed could also be supported by the ability to perceive the strength of a memory trace or the amount of time that has passed since the experience (Roberts, 2002). Thus, jays may have learned that weak (or old) memory traces for the preferred food signal that it has likely degraded, whereas strong (or recent) memory traces signal that the food is still good. To address this issue, Clayton, Yu, and Dickinson (2003b) investigated how jays respond when tested at times intermediate between the short and long times since the initial learning events. Jays made categorical judgments, generalizing intermediate times to be equivalent to either the short or long initial duration, rather than showing a gradient of choices indicative of "forgetting." However, this result does not require us to conclude that animals cannot detect the gradual changing strength or age of a memory. The jays could have had an internal gradual gradient and then applied it in making a categorical decision about which of two responses to emit in a binary choice situation. In our view, one cannot eliminate the confound of differential memory strengths in tests on memories that occurred at different times; instead, it must be demonstrated directly that the animals cannot *use* cues about memory strength or age to accurately make the critical memory judgments. This criterion was satisfied in the experiment on judging the order of a series of odors described above (Fortin et al., 2002).

Recently, others have suggested that memory for the "place" or "context" of events constitutes another feature of episodic memory. Each of these efforts has demonstrated a critical role for the hippocampus in memory for events defined by the context in which they occurred. Gaffan (1994) trained monkeys on a set of discrimination problems composed of objects stimuli presented on a computer screen with different kinds of background patterns. Animals with the hippocampus disconnected

by fornix lesions learned object discriminations at the normal rate when the background simply varied and did not predict the location of the objects or their reward values, but, the same animals were impaired when the background context predicted the location of the rewarded object. Day, Langston, and Morris (2003) initially allowed rats to find different flavored rewards at specific locations on a open platform and then tested their memory for the location of those events cued by the flavor associated with one of the locations. After a single exposure, rats could identify the location in which a flavor had previously been consumed. By contrast, inactivation of the hippocampus or blockade of NMDA receptors prevented encoding of the flavor-place association.

Other studies have demonstrated critical hippocampal involvement in processing contextual information independent of the spatial position of an object. Mumby, Gaskin, Glenn, Scharmek, and Lehmann (2002) initially exposed rats to two objects in particular places in one of two environmental chambers. In subsequent recognition testing, the place of the object within a context or the context was changed. Normal rats show increased exploration of objects moved to new places or in novel contexts. By contrast, rats with hippocampal damage failed to show recognition following a shift in context or place. Another study failed to find a deficit in object–place recognition following hippocampal disconnection, but the same animals had a severe deficit in recognition based on a combination of contextual and place cues (Eacott & Norman, 2004). Perhaps the strongest evidence that the hippocampus is critical for learning the context of important events comes from studies of fear conditioning (Phillips & LeDoux, 1994). These studies are based on the conditioning protocol in which a tone and shock are paired repeatedly such that rats become fearful of the tone. In addition to a conditioned fear for the tone cue, rats also become fearful of the context in which the tones and shock were presented, evidenced as freezing and other indices of fear when the animal is returned to the environment where conditioning occurred. Damage to the hippocampus eliminates the contextual fear conditioning, without affecting conditioned fear to the tone.

These findings are consistent with evidence from studies of memory for spatial and contextual information in a human amnesic patient. In one experiment, the patient toured a virtual reality town, playing a game in which he retrieved objects from people he met in the environment (Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001). After retrieving several objects, the subject was tested on memory of the events. In each test, he could normally recognize which of two objects was retrieved and could recognize particular scenes of the environment, but performed poorly on identifying which of two objects was given earlier, or by a particular person, or in a particular place. In another experiment, the ability of this patient to recognize objects in scenes was further tested (King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002). Again the subject initially received objects at particular places in a virtual reality town. In subsequent testing, he could normally recognize those objects when presented from the original view, but was impaired when perspective of the scene was shifted. These findings suggest that the patient could use intact pattern-matching to identify familiar scenes but could not recollect the scene when required to re-orient his frame of reference to a novel perspective. These studies are appealing

in that they demonstrate a common role for the hippocampus in episodic and contextual memory across species.

In closing, it should be kept in mind that the hippocampus is involved in more than episodic recollection. There is now substantial evidence that the hippocampus contributes to the flexible expression of semantic memories for spatial, contextual, and non-spatial memory (Eichenbaum & Cohen, 2001). Therefore, susceptibility to hippocampal damage is not, in and of itself, a *sufficient* criterion for the existence of episodic memory. However, because episodic memory in humans is known to depend on the hippocampus, demonstrating the role of the hippocampus for any putative episodic memory processing function should be considered a *necessary* component of confirmatory evidence.

Finally, while it is impossible to demonstrate the subjective experience of recollection in animals, the findings described here provide evidence for several features of episodic memory processing in non-human animals. At the very least, these findings reveal the existence of fundamental cognitive processing mechanisms in animals that underlie the emergent property of subjective experience in human recollection. However, we take a stronger position in accord with the old dictum, "If it quacks like a duck and walks like a duck, it's a duck." We contend: Animals exhibit defining features of human episodic memory, and these features of their memory require hippocampal function as they do in human episodic memory. Therefore, animals experience episodic recollection.

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