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OUTLOOK

Rats can replay episodic memories of past odors

Thomas R. Zentall [1]

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Summary
Panoz-Brown et al. (*Current Biology, 28,* 1628–1634, 2018) present evidence to support the hypothesis that rats can replay their episode memory to determine which of a series of odors was at a particular location in the sequence. They also show that the hippocampus is likely involved in allowing the rats to replay those memories.

Keywords Memory · Episodic memory · Memory replay

Episodic memory involves being able to mentally travel back in time to recover personal memories of past experienced events. They can be distinguished from semantic memory consisting of memory for information or facts that are known but not remembered as an experience. Episodic memory is easier to assess in humans than in other animals because language can identify the event in question (e.g., asking "What did you have for dinner last night?").

To assess episodic memory in rats, Panoz-Brown et al. (2018) used a series of trial-unique, successively presented odors. At the end of the sequence, to obtain the optimal amount of reward, given one context, the rats had to select the second from the last odor in the sequence (rather than a different odor from the sequence); given a different context, the rats had to select the fourth from the last odor in the sequence (rather than a different odor from the sequence). The use of a variable number of odors from trial to trial made it impossible for the rats to predict the target odor when it occurred. Thus, not until the entire sequence of odors had been experienced was it possible for a rat to identify the target odors, and not until the context was experienced could the correct odor be identified.

✉ Thomas R. Zentall
zentall@uky.edu

[1] Department of Psychology, University of Kentucky, Lexington, KY 40506, USA

One of the earliest uses of the sequential presentation of stimuli with a following test of item memory had human subjects respond based on whether they had seen a particular stimulus item in a just-experienced list or not (Sternberg, 1966). The results with that procedure suggested that subjects replayed the entire sequence at the time of test because the latency of their response was a direct function of the length of the list. Furthermore, surprisingly, response latencies were comparable, whether the item was in the list or was not in the list. This suggests that when the item was in the list, subjects replayed the entire list because had they responded as soon as they reached the target item, latencies should have been shorter, on average, when the target item was in the list, than when the item was absent. It would be interesting to determine if rats too replay the whole list before deciding which odor is appropriate for the context presented.

To provide evidence that the rats were actually replaying episodic memories, Panoz-Brown et al. (2018) proposed five tests of the replay of episodic memories that could be applied to their experiments. First, an animal that replays episodic memories should remember the order of multiple unique events. In this case, the sequence of odors. Second, the animal should rely on episodic memory rather than nonepisodic memory alternatives to remember the order of events. That is, the strength of the memory should not be a reliable cue to the correct odor. Third, episodic memory replay should be a part of long-term memory. Thus, a delay between experiencing the sequence and the test should not be disruptive of accuracy. Fourth, episodic memory replay should be resistant to interference from other memories (events experienced between presentation of the sequence and testing). Fifth, because the hippocampus is assumed to be involved in the storage of episodic memories, their replay should be dependent upon the

hippocampus. That is, if the hippocampus is disabled, then it should disrupt test accuracy.

In their first experiment, Panoz-Brown et al. (2018) demonstrated that rats could accurately choose either the second to the last or fourth from the last odor in the trial sequence, depending on a context cue (instruction) provided. To control for the possibility that the rats were using memory strength cues in the two test contexts (i.e., based on time from the end of the odor sequence), in Experiment 2 the authors doubled the interitem interval such that the delay between the odor that was second from the end would be same as the delay of the odor that was fourth from the end during training. In Experiment 3, the authors tested the rats for their long-term memory for the odor sequence by delaying the test for 60 min following presentation of the odor sequence. In Experiment 4, they tested the memory of the experienced sequence for resistance to interference by inserting an unrelated new-old, odor recognition task between experiencing the sequence and testing. In Experiment 5, the authors asked whether episodic memory replay is dependent on the hippocampus by chemically suppressing activity in the hippocampus. Interestingly, although suppression of the hippocampus significantly reduced the rats' accuracy, the rats were still reasonably accurate on the episodic memory replay task. The results of all five experiments were consistent with the hypothesis that the rats were replaying an episodic memory.

The authors used an interesting and creative form of training on this complex task. To facilitate acquisition, they used a modified correction procedure. To maintain incentive motivation, if the rat's initial choice was correct, then it was provided with a pellet of food, and then it was given an additional five pellets. If the rat chose the incorrect odor, however, it was not fed but it was allowed to go to the unchosen odor and receive one pellet of food, but it would not receive the additional five pellets. Thus, reinforcement could be obtained on all trials, but it could be obtained sooner and of a larger amount when the correct response was made first. The necessity of this reinforcement procedure compared with the more typical reinforcement versus nonreinforcement method is not clear, but it is an interesting variation that is worthy of study in its own right.

It has been argued that a true measure of episodic memory requires that, at the time of experiencing the target event, there should be no expectation that the event will have to be remembered (e.g., asking a human subject "What did you have for dinner last night"; see Zentall, Clement, Bhatt, & Allen, 2001). Although this requirement was not met in the present experiments, in a cleverly designed experiment, Zhou, Hohmann, and Crystal (2012) demonstrated that rats can recover memories that are not expected to be recalled at the time that they are experienced.

The key to encouraging animals to use their cognitive ability is, in part, to understand the naturally occurring behavior of the animal, so that the stimuli, responses, and reinforcers are appropriate for the animal. The use of olfactory stimuli satisfies that criterion because olfactory stimuli are more discriminable and more memorable for rats (see, e.g., Slotnick & Katz, 1974) than are more typically used, visual or auditory stimuli that are easier to control (present and remove) and more discriminable to humans.

Evidence for the replay of episodic memory by rats presented by Panoz-Brown et al. (2018) represents a model of how one should approach the exploration of comparative cognition. A challenge to researchers who study comparative cognition is, by necessity, how to study processes that cannot be assessed directly. Thus, typically, behavioral evidence for a cognitive process requires that alternative mechanistic processes be ruled out. This means that it is essential that the measures of assessment be appropriate to identify the underlying mechanisms. In this multiexperiment study, the procedures used need to be sufficiently complex to isolate the underlying process, yet they also need to be simple enough to encourage the subjects to use the presumed cognitive process necessary to increase the probability of reinforcement. The research by Panoz-Brown et al. to study the replay of episodic memories by rats does an excellent job of balancing the need to rule out simpler means for the animals to correctly identify the target stimulus, yet appropriately tap into the animal's cognitive ability.

The elegance of these episodic memory replay experiments is that, although the theoretical questions being asked are complex and elusive (does the rat have episodic memories that it can replay), the actual procedures are relatively simple: Experiencing the sequence of odors one at a time and then choosing between two odors, one correct, the other an incorrect foil from the same sequence that had been experienced either before or after the target odor. More generally, this article by Panoz-Brown et al. (2018) provides an excellent model for how to design and conduct a series of experiments to answer a complex question in comparative cognition.

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