Episodic-Like Memory in Rats: Is It Based on When or How Long Ago?

William A. Roberts *et al.*

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cannot yet differentiate this account from alternative interpretations.

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Supporting Online Material

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Materials and Methods
Figs. S1 and S2
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Episodic-Like Memory in Rats: Is It Based on When or How Long Ago?

William A. Roberts,[1]* Miranda C. Feeney,[1] Krista MacPherson,[1] Mark Petter,[2] Neil McMillan,[1] Evanya Musolino[1]

Recent experiments with rats suggest that they show episodic-like or what-where-when memory for a preferred food found on a radial maze. Although memory for when a salient event occurred suggests that rats can mentally travel in time to a moment in the past, an alternative possibility is that they remember how long ago the food was found. Three groups of rats were tested for memory of previously encountered food. The different groups could use only the cues of when, how long ago, or when + how long ago. Only the cue of how long ago food was encountered was used successfully. These results suggest that episodic-like memory in rats is qualitatively different from human episodic memory.

Although Tulving (*1*) initially defined episodic memory as a person's ability to remember a personal past event (what) including where and when it happened, he later amended this definition to include autonoetic consciousness or the feeling of retrieving a personal episode (*2*). It was argued further that episodic memory is found only in humans (*3*). However, recent research with birds and rodents has brought this position into question. By using Tulving's original criteria of what-where-when, it has been shown in behavioral experiments that scrub jays (*4*–*6*) and rats (*7*–*10*) remember where and when they cached or discovered foods of differing palatability. Because these experiments could not involve an assessment of autonoetic consciousness, their findings have been taken as evidence for episodic-like memory, a form of memory in animals that may have some of the properties of human episodic memory (*11*).

Of particular importance in these studies was the discovery that animals could remember when they had cached or encountered a favored food. Memory for when suggests that animals can mentally travel in time or locate a past event within a temporal framework of hours and days (*12*). An alternative possibility is that, instead of remembering when an event happened within a framework of past time, animals are keeping track of how much time has elapsed since caching or encountering a particular food item at a particular place and are using elapsed time to indicate return to or avoidance of that location (*12*). The cues of when and how long ago are typically confounded in studies of episodic-like memory. Thus, animals might be remembering how long ago an event occurred by keeping track of elapsed time using accumulators, circadian timers, their own behavior, or the strength of a decaying memory trace (*13*–*17*). If this is the case, then episodic-like memory in animals may be quite different from human episodic memory in which people can reconstruct past experiences within an absolute temporal dimension (*18*–*20*).

In two experiments, we asked whether the temporal cues used by rats to show episodic-like memory were when the study phase occurred, how long ago it occurred, or whether rats needed both when and how long ago cues. Three groups of 10 Long-Evans hooded rats each were tested (*21*), in one procedure in which the cue of when was relevant and the cue of how long ago was made irrelevant, a second in which how long ago was relevant and when was irrelevant, and a third in which rats could use when + how long ago (Fig. 1). Within daily trials, rats were allowed to enter four randomly chosen arms of an eight-arm radial maze during a study phase that could occur at 9 a.m. or 12:30 p.m. Three of the arms contained two Noyes 45-mg reward pellets, and the fourth arm contained the highly preferred reward of a cube of cheese (*10*). The rats were returned to the maze for a test phase at 9:30 a.m., 1 p.m., or 4:30 p.m. On the test phase, all eight arms were open, and rats could choose freely among them. The four arms closed during the study phase now contained two reward pellets, and the three arms that contained pellets during the study phase were empty.

Groups When and How Long Ago (HLA) had study phase trials at either 9 a.m. or 12:30 p.m. and test phase trials at 9:30 a.m., 1 p.m., or 4:30 p.m. (Fig. 1). On the arm where a rat consumed cheese in the study phase, another piece of cheese was placed on the same arm to replenish (R) it or the arm was empty, as the cheese had been pilfered (P); these conditions were found at different times for subgroups A and B within each group. Notice that the When group always had the cheese arm replenished after entering it at 9 a.m. (subgroup B) or at 12:30 p.m. (subgroup A) and pilfered after entering it at 12:30 p.m. (subgroup B) or at 9 a.m. (subgroup A). These rats then could only consistently return to the replenished cheese arm early on the appropriate trials if they used "when" as a cue and not how long ago the cheese arm had been encountered. The opposite arrangement was in effect for rats in the HLA group; subgroups A and B always had the cheese arm replenished after 30 min or 4 hours, and when the rats first encountered the cheese arm was made irrelevant. Rats in the When + HLA condition were tested under a standard procedure (*10*) in which both the time of the study phase and the interval until testing could indicate whether the

[1]Department of Psychology, University of Western Ontario, London, Ontario, N6A 5C2, Canada. [2]Department of Psychology, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada.

*To whom correspondence should be addressed. E-mail: roberts@uwo.ca

cheese arm would be replenished or pilfered in both subgroups. It should be further noted in this design that tests at 1 p.m. provide the most important data. When tested at 9:30 a.m. or 4:30 p.m., rats in both When and HLA groups could use time of day as a cue to indicate replenishment of the cheese reward. At 1 p.m. tests, however, time of test is irrelevant as a cue, and only when or how long ago cues can be used to determine whether the cheese reward will be replenished or pilfered.

Training trials in which the cheese reward was always replenished or always pilfered were presented initially in blocks of 16 days. Over the initial 16 days, only trials in which cheese was replenished were presented, and, over the next 16 days, only trials in which the cheese was pilfered were presented. Over a final block of 40 days, both replenished and pilfered trials at 30-min and 4-hour retention intervals were randomly mixed together. Sequences of rats' entrances into the arms of the maze during test phase trials were recorded. Rats showed a strong preference for the arms that had been closed during the study phase and that now contained pellets (table S1). Their readiness to return to the arm where cheese had been found during study was evaluated by two measures: the probability of returning to the cheese arm in the first four arms visited, and the mean rank of entry into the cheese arm during successive arm choices. Early return to the cheese arm is indicated by a high probability of visiting it in the first four choices and by a low rank of entry.

Performance over the last 20 trials of training is shown in Fig. 2, with the proportion of cheese arm entries in the first four visits shown in 2A and the mean rank of entry into the cheese arm shown in 2B. Both measures show the same pattern. When tests at all times of day are analyzed, all three groups show a significant tendency to enter the cheese arm earlier when cheese is replenished than when it is pilfered [$t(9) \geq 2.48$ for proportion; $t(9) \geq 3.21$ for mean rank of entry]. When tests at 1 p.m. are considered, however, the When group shows no difference between replenish and pilfer trials [$t(9) = 0.29$ for proportion; $t(9) = 0.9$ for mean rank of entry], but the HLA and When + HLA groups show significant effects [$t(9) \geq 2.72$ for proportion; $t(9) \geq 2.67$ for mean rank entry].

The first experiment indicated that rats used how long ago cheese was encountered as a cue but not when during the day it was encountered. It is possible that rats might be sensitive to when a preferred reward was found if the encounter occurred on the previous day. In experiment 2, we examined memory for when versus how long ago over an interval longer than 24 hours (Fig. 3). The When, HLA, and When + HLA groups ($n = 5$) were tested again. In the When and HLA groups, rats were given the study trial at 9 a.m. or 12 p.m. The short retention interval was 1 hour, with test trials given at 10 a.m. or 1 p.m. of the same day. The long retention interval was 28 hours, with test trials given at 1 p.m. or 4 p.m. of the next day. As in experiment 1, the time of day at which cheese was encountered was the relevant cue for the When group, the time that elapsed between the study and test phases was the relevant cue for the HLA group, and both cues were relevant for the When + HLA group. From the start of training, the different types of trials were presented in random order over days; each group received 56 total trials, 28 on which cheese was replenished and 28 on which cheese was pilfered.

Again, tests at 1 p.m. were most important because they controlled for time of day as a cue for cheese replenishment.

Data for the final 28 trials of training are shown in Fig. 4. The findings of experiment 2 largely replicated those of experiment 1. When tests at all times of day were considered, both the

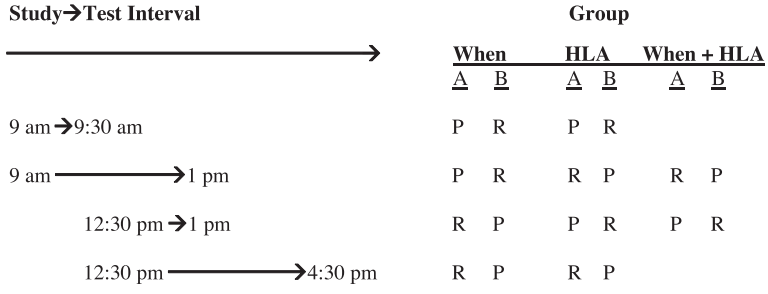

Fig. 1. Design of experiment 1 for the study of the temporal basis of episodic-like memory in rats. Three groups (When, HLA, and When + HLA; each $n = 10$) explored, in the study phase, four randomly chosen arms at 9 a.m. or 12:30 p.m. and were given a choice in the test phase among all eight arms at 9:30 a.m., 1 p.m., or 4:30 p.m. Subgroups (A and B; $n = 5$) found that the cheese on one arm in the study phase was either replenished (R) or pilfered (P) in the test phase.

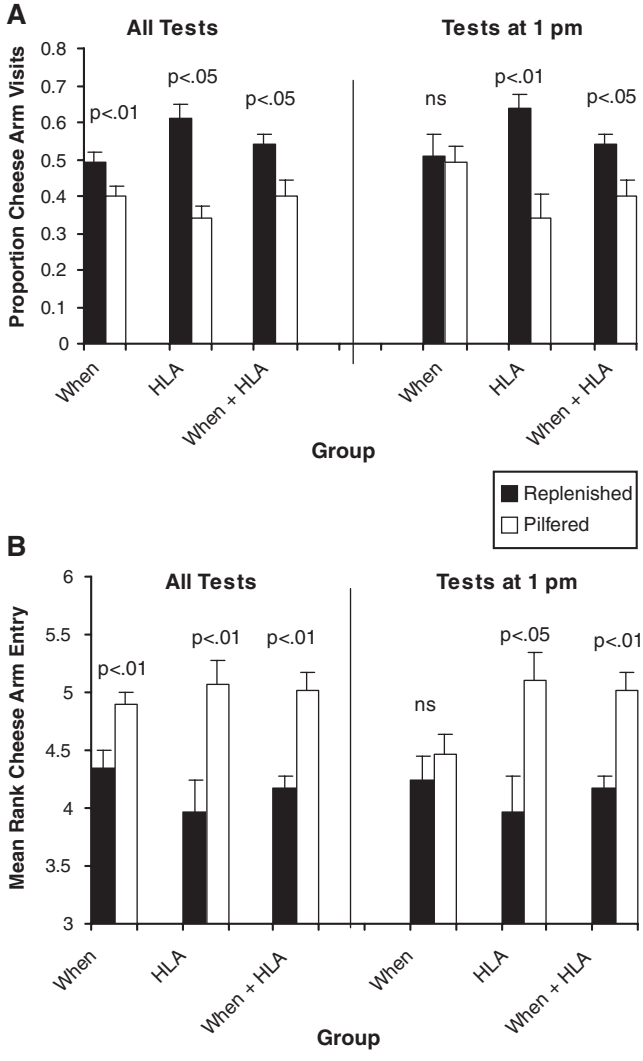

Fig. 2. Results of experiment 1. (**A**) Proportion of visits to the cheese arm in the first four visits. (**B**) Mean rank of entry into the cheese arm. All error bars are SEM.

proportion of cheese arm visits in the first four arm entries and the mean rank entry show no significant effect of when cheese was found in the maze [$t(4) = 0.2$ for proportion; $t(4) = 0.48$ for mean rank entry]. However, the HLA and When + HLA groups showed significantly earlier visits to the cheese arm on replenish trials than on pilfer trials [$t(4) \geq 2.32$ for proportion; $t(4) \geq 2.73$ for mean rank entry]. The same results appear when tests at 1 p.m. only are examined, with no effects of when the cheese arm was visited [$t(4) = 0.75$ for proportion; $t(4) = 0.12$ for mean rank entry], but significant effects of HLA and When + HLA [$t(4) \geq 2.63$ for proportion; $t(4) \geq 3.00$ for mean rank entry].

The findings of two experiments indicate that rats were not sensitive to when during the day they first discovered cheese on an arm of the radial maze. By contrast, they were able to use elapsed time or how long ago the cheese was found to indicate that it would be replenished or pilfered on the test phase. The difference between the When and HLA groups suggests that the success of the When + HLA group and rats tested in previous episodic-like memory experiments (*7*–*10*) was caused by animals keeping track of the time between study and test phases and not by memory for when the study phase occurred. Rats have been shown to be able to track the time that has elapsed between a signal and the delivery of food over both short and long time intervals, and several possible mechanisms may account for this ability, including internal accumulators (*13*), circadian oscillators (*14*, *15*), the animal's own behavior (*16*), and the strength of a memory trace (*17*). Although humans may reconstruct the timing of a past experience using memory for absolute time, order of events, and elapsed time (*20*), the implication of the studies reported here is that rats do not need to remember when a food was encountered within a day or between days in order to show episodic-like memory. These findings then cast into doubt any similarity between episodic-like memory in rats and episodic memory in humans. Humans can specify when an event occurred within a past temporal framework of hours, days, and years (*20*), but rats appear to remember only how much time has gone by since an important event occurred.

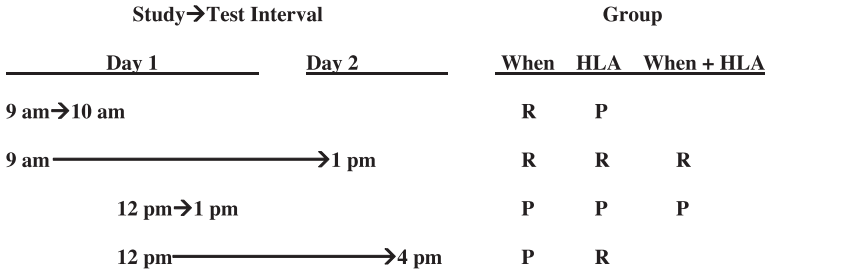

Fig. 3. Design of experiment 2 for the study of the temporal basis of episodic-like memory in rats between days. Three groups (When, HLA, and When + HLA; each $n = 5$) explored, in the study phase, four randomly chosen arms at 9 a.m. or 12 p.m. and were given a choice in the test phase among all eight arms at 10 a.m., 1 p.m., or 4 p.m. Tests between days made the retention interval 28 hours long. Rats found that the cheese on one arm in the study phase was either replenished (R) or pilfered (P) in the test phase.

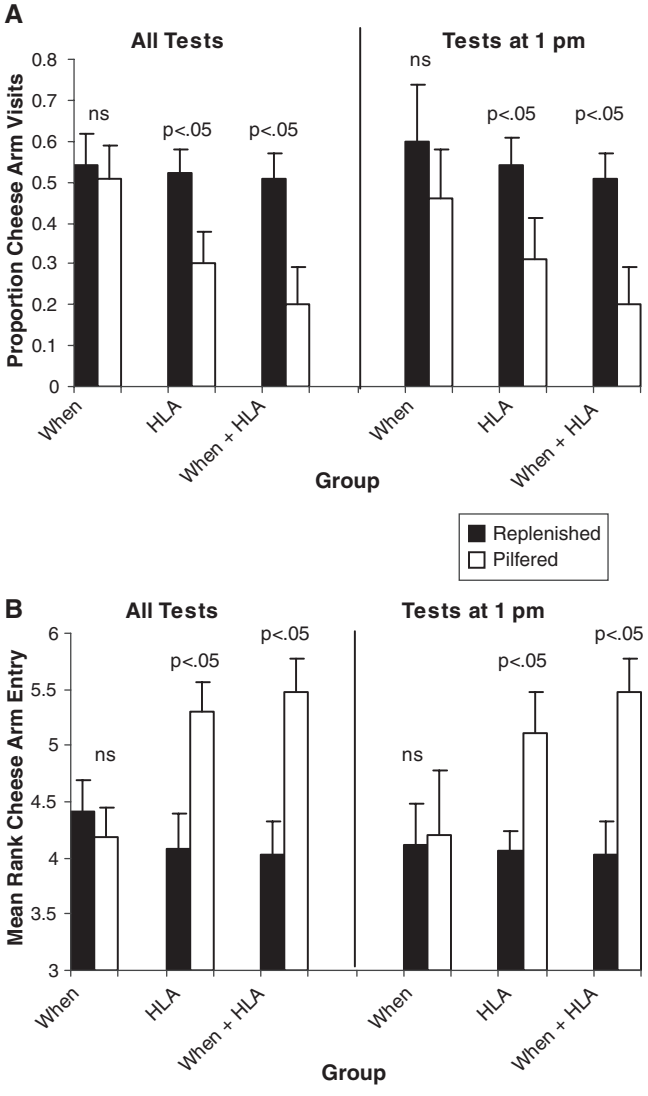

Fig. 4. Results of experiment 2. (**A**) Proportion of visits to the cheese arm in the first four visits. (**B**) Mean rank of entry into the cheese arm. All error bars are SEM.

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Materials and Methods
SOM Text
Table S1

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