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Testing for episodic-like memory in rats in the absence of time of day cues: Replication of Babb and Crystal

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Abstract

Two experiments were performed to look for evidence of episodic-like memory in rats. On each of a series of trials on an eight-arm radial maze, rats in two groups entered four open arms in Phase 1, with reward pellets on three arms and a favored reward (chocolate in Experiment 1 and cheese in Experiment 2) on the remaining arm. Phase 2 retention tests were given 30 min or 4 h after Phase 1, with all eight arms open. The four arms not entered in Phase 1 all contained reward pellets, and the three arms that contained pellets in Phase 1 were empty. In the replenish short group, the favored reward was replenished at the same location where it was found in Phase 1 at the 30 min retention interval but was absent (Experiment 1) or degraded (Experiment 2) at the 4 h retention interval. In the replenish long group, the favored reward was replenished at the 4 h retention interval but rials that randomly mixed short and long delays, rats in both experiments learned to return earlier to the arm containing the favored reward at the retention interval when it was absent or degraded. These results replicate earlier findings [Babb, S.J., Crystal, J.D., 2005, Discrimination of what, when, and where: implications for episodic-like memory in rats. Learn. Mot., 36, 177–189] and provide evidence of episodic-like memory in rats.

Keywords: Episodic-like memory; Radial maze; Rats

1. Introduction

Tulving first identified episodic memory as the ability to mentally journey backwards in time and to retrieve information regarding specific personal events (Tulving, 1972, 1983, 1984, 1985). Episodic memory was contrasted with semantic memory, which Tulving referred to as memory for general world knowledge, such as the names of major capital cities or the rules of dining etiquette. It was suggested that episodic memories, unlike semantic memories, contained information about where and when specific events occurred. Tulving (1983, 1985) also argued that episodic memory is characterized by additional cognitive features, namely self awareness or autonoetic consciousness. Autonoetic consciousness was defined as that property of episodic memories that provides an individual with an impression of awareness of the past through feelings of familiarity or knowing. Many researchers have pointed out that feelings of familiarity or knowing are impossible to test in non-verbal animals (e.g., Babb and Crystal, 2005; Schwartz et al., 2005; Suddendorf and Corballis, 1997). As a result, Clayton and Dickinson (1998) developed the behavioral criteria of memory for what, where, and when to test for episodic-like memory in animals. According to this definition, episodic recollection of an event involves remembering features of the event (what), the location at which the event occurred (where), and the time the event took place (when). The advantage of this definition is that these features of memory can be tested for in behavioural experiments, without the need for verbal report of subjective impressions.

Using the what, where, and when criteria to test for episodiclike memory, Clayton and Dickinson (1998, 1999), (Clayton et al., 2001; De Kort et al., 2005) have provided evidence to suggest that scrub jays, a corvid that caches food and later recovers it, can remember these critical details of food storing events. Scrub jays were allowed first to cache both preferred perishable wax worms and less preferred non-perishable peanuts in different locations. Memory was tested by re-presenting the jays with the caching apparatus either 4 h or 124 h after caching. Peanuts were fresh after both delays, whereas worms were fresh after

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4 h, but were degraded when encountered after 124 h. When the jays were re-exposed to the caching tray after 4 h, they searched at the worm locations prior to searching at the peanut locations. Conversely, after a 124 h delay, the jays preferred to visit peanut cache sites first. The differential search patterns displayed after the two delays suggest the jays had learned when the two foods would be edible and exhibited an ability to recall where food items of each type were and when the caching episode had taken place.

Attempts to find evidence of episodic-like memory in nonhuman mammals have met with mixed success. In an experiment conducted by Eichenbaum et al. (2005), evidence of episodic-like memory in rats was found. In that study, rats sampled a series of four different cups containing distinctive odors, each in a different spatial location. When tested with a choice between a random pair of cups placed in their respective original locations, rats were rewarded for approaching the member of each random pair, which occurred earlier in the sequence. Rats learned to prefer the odor of the earlier visited cup, although the odors and locations of cups varied from one trial to the next. Eichenbaum et al. (2005) concluded that the rats remembered the order of unique sequences of odors and places and that this ability constituted episodic-like memory.

Although the Eichenbaum et al. (2005) study provides evidence to support the existence of episodic-like faculties in rats, the paradigm used by Eichenbaum and colleagues varied greatly from that of Clayton and Dickinson (1998). In another study with rhesus monkeys, Hampton et al. (2005) tested monkeys' memory of what, where, and when using the scrub jay paradigm developed by Clayton and Dickinson (1998). Monkeys were guided into a large room where they found a preferred and a less preferred food reward in a trial-unique array of three locations. Monkeys were returned to the test room 1 and 25 h later for test trials. After 25 h but not 1 h, the preferred food was replaced with a distasteful food, while the less preferred food was still present. Results showed that rhesus monkeys remembered the type of food and where the food was at both delay intervals, but failed to demonstrate memory for when a food was encountered. They searched at the preferred food site first at both delays.

In a series of experiments with rats, Bird et al. (2003) allowed rats to hoard food in each of four available end boxes on an eight-arm radial maze. On retrieval tests, all eight arms were accessible and rats were allowed to retrieve the food items hidden earlier on the four selected arms. Findings indicated that the rats searched the maze arms where food had been hidden before arms that did not contain food. In another experiment, rats carried preferred cheese chunks and less preferred pieces of pretzels to different arms. Retrieval tests were given 45 min after the food was carried to the arms. The results showed that the rats entered the cheese arms before the pretzel arms. The findings from these two experiments suggest that rats remembered both where food was hidden and what type of food item was hidden in each location.

The final experiment was designed to test rats for memory of when food items were hidden (Bird et al., 2005, Experiment

6). Two groups of rats were trained to carry pieces of cheese and pretzel to different arms before being given retrieval tests either 1 h or 25 h later. One group of rats, the 1 h degrade group, encountered unpalatable cheese that had been soaked in bitter quinine after 1 h but discovered fresh, edible cheese after 25 h. In contrast, conditions were reversed for the second group of rats; the 25 h degrade group encountered bitter cheese after 25 h but edible cheese after 1 h. The pretzels were always fresh for both groups. The rats failed to show memory for when food items were hoarded, as neither group of rats developed a tendency to make earlier visits to pretzel arms than to cheese arms at the delay when the cheese was degraded.

Recently, an interesting study similar in design to that of Clayton and Dickinson's (1998) work with scrub jays has provided evidence for episodic-like memory in rats using the eightarm radial maze (Babb and Crystal, 2005). In the first phase, rats visited four randomly chosen arms, three of which contained reward pellets and one of which contained the preferred reward chocolate. After either a short 30 min or long 4 h delay, rats were returned to the maze for a second phase in which all eight arms of the radial maze were available. After a short delay, the four arms that did not provide food during the first phase contained reward pellets. After a long delay, the four unentered arms contained pellets and the chocolate arm of Phase 1 was replenished with fresh chocolate. The results showed that rats made more visits to the chocolate location after the long than after the short delay, suggesting memory of what, where, and when. Next, the rats received a taste-aversion treatment in which the chocolate was paired with lithium chloride. Subsequent testing used the long delay at which they had previously revisited the chocolate arm at a high rate. Rats now showed a significant reduction in revisits to the chocolate location. The researchers concluded that the reduction of revisits to the chocolate location after the taste-aversion treatment revealed further evidence of memory for what, where, and when. In this case, episodic-like memory was used flexibly. When the significance of chocolate was changed from a preferred food to a food to be avoided, rats avoided the location where chocolate had last been found.

One alternative explanation for the results found by Babb and Crystal (2005) is that the rats used timing mechanisms to discriminate between the short and long delay trials instead of memory for when rewards were found. On both the short and long delay trials, rats were placed on the maze at the same time for Phase 1 but were returned to the maze for Phase 2 in the morning after a short delay and in the afternoon after a long delay. Thus, rats may have learned to return to the chocolate arm when returned to the maze in the afternoon, but to not return to the chocolate arm when returned to the maze in the morning. Rats' ability to sense their own circadian rhythms may allow them to use time of day as a cue.

Babb and Crystal (2006a) examined this issue in a follow-up study by using retention intervals of 1 and 25 h, resulting in the rats always receiving the second phase at the same time of day. The remainder of the procedure was the same as in the previous experiment. The results showed that, just as in the original experiment, rats made more visits to the chocolate location after the long delay than after the short delay. Next, the rats were Download English Version:

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