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Discrimination of what, when, and where: Implications for episodic-like memory in rats ☆

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Abstract

We investigated the discrimination of what, when, and where in rats ($n = 5$) using an eight-arm radial maze. Rats received daily training consisting of forced-choice visits to four baited arms, one of which was randomly chosen each day to contain chocolate (Phase 1). In Phase 2, all eight arms were available. After a short (30 min) retention interval (RI), the four arms that were not available in Phase 1 provided food. After a long (4 h) RI, the four remaining arms plus the arm containing chocolate provided food (i.e., the chocolate arm replenished). The rats visited the chocolate location after the long RI more than after the short RI. Next, chocolate was paired with lithium chloride, and subsequent testing used the long RI. The rats visited the chocolate location less after the taste-aversion manipulation than in previous training, demonstrating knowledge of what, when, and where. Implications for episodic-like memory are discussed.

Keywords: What–when–where; Episodic memory; Episodic-like memory

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Gallistel (1990) proposed that when an event occurs, animals record the time and place at which the event occurred, together with the features of the event. According to this proposal, the content of memory is a record of what occurred, when it occurred, and where it occurred. Memories of what, when, and where an event occurred may be recalled later and may form the basis for predicting future events (e.g., classical conditioning) according to Gallistel. Information about the temporal–spatial features of a specific event is one aspect of episodic memory.

Tulving (1972) distinguished between episodic memory (the encoding and retrieval from memory of unique, personal past experiences) and other types of memory. This early distinction focused on the difference between personally experienced events and knowledge of general facts about the world. In particular, Tulving (1972) proposed that "Episodic memory receives and stores information about temporally dated phases or events, and temporal–spatial relations among these events" (p. 385).

Although knowledge of what, when, and where remains an important component of episodic memory (Nyberg et al., 1996), it is not the only feature of episodic memory. In particular, Tulving and colleagues (e.g., Tulving, 1983; Tulving & Markowitsch, 1998) have focused on three additional features of episodic memory: the ability to recognize subjective time, autonoetic consciousness, and knowledge of a "self," all of which are deemed necessary for mental time travel (i.e., the ability to subjectively re-experience an event). According to this proposal, these features distinguish between recalling a personal past experience and remembering an impersonal fact. However, these attributes are difficult, if not impossible, to test in non-verbal animals (Hampton & Schwartz, 2004; Roberts, 2002; Suddendorf & Busby, 2003; Suddendorf & Corballis, 1997). Consequently, Clayton and colleagues (Clayton, Bussey, & Dickinson, 2003; Clayton, Griffiths, & Dickinson, 2000; Clayton, Griffiths, Emery, & Dickinson, 2001) have argued that behavioral studies of episodic memory should focus on knowledge of what, when, and where as criteria for episodic-like memory in animals.

Studies with food-storing birds (Clayton & Dickinson, 1998, 1999a, 1999b; Clayton, Yu, & Dickinson, 2001, 2003) have shown that scrub jays can remember what type of food they cached, where they cached it, and when they cached it; there is evidence that food-storing birds have an adaptive specialization of memory (e.g., Pravosudov & Clayton, 2002; Shettleworth, 1998). If characterizing episodic memory in animals is based on the information encoded rather than the subjective experience that accompanies the memory, then there is evidence that scrub jays possess episodic-like memory.

Scrub jays were given the opportunity to cache different food types and recover them after a retention interval (RI; Clayton & Dickinson, 1998). Birds in the degrade group were trained to expect that wax worms, a preferred food, decayed after a delay of 124 h, whereas peanuts, a less preferred food, did not. The birds were then allowed to cache either peanuts or wax worms on one side of a visuospatially distinct tray. After a retention interval of 120 h, the birds were then allowed to cache the second food type in the opposite side of the tray. Four hours later, the birds were allowed to recover food from one side of the tray. The birds searched for the food type that was preferred only if it was still fresh (i.e., birds recovered more worms when they cached

peanuts before worms, but more peanuts were recovered when the birds had cached worms before peanuts).

To ensure that the different search strategies after different delays were not due to different levels of forgetting of worm and peanut caches (i.e., relative familiarity), a replenish group was created, in which the birds never had the opportunity to learn that the wax worms decay after long periods of time. Unlike the birds in the degrade group, the birds in the replenish group inspected the worm side first in all delay conditions.

In the wild, the longer caches are left without being recovered, the more likely they are to be stolen by another animal. Therefore, a pilfer group was trained to expect that wax worms had been removed from the tray after 124 h. The pilfer group directed more of their first inspections to the peanut side of the tray if worms were cached long enough to be pilfered.

These data suggest scrub jays can remember what type of food they cached, where in the tray they cached, and when they cached it. The same conclusion was reached in a similar study that used three food types that became unavailable (degraded or pilfered) after three RIs (Clayton, Yu, et al., 2001).

Clayton, Yu, and Dickinson (2003) provided evidence that information about the status of a stored food type can be updated after the food has been cached. Clayton and colleagues gave scrub jays the opportunity to store crickets and peanuts, and recover them after RIs of 2, 3, and 5 days. For one group of birds, the crickets degraded after 2–3 days but not after 5 days; for another group, the stored food was always fresh at recovery. As in previous studies, this experience resulted in a preference for peanuts after the longest delay for birds that had experience with the decayed crickets. Next, the ability to flexibly update memory about the stored food was assessed by introducing new information during the RI. The birds cached peanuts and crickets in three trays across successive days and recovered their caches from the first two trays after a 3-day RI. For one group, the crickets remained fresh and palatable; for the second group, the crickets decayed. The birds that had found fresh crickets in the first two trays continued to search for crickets in the third tray. However, the birds that had found decayed crickets in the first two trays searched preferentially for peanuts in the third tray. These data suggest that the birds integrated information about the cached food with new information presented during the RI.

Clayton and Dickinson (1999a) provided additional evidence that scrub jays could remember the types of food that they cached. The motivation to consume a particular food type was manipulated between the time of caching and recovery by prefeeding the birds with one of two food types. The birds cached peanuts and dog kibble, and they were then prefed one of the foods after a retention interval (4 or 172 h). After both RIs, the birds directed their first searches to the tray that contained the food they had not been prefed. These data suggest that the birds inspected the trays based upon their ability to recall the contents of the caches and the current incentive value of the food.

To determine if the birds could remember which type of food had been recovered, they were allowed to cache three peanuts on one side of each tray, and three dog-food kibbles on the other side of each tray. After a 3 h RI, the birds were given two recovery phases in which they were allowed to recover kibble from one tray and

peanuts from the other tray. The birds were then prefed one of the food items and then presented with both caching trays. The birds directed their searches to the tray that still contained the preferred (i.e., non-prefed) food. Therefore, the birds were able to encode information about the type of food they cached, update their memory of whether or not the cache site contained food, and integrate the information about the content of the cache with the incentive value of the food at recovery.

The present study was designed based on Clayton and colleagues' approach to episodic-like memory. The purpose of the present experiment was to document knowledge of what, when, and where using rats as subjects, without relying on food-caching. Rats were trained to find a food pellet at each of eight arms in a radial maze (Olton & Samuelson, 1976); one of the arms, randomly selected, was baited with a chocolate pellet, a preferred food type. Daily testing was divided into forced-choice (which always included chocolate) and free-choice phases, separated by a retention interval. The rats were trained to discriminate between a short and long retention interval. After the long retention interval, the chocolate replenished (i.e., revisiting the chocolate location resulted in a pellet). After the short retention interval, the chocolate bait did not replenish. After the animals had learned to selectively revisit the chocolate location following a long retention interval, chocolate was paired with lithium chloride (LiCl; Batson, Best, Phillips, Patel, & Gilleland, 1986; Melcer & Timberlake, 1985). The goal was to change a rat that revisited the chocolate location into a rat that did not revisit the chocolate location. By not revisiting the chocolate location after LiCl treatment, the rats would demonstrate knowledge of what, when, and where.

Method

Subjects

Five male Long Evans rats (Harlan, Madison, WI) were individually housed in a colony with light onset at 07:00 and offset at 19:00. The rats were given unlimited access to 5001 Rodent Diet (Lab Diet, Brentwood, MO) for one week, and then given 20 g for 1 day and 15 g/day on subsequent days. Water was available at all times, except during brief testing periods. The rats were approximately 6 months old at the beginning of the experiment with an average weight of 326 g. The rats had served (69 days) in a previous, related study (Babb & Crystal, 2003). In addition, the rats received pilot testing to expose the rats to the contingency that chocolate replenished on multiple visits. The animals were given several two-alternative forced choices between chocolate, new, and old locations. Because the rats continued to make only a single revisit to the chocolate location, the procedure described below required only a single revisit to the chocolate location.

Materials

Testing was conducted in an eight-arm radial maze. The central hub (white polypropylene octagonal base [28.6 cm in diameter, 11.4 cm sides], metal walls [33.3 cm

high], and a clear polycarbonate lid, MED Associates, ENV-538) was equipped with eight computer-controlled guillotine doors (ENV-540). The arms (76.2 cm long, 8.9 cm wide with 17.5 cm high clear polycarbonate walls and topped with polycarbonate) radiated from the center hub with equal spacing between each arm. A food trough (ENV-200R1M) was placed at the end of each arm. A photobeam (ENV-254, approximately 1 cm inside each food trough, 1 cm from the trough bottom) detected head entries. A 45 mg pellet dispenser (ENV-203) was placed behind each food trough. Additional photobeams were located in each arm at 3.8 and 5.1 cm from the guillotine doors.

The maze was positioned on stools 81.3 cm above the floor. White noise (67 dB from a speaker located in the ceiling above the hub) masked outside noise. A 500 MHz computer in an adjacent room, running MED-PC for Windows (Version 1.15), controlled experimental events (guillotine doors and food) and recorded the data (photobeam breaks) with 10 ms resolution. A video camera in the ceiling above the center of the maze was used to observe the rats.

Procedure

Training consisted of two shifts per day for each rat. The rats were individually placed in the maze beginning at 09:00 for Phase 1 (forced-choice). Four doors (randomly chosen for each rat each day) were then opened, with the restriction that one of the arms dispensed chocolate pellets (F0299, Bio-Serv, Frenchtown, NJ); all other arms dispensed regular pellets (PJA/I-0045, Research Diets, New Brunswick, NJ). A pellet was delivered to each of the accessible food troughs contingent on the first head entry into the photobeam located in each of the troughs. The animals were later returned for Phase 2 (free-choice) in which all eight doors were open; food was available at each of the arms not previously accessible in the forced-choice phase. The interval between the forced- and the free-choice phases served as a discriminative cue. On days with a short retention interval (SRI), the interval between Phases 1 and 2 was 0.5 h, and the only arms that provided food were the four arms not available in Phase 1. On days with a long retention interval (LRI), the interval between Phases 1 and 2 was 4 h; the free-choice phase was identical to the SRI condition, except that the chocolate arm replenished (i.e., the chocolate was available during the free-choice phase at the location that provided chocolate during the forced-choice phase). The rat was required to visit each arm to collect the remaining pieces of food after a retention interval; the free-choice phase ended after four or five pellets were collected in SRI or LRI, respectively. On any given day, either SRI or LRI (but not both) was tested.

The rats received alternating blocks of SRI followed by blocks of LRI sessions. Each block differed only in retention interval and consisted of 7–12 days of training. A total of 17 and 19 SRI and LRI sessions were conducted, respectively. The animals were then given 42 days of mixed SRI and LRI conditions. The order of SRI and LRI was randomized across days. We analyzed the last 17 days of mixed training.

Next, the rats received pairings of chocolate and LiCl. The animals were fed 50 g of chocolate pellets for 30 min, and 10 min after removing the food they were injected

with an isotonic solution of LiCl in distilled water (0.75 mol/L, 0.6 ml/100 g of body weight ip). The animals were given LiCl treatments as described above for 3 days, with at least 1 day of regular food and no LiCl in between each LiCl treatment day. Testing resumed after the third day of regular food following the third LiCl treatment. Testing after LiCl treatments was conducted for 3 days. The animals were tested with the LRI condition described above; however, the free-choice phase ended when the animals had visited four locations, and the chocolate dispenser was disabled.

For comparison, a pilot study with experimentally naïve Long Evans rats ($n = 6$) documented that animals consumed more chocolate pellets than regular pellets. The rats were given two bowls, each containing 50 chocolate or 50 regular pellets, respectively. The bowls were removed and the pellets were counted after 5 min or after one bowl was depleted. Each rat ate all available chocolate pellets. The percentage of chocolate pellets consumed was 97.4% ± .01 (mean ± SEM). A preference test was given after the LiCl treatment (described above) to evaluate the effectiveness of the taste-aversion manipulation. The percentage of chocolate pellets consumed was 2.5% ± .02 (mean ± SEM); each rat ate all available regular pellets.

Throughout the experiment, the arms of the maze were cleaned with Nolvasan (Fort Dodge Animal Health, Fort Dodge, Iowa) each day between forced- and free-choice phases. A plastic bag with holes, and filled with chocolate and regular pellets was taped on the stool at the end of each arm beside the filled pellet dispensers (i.e., food odors were constant throughout all parts of the experiment).

Throughout this article, the criterion for statistical significance is .05.

Results

The proportion correct in the first four choices after the retention interval is presented in Table 1. There were no significant differences in these proportions, $F(4, 16) = 1.41$. During block testing with SRI, the proportion of visits to the chocolate location in the first four choices was .25. During block testing with LRI, the proportion of visits to the chocolate location in the first four choices was .54.

Fig. 1(top panel) plots the proportion of first four choices that included chocolate during mixed SRI and LRI testing. The rats visited the chocolate site more often in LRI than in SRI conditions, $t(4) = 2.90$.

Table 1
Mean (and SEM) of proportion correct in the first four choices after the retention interval

	Retention interval	
	Short	Long
Block	0.89 (0.02)	0.86 (0.03)
Mixed	0.91 (0.03)	0.91 (0.02)
Lithium chloride		0.78 (0.07)

Note. After a short RI, a visit to the four arms that were not available in Phase 1 was defined as correct. After a long RI, a visit to the four remaining arms plus the arm containing chocolate was defined as correct.

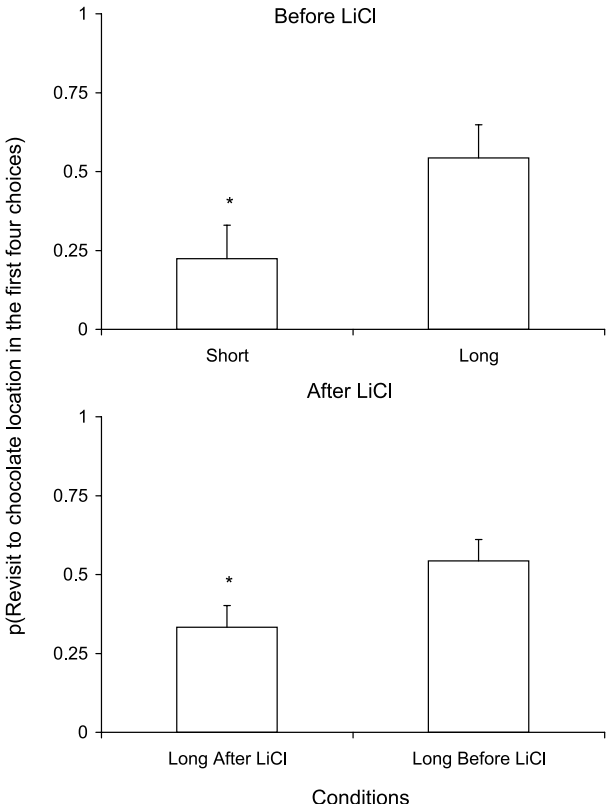

Fig. 1. Mean proportion of chocolate revisits in the first four choices of Phase 2 in mixed testing is plotted as a function of experimental conditions. Top and bottom panels display data from testing without and with LiCl treatment, respectively (see text for details). Error bars represent 1 SEM. *$p < .05$

The probability of revisiting chocolate in the first four choices from LRI in testing after the lithium chloride is shown in Fig. 1(bottom panel). After LiCl, the rats revisited chocolate in LRI less often than they did prior to LiCl in LRI, $t(4) = 3.07$.

The probability of revisiting chocolate was not statistically different between SRI before LiCl treatment and LRI after LiCl treatment, $t(4) < 1$. The proportion correct in the first four choices after the retention interval was lower after LiCl compared to pre-LiCl performance; however, this difference was not significant, $t(4) = 1.37$ (see Table 1).

The rats ate the chocolate when they encountered it in the forced-choice phase (i.e., prior to the retention interval). Therefore, encountering a chocolate pellet was not sufficient to reject eating it. Nevertheless, when tested after the retention interval, the rats avoided the location known to contain chocolate, reversing their initial preference to choose the chocolate location after a long RI.

It is unlikely that the different proportions of visits to the chocolate location in SRI and LRI conditions are due to more forgetting of forced-choice locations after LRI than SRI. The proportion correct did not decline reliably across the retention

intervals (see Table 1), $t(4) < 1$. However, the comparison of SRI and LRI in Table 1 includes a different number of correct locations per trial (4 and 5, respectively); a visit to the chocolate location counted as a correct choice after a long retention interval but as an incorrect choice after a short retention interval. These differences complicate the comparison of the proportions in Table 1. Therefore, we examined the proportion correct excluding the chocolate location in mixed SRI (0.96 ± 0.01; mean $\pm$ SEM) and LRI (0.90 ± 0.02) conditions. The proportion correct at non-chocolate locations did not decline reliably across the retention intervals, $t(4) = 2.08$. Therefore, the higher rate of revisits to the chocolate location after the long retention interval cannot be due to forgetting which location contained chocolate.

Discussion

Rats were required to visit four randomly chosen locations, one of which was randomly selected to provide chocolate. The animals were later returned to the maze after either a short or long retention interval, with all eight locations available. After the short retention interval, only the four locations not available in the first phase provided food; after the long retention interval, the four locations not available in the first phase, plus the chocolate location, provided food. The rats made more visits to the chocolate location after the long than after the short retention interval. Next, the animals received a taste-aversion treatment, in which chocolate was paired with lithium chloride. The animals were subsequently tested using the long retention interval (i.e., a condition in which the rats previously revisited the chocolate at a high rate). The rats made fewer revisits to the chocolate location after the lithium chloride treatment than in previous testing. The animals could not have reduced the rate of revisits to the chocolate location without knowledge of what, when, and where.

One potential alternative explanation is that the animals were using relative familiarity to guide their behavior after the different retention intervals. The rats could have solved the task by using the conditional rule: do not revisit if familiarity with chocolate is high (i.e., after a short delay), and revisit if familiarity is low (i.e., after a long delay). However, the conditional rule cannot explain performance after lithium chloride. Post-LiCl testing was conducted with a long RI. Therefore, the conditional rule predicts revisits to chocolate at a high rate, rather than the observed low rate. Because chocolate revisits declined after LiCl treatment, in conditions that controlled the level of relative familiarity, knowledge of what, when, and where is a single parsimonious interpretation for the selective revisits to chocolate before LiCl (Fig. 1, top panel) and the decline in visits to chocolate after LiCl (Fig. 1, bottom panel).

An aspect of episodic memory involves encoding of unique events. In the present experiment, the rats demonstrated memory of the daily location of the chocolate. For food-caching animals, retrieval of the food cache depends on a single, brief encoding event. Clayton and colleagues placed distinctive Lego structures at each caching tray to provide unique encoding events (Clayton & Dickinson, 1998, 1999a, 1999b; Clayton, Yu, et al., 2001, 2003). We approached this issue in a previous study by providing rats with trial-unique objects in each arm of the radial maze. However, we found that

rats navigated with respect to a representation of spatial locations and did not follow trial-unique cues (Babb & Crystal, 2003).

The observation of what–when–where information contrasts with other recent reports with rats. Roberts and Roberts (2002) assessed the ability of rats to remember the order in which they entered arms on a radial maze. The rats were unable to discriminate the first arm they encountered from the other arms. Bird, Roberts, Abroms, Kit, and Crupi (2003) induced rats to carry food items (cheese and pretzels) from the center of a radial maze to boxes at the end of each arm; the rats were removed from the maze arm before the food was fully consumed. The rats hid and retrieved cheese preferentially over pretzels. However, the rats were insensitive to pilfering of the food. When Bird and colleagues degraded cheese at one delay interval but not the other, the rats did not selectively avoid locations with the degraded food. Taken together, the experiments by Roberts and colleagues provide evidence for knowledge of what type of food they hid and where they hid it, but no evidence that rats remembered when they hid it.

In contrast, Eichenbaum and colleagues (e.g., Ergorul & Eichenbaum, 2004; Fortin, Agster, & Eichenbaum, 2002) have documented that rats quickly learn the sequence of randomly ordered odors. After being presented with a sequential order, the rats learned to select an odor that had not been presented in the sequence. The rats were then divided into hippocampal lesion or sham groups. The rats with the hippocampal lesions performed as well as the control rats on an odor recognition task, but were impaired on tests of sequential order. These data are consistent with the hypothesis that the hippocampus is involved in memory for sequences of events. Eichenbaum and Fortin (2003) argued that memory for the sequential order of unique events provides a model for episodic memory.

The present experiment documents knowledge of what, when, and where. However, it does not identify the mechanisms responsible for these types of knowledge. In the paragraphs that follow, we outline several potential mechanisms that may subserve knowledge of what, when, and where.

Two types of timing mechanisms may be proposed to discriminate between the short and long retention intervals. The rats may have used an interval timing mechanism (Gibbon, 1991) to discriminate 0.5 and 4 h. Alternatively, the rats may have used a circadian oscillator (Mistlberger, 1994) to discriminate time of day (e.g., morning vs. afternoon).

The rats restricted their revisits to conditions in which chocolate replenished, and the rate of revisits to chocolate was reduced after LiCl treatment. This suggests that the content of "what" consisted of knowledge of chocolate. However, the mechanism remains to be identified. For example, the animals may have been using a response–outcome association to avoid revisiting the chocolate location after LiCl treatment (Colwill & Rescorla, 1985). According to this view, the animals did not revisit the chocolate location after the long retention interval because the outcome was undesirable.

The location of the chocolate arm varied randomly from day to day. The content of "where" is the location of the chocolate arm. However, the mechanism of spatial navigation remains to be identified. For example, the rats may have navigated with

respect to a spatial representation of the global geometric framework (i.e., a cognitive map), dead reckoning (i.e., path integration) or landmarks (Gallistel, 1990).

The present experiment documents the use of what–when–where information. In the paragraphs that follow, we outline the implications for episodic-like memory.

Knowledge of what, when, and where is a necessary condition for the establishment of episodic memory. However, it is not a sufficient condition. For example, in the present study, there is no information about the subjective state of the animal when the animal makes a decision to revisit the chocolate location. We have no method to know if the animal is engaged in mental time travel or if it is subjectively re-experiencing the previous event of finding chocolate. Therefore, it is possible that a three-way conditional discrimination of what, when, and where occurs in the absence of any accompanying subjective states. Clayton, Bussey, Emery, and Dickinson (2003) have argued that reconstructive generative processes and meta-representations at retrieval should not be considered necessary criteria for episodic memory.

Clayton, Bussey, and Dickinson (2003) have argued that behavioral criteria for episodic-like memory include content, structure, and flexibility. According to this proposal, the content is a recollection of what occurred, where it occurred, and when it occurred based on a specific past experience. The structure is an integrated what–where–when representation. Flexibility proposes that episodic memory is embedded within a declarative-memory framework which involves flexible use of information.

We view the present demonstration of what–when–where in rats as meeting Clayton, Bussey, and Dickinson (2003) content criterion. In contrast, Clayton, Yu, et al. (2001) have demonstrated that scrub jays can distinguish between multiple episodes in which they cached the same food type in different locations; these data suggest that what–when–where information is integrated. Clayton, Yu, et al. (2003) have demonstrated that when scrub jays are presented with new information about the perishability of worms after having stored the worms, the birds switched their preferences for worms and peanuts accordingly; these data suggest flexibility in updating information after the time of encoding. Additional research with rats will be needed to assess the integrated and flexibility criteria. One approach toward addressing these questions is to satiate the rats to a specific food type during the RI (Balleine & Dickinson, 1998; Colwill & Rescorla, 1985). In pilot studies, we were unable to identify parameters to satiate rats to chocolate.

Zentall, Clement, Bhatt, and Allen (2001) have emphasized another feature of episodic-like memory. In particular, it should be possible to answer an unexpected question based on episodic memory. Zentall and colleagues argued that what–when–where information could be based on the acquisition of a set of explicitly trained if–then rules; the rules could be applied when a food item is initially encountered. To avoid the concern, Zentall and colleagues trained pigeons to respond differently after having pecked or not pecked (i.e., nonverbally answering the question "Did you just peck or refrain from pecking?"). In a separate discrimination, the pigeons were placed in a situation in which they pecked one stimulus but not another, without requiring them to do so. Next, the pigeons were given the opportunity to report whether they had pecked or not. The data suggest that the pigeons could remember a specific detail about their past experience. The current study, like

Clayton and Dickinson's (1998, 1999b) initial demonstrations of what–when–where information, could be solved by rule-based learning at the time a food item is encountered.

Roberts (2002) offered a related rule-based criticism of Clayton and colleagues' demonstration of episodic-like memory. In particular, Roberts argued that the scrub jays may have learned that a relatively weak memory trace for meal worm locations predicts decayed worms and that a relatively strong memory trace predicts palatable worms. A conditional rule can be constructed to describe our training data, applying Roberts's explanation. In particular, the memory trace for a chocolate location would be relatively strong after a short RI and relatively weak after a long RI. Therefore, the rat could adopt the rule, "if the memory of the chocolate location is weak, revisit that location." However, the use of this rule does not predict the data observed after LiCl treatment. Testing after the LiCl treatment used a long RI. Therefore, application of the rule outlined above would predict revisits at a high rate, rather than the observed low rate. LiCl treatment may change the memory representation of chocolate (e.g.,Trapold & Overmier, 1972). However, if LiCl treatment affects the strength of the memory trace, it is not clear whether the memory trace is strengthened or weakened.

Episodic memory is the first kind of memory to degenerate with age, and the last to be acquired as a child (Tulving, 2002). Patients with neurodegenerative diseases such as Alzheimer's show a loss of episodic memory. The hippocampus plays an important role in the acquisition of new memories; it incorporates temporal information from the frontal lobes, thus providing a basis for "when" (Burgess, Maguire, & O'Keefe, 2002). The hippocampus has been implicated in spatial memory tasks, and may provide a basis for "where" (O'Keefe & Nadel, 1978). The right hippocampus processes spatial locations, while the left hippocampus is involved in episodic memory (Burgess et al., 2002; Maguire, 2001). The left and right prefrontal cortices are implicated in encoding and retrieval of episodic memory, respectively (Tulving, 2002).

Development of a rodent model for episodic memory could lead to a better understanding of the neural, molecular, and behavioral mechanisms of episodic memory (Griffiths & Clayton, 2001). The availability of a rodent model could also permit the screening of putative pharmacotherapies for human memory disorders such as Alzheimer's (Clayton & Griffiths, 2002).

The present study demonstrates that rats possess what, when, and where components of episodic memory. This study adds to the growing literature which suggests that animals may possess episodic-like memory (Clayton & Dickinson, 1998; Clayton & Dickinson, 1999a, 1999b; Clayton, Yu, et al., 2001, 2003). Although it may be impossible to demonstrate autonoetic consciousness in animals, relying on Tulving's (1972) definition of episodic memory may represent a critical strategy for testing episodic-like memory in rats.

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