Rhesus monkeys (*Macaca mulatta*) demonstrate robust memory for what and where, but not when, in an open-field test of memory ☆

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Abstract

We adapted a paradigm developed by Clayton and Dickinson (1998), who demonstrated memory for *what, where,* and *when* in scrub jays, for use with rhesus monkeys. In the study phase of each trial, monkeys found a preferred and a less-preferred food reward in a trial-unique array of three locations in a large room. After 1 h, monkeys returned to the test room, where they found foods placed as during study. Twenty-five hours after the study phase monkeys again searched the room, but now the preferred food was replaced with a distasteful food remnant, while the less-preferred food was still present. Although monkeys remembered the locations of the foods for up to 25 h, they did not learn that the preferred food was available after the short, but not after the long delay. Thus, monkeys demonstrated long-term memory

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for the type and location of food but failed to demonstrate sensitivity to when they acquired that knowledge.
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In humans it is comparatively easy to distinguish between semantic and episodic memory based on reports of the experience accompanying memory retrieval (Tulving, 1972, 1983; Wheeler, 2000). Semantic memory consists of facts about the world: water is scarce in the desert, seafood must be fresh to be safe. In contrast, episodic memory consists of events from one's personal past: running out of water on a desert hiking trip, the time you were sickened by spoiled clams at a beach party. Accordingly, humans demonstrate episodic memory by reporting that they *remember* the specific episode in which information was acquired and can re-experience that episode. Humans demonstrate semantic memory by reporting that they simply *know* a given fact about the world, without necessarily having the ability to retrieve the specific context in which that knowledge was acquired (Tulving, 1985).

There have been a number of attempts to determine whether a system like the human episodic memory system can be identified in nonhuman animals (e.g., Agster, Fortin, & Eichenbaum, 2002; Bierley, Kesner, & Novak, 1983; Bird, Roberts, Abroms, Kit, & Crupi, 2003; Clayton & Dickinson, 1998; Fortin, Agster, & Eichenbaum, 2002; Gaffan, 1994; Kesner, Gilbert, & Barua, 2002; Roberts & Roberts, 2002; Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002; Zentall, Clement, Bhatt, & Allen, 2001). A major obstacle in this area of research is our inability to measure whether nonhuman animals consciously re-experience events, as required by prominent definitions of episodic memory (Tulving, 2002a, 2002b; Tulving & LePage, 2000). That is, given that nonhuman animals do not report verbally on the results of introspection, it may not be possible to apply the same criteria to identify episodic memory as are used with human subjects (Hampton & Schwartz, 2004; Roberts, 2002; Suddendorf & Busby, 2003; Suddendorf & Corballis, 1997; Zentall et al., 2001).

Because "mental time travel" and "re-experiencing" are not available for measurement in nonverbal species, Clayton and Dickinson (1998) have proposed a behavioral measure that can be applied in studies of nonhumans that may capture critical features of memory for specific events in an individual's life. In congruence with other recent approaches (e.g., Fortin et al., 2002; Zentall et al., 2001), Clayton and Dickinson (1998) specify behaviorally what an animal with episodic memory could do that one without it could not do. In their studies, scrub jays (*Aphelocoma californica*) arguably evidence memory for specific episodes in their personal past by simultaneously demonstrating knowledge of *what* happened, *where* it happened, and most critically *when* it happened (WWW memory hereafter; Clayton & Dickinson, 1998; Clayton & Dickinson, 1999a, 1999b, 1999c; Clayton, Yu, & Dickinson, 2001, 2003). Scrub jays cached wax moth larvae (which the birds' previous experience had shown

to be delicious, but perishable) and peanuts (less preferred, but not perishable) in sand-filled ice-cube trays. When given the opportunity to retrieve the previously hidden food, the birds searched first in locations where the still tasty larvae had been hidden if only a short time had elapsed since caching. In contrast, if a long delay interval elapsed followed caching larvae, the birds searched first in the locations where peanuts had been hidden, demonstrating that they knew what foods had been hidden in which locations, and how long ago (Clayton & Dickinson, 1998). Critically, the delay intervals used were hours to days, outside the range in which interval timing mechanisms have been shown to operate (Roberts, 1998), and tests were arranged to prevent use of time of day to guide food choice. Clayton and Dickinson argued that WWW memory is memory of a specific episode (Clayton & Dickinson, 1998). However, in recognition of the fact that they had no direct evidence that the birds consciously recollected the personal past, they called it "episodic-like" memory. The general pattern of behavior expected in a "what-where-when" memory experiment is shown in Fig. 1.

   In the present study, we used an adaptation of the WWW memory paradigm developed by Clayton and Dickinson (1998) to evaluate memory in rhesus monkeys. We used a "foraging" task involving whole-body locomotion, which we assumed would engage memory for events to a greater extent than do tests traditionally used with monkeys, which involve manual responses to objects on a test tray or on a touch screen. While moving about in a large room, monkeys learned the locations of two foods differing in palatability. After learning, the monkeys were allowed to revisit the room after both a short and a long delay interval on each trial. Using the logic of Clayton and Dickinson, both the preferred and less-preferred foods were available after a short delay interval, whereas only the less-preferred food was available after the long delay interval. In addition, we hypothesized that if the monkeys possess knowledge of what, where, and when, they would learn, over the course of training, to avoid searching for the preferred food after the long delay, but would continue to search for this food at the short delay (Fig. 1). Furthermore, as part of a larger effort aimed at under-
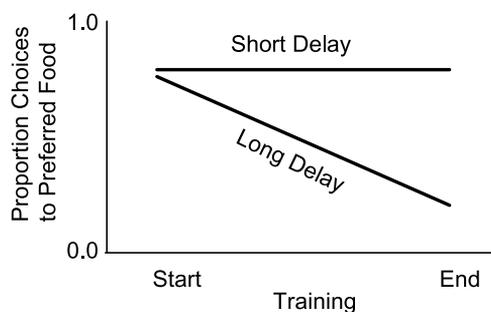

Fig. 1. Hypothetical data from subjects demonstrating memory for "what," "where," and "when." As training progresses, subjects learn that a preferred food is available only after a short delay, while a less preferred food reward is available after both long and short delays. Eventually, subjects learn to search locations containing the preferred food only after a short delay, thereby demonstrating that they know what foods are in which locations, and how long ago they learned this information.

standing the role of the monkey hippocampus in memory, we compared the performance of a group of intact monkeys with that of a group of monkeys with excitotoxic lesions of the hippocampus, a brain structure implicated in human episodic memory (Davachi, Mitchell, & Wagner, 2003; Ranganath et al., 2004; Tulving, 2002b; Vargha-Khadem, Gadian, & Mishkin, 2001; Vargha-Khadem et al., 1997).

Materials and methods

Subjects

Ten adult rhesus monkeys (*Macaca mulatta*; age 4–6 years, mean 4.6), 8 males and 2 females, were studied. The monkeys had previously participated in spatial memory experiments conducted in the same environment used here (Hampton, Hampstead, & Murray, 2004). Monkeys were housed in single-sex, socially compatible pairs, with one monkey in each pair randomly assigned to the surgery condition and the other monkey to the control condition. To ensure motivation, monkeys were maintained on a controlled diet and desirable food rewards were used during testing. Before testing each day, a screen divider was placed in the home cage to separate each pair. After testing, monkeys were fed while still separated to prevent food competition and then reunited after all food had been consumed. Water, and a variety of enrichment devices such as toys and mirrors were continuously available in the home cage.

Surgery

Five monkeys received bilateral excitotoxic lesions of the hippocampus. The surgical procedures have been previously described in detail (Hampton, Buckmaster, Anuszkiewicz-Lundgren, & Murray, 2004; Hampton, Hampstead, et al., 2004). Briefly, stereotaxic coordinates for the injection of excitotoxin were generated using magnetic resonance imaging (MRI). Under deep anesthesia, and in aseptic conditions, either the excitotoxin ibotenic acid or *N*-methyl-D-aspartic acid (NMDA) was injected bilaterally into the hippocampus. Monkeys were monitored closely during recovery and given a postoperative treatment regimen that included antibiotics, anti-inflammatory agents, and analgesics. About a week after surgery, MRI was again used to assess the placement of the injections, and to plan additional surgeries if necessary. The extent of the hippocampal damage was estimated from T1-weighted scans obtained about 10 months after surgery. The majority of the hippocampus was damaged in all cases, with estimated cell loss ranging from 65 to 85% (see Hampton, Buckmaster, et al., 2004 for details; Málková, Lex, Mishkin, & Saunders, 2001).

Test room

Testing was conducted in a large room (4.0×5.1 m; Fig. 2). One corner of the room was occupied by the experimenter and was separated from the rest of the room by a chain-link fence. The fence was covered with tarpaulin so that the monkeys
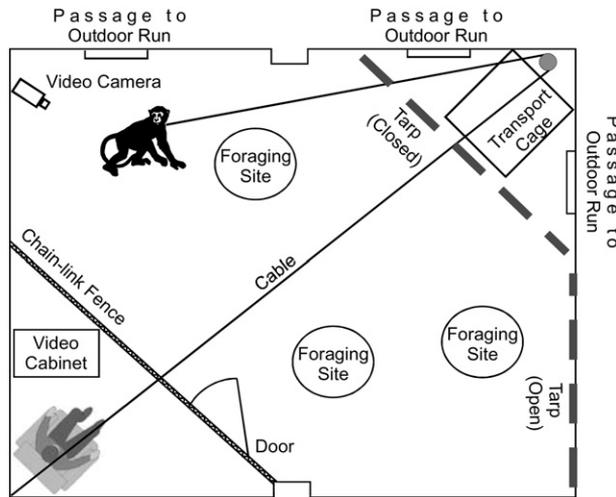
Fig. 2. Schematic diagram of the test room (4.0 × 5.1 m), indicating the location of the observer, the tether system by which monkeys could be returned to the transport cage, and a representative array of foraging sites. A tarp prevented monkeys from seeing the experimenter and a closed-circuit video system was used to observe the monkeys. Objects are not to scale.

could not see the experimenter. A camera was mounted high on the wall of the test room, permitting observation of the monkeys via closed-circuit television. Two slide projectors were used to project images on the walls and floor of the room in an effort to provide additional landmarks and spatial context.

For each session, a monkey was brought to the test room in a large wheeled transport cage, which was secured to the wall in one corner of the room. A second tarpaulin, mounted on the wall near the transport cage, could be used to block the monkey's view of the test room. A tether that connected via a system of pulleys to the opposite corner of the room was clipped onto the monkey's collar. This arrangement permitted the experimenter to pull the monkey in the direction of the transport cage if necessary. The monkeys moved freely about the room on the tether, and retrieved food from "foraging sites," each consisting of a 25-pound weight-lifting plate covered with an inverted plastic flower pot that could easily be displaced to reveal the food hidden underneath. Upon displacing the flower pot, a large quantity of food was clearly visible, but not obtainable, within a clear plastic container. A smaller portion of the same food served as the reward and was placed in front of this container. This design allowed control of the amount of food consumed while indicating to the subject that more food remained at the site after the reward was removed.

Procedure

Food preference

Prior to the beginning of formal training, food preferences were determined for each monkey individually. Monkeys were offered two different foods which casual

observation suggested differed in palatability. The foods were placed on the floor a short distance in front of the transport cage. An initial trial was given at the start of each session in which only the presumed less-preferred food was available, to ensure that the monkeys would eat it. The presumed preferred food was added after the monkey had completed the initial trial. Monkeys were then given 12 choice trials per day and were allowed to consume only one food on each trial. The locations of the two foods were counterbalanced. Various food combinations were used (e.g., banana versus food pellets; grapes versus peanuts) until each subject made more than 85% of choices to a given food over three consecutive days (36 trials). On the basis of food choices, each monkey was assigned one of two preferred foods (e.g., slice of banana; 2 or 3 grapes) and one of three less preferred foods (e.g., one peanut; a proprietary flavored primate treat; several 190 mg standard primate food pellets).

Training

After food preferences had been established, monkeys were acclimated to the testing environment. Three foraging sites were available. Two of these sites were baited with the foods selected for that monkey on the basis of food preference testing, while the third site remained unbaited. Monkeys were allowed to visit the array of sites up to three times to encounter and procure both the preferred and less-preferred food. Monkeys were returned to the transport cage between each choice, and the experimenter removed the flower pot from the most recently chosen site so that it could not be selected again. A run was complete when monkeys had visited both baited sites. Monkeys were given a total of 12 such runs each session. After each run, monkeys were returned to the transport cage, the tarp was placed to obstruct their view, the sites were rebaited, the tarp was removed, and the next run was initiated. Training was considered complete when monkeys had (1) completed at least 10 sessions and (2) visited the site containing the preferred food first on at least 3 of the last 4 runs of a given session (i.e., runs 9–12), three sessions in a row. For each session, a novel arrangement of three foraging sites was used and two unique images were displayed via the slide projectors. In addition, the test room lights were dimmed slightly to increase the salience of the projected images.

Main experiment

Each trial consisted of a study phase, during which monkeys could learn the location of both the preferred and less-preferred food for that trial, followed by two test phases, the first 1 h and the second 25 h later. Thus, a single trial took two days to complete. The projected images and baited locations remained the same between study and test on a given trial, but were unique to each trial. Each monkey completed a total of 30 trials (60 days of testing).

Study phase

The methods for the study phase were the same as in training, with two exceptions. First, the random selection of foraging sites was constrained so that adjacent sites were at least two feet apart. Second, because animals learned the locations of the foods rapidly during training, the total number of study runs on each trial was

reduced from 12 to 8. Monkeys were returned to their home cages after completing the study runs.

Test phase
One hour delay. One hour after completing the study runs, each monkey was returned to the test room and the tarp was pulled across the front of the cage. The sites were baited with the same two foods used during study. To prevent auditory cues from indicating the location of the baited sites, we used a false baiting procedure in which the experimenter visited each site, lifted the flower pot and dropped it back into place, while baiting the appropriate sites along the way. The tarp was then removed, and the monkey was allowed to search the array for food. As during study, the monkeys were returned to the transport cage between choices, and the flower pot associated with the last choice was removed. The test was terminated once the monkey had visited both baited sites. The experimenter scored both the locations of the visited sites and the order in which they were visited.

Twenty-five hour delay. Twenty-five hours after completing the study phase of each trial, monkeys were returned to the test room and given a second test. Thus, this 25-h delay test occurred at the same time of day as had the 1-h delay test, but one day later. Methods were the same as for the 1-h test except that the preferred food had now "degraded," i.e., had been replaced by a distasteful food remnant that was sprayed with a commercially available bitter flavor compound (e.g., grape stalk for grapes; stem and dried peel for banana; Fig. 3). The less-preferred food remained unchanged. The trial was completed once the monkey had visited both baited sites.

Statistics
Proportion correct scores were arcsine transformed before analysis to conform with statistical assumptions (Kirk, 1984).

Fig. 3. Foraging sites with example preferred and less-preferred foods. The sites consisted of a clear plastic box on top of a 25 pound lifting weight. Inside the clear box was a relatively large amount of food, whereas outside each box was one "bite" of each of the two foods. In the experiment proper, bites of both foods were available at study, and after a 1-h delay interval. However, after a 25-h delay interval, only the less-preferred food was available; at the location previously occupied by the preferred food, only a distasteful food remnant remained.

Results and discussion

Training

The 10 monkeys considered together required a mean of 13.0 sessions to attain criterion. The two groups did not differ on this measure ($t_8 = 0.96$; group Con 12.2 sessions; group Hp 13.8 sessions).

Study phase

During the 8 study runs of each trial, the monkeys rapidly learned to look first in the location holding the preferred food. The two groups did not differ in the number of first looks to the site with the preferred food (Fig. 4, upper lines). A repeated measures ANOVA with between-subjects factor Group (Con, Hp) and within-subjects factor Run (1–8) revealed a significant main effect of Run, but no significant effect of Group and no significant interaction between Group and Run (Group $F_{1,8} = 2.05$; Run $F_{7,56} = 49.32$, $p < .01$; Group × Run $F_{7,56} = 0.74$). The monkeys also learned to avoid the unbaited site, indicating that they had encoded not only the location of the preferred food, but also the location of the less-preferred food (Fig. 4, lower lines). A repeated measures ANOVA with between-subjects factor Group (Con, Hp) and within-subjects factor Run (1–8) revealed that group Hp was mildly impaired in learning to avoid the unbaited site (Group $F_{1,8} = 10.46$, $p < .05$). In addition, as expected, the number of first looks to the unbaited site declined significantly across the 8 runs, but there was no significant interaction between Group and Run (Run $F_{7,56} = 18.45$, $p < .01$; Group × Run $F_{7,56} = 0.57$). By the end of the 8 training runs, both groups visited the unbaited site less often than would be expected by chance (Con $t_4 = 15.76$, $p < .01$; Hp $t_4 = 5.11$, $p < .01$). Thus, despite their deficit in spatial memory (Hampton, Buckmaster, et al., 2004), with the present "repeated runs" pro-
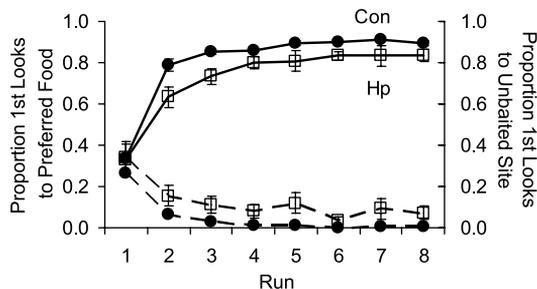

Fig. 4. Acquisition of the location of the preferred food (upper, solid lines and left ordinate) and the location of the empty site (lower, dashed lines and right ordinate) during the study phase of trials. Data shown are from the first choice of each "run," where a run consisted of up to three visits to the foraging array during which the monkey would discover and eat both the preferred and less-preferred food reward. Group Con is indicated by filled circles; group Hp is indicated by open squares; Error bars are standard errors.

cedure the hippocampectomized monkeys, like the controls, were able to encode the locations of both the preferred and less-preferred foods during the study phase.

Test phase

For purposes of data analysis, the 30 trials were divided into three 10-trial blocks (Fig. 5). A repeated measures ANOVA with Group (Con, Hp) as a between-subjects factor and Delay (short, long) and Block (1–3) as within-subjects factors revealed no significant main effect of Group or Block and no significant interactions, although the effect of Delay was significant (Group $F_{1,8} = 4.17$; Block $F_{2,16} = 2.18$; Block × Group $F_{2,16} = 0.23$; Delay $F_{1,8} = 15.04$, $p < .01$; Delay × Group $F_{1,8} = .06$; Block × Delay $F_{2,16} = 0.32$; Block × Delay × Group $F_{2,16} = 0.71$). To maximize statistical power, the ANOVA was recalculated, removing Group as a factor, and again the effect of Delay was significant but did not interact with Block (Block $F_{2,18} = 2.38$; Delay $F_{1,9} = 16.80$, $p < .01$; Block × Delay $F_{2,18} = 0.33$). Thus, neither group of monkeys showed the progressive decrease in the probability of visiting the preferred food location on long compared to short delays that would indicate WWW memory (compare Figs. 1 and 5). Such a result would be evident statistically in a Block × Delay interaction, but Delay was the only significant effect.

Use of WWW memory predicts fewer searches directed at the location of the preferred food on long-delay trials, compared to short-delay trials. Although we found a significant effect of delay interval, it was small and it did not grow in magnitude over training as would be predicted by use of WWW memory. Still, the main effect of delay requires some explanation. There are two main possibilities—first, that it reflects knowledge of the time of the test relative to the study phase and, second, that it reflects forgetting. As for the former explanation, we predicted a gradual emergence of the different choices on long versus short delay trials because it is only through experience that the monkeys could learn that the preferred food was not available at the long delay. Furthermore, even if monkeys acquired this knowledge in the first few trials of the experiment, the initial small difference in choice behavior
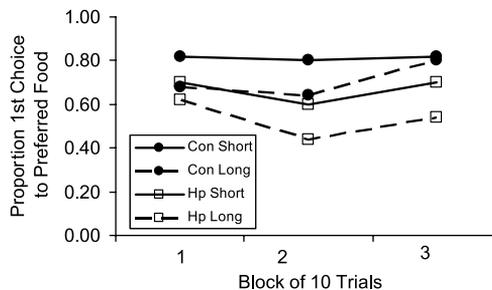

Fig. 5. Proportion of first looks to the site where the preferred food had been located during study (see figure for key). Use of WWW memory could be inferred if preference for the location of the preferred food declined selectively on long delay trials as training progressed. Con, intact control monkeys; Hp, monkeys with selective hippocampal lesions.

between long and short delays should have increased with training if monkeys had WWW memory. Indeed, the data from Group Con are a particularly bad fit for the emergence of "when" memory because the probability of searching in the site of the preferred food at the long delay actually increased, on average, in the last block of training (Fig. 5), a pattern opposite that predicted by use of WWW memory. Still, we cannot entirely rule out the possibility that the main effect of Delay reflects a weak form of "when" memory. The second possibility is that the main effect of Delay reflects forgetting, over the interval between the short- and long-delay tests, of either the locations of the foods or of their identities or both. Unlike the case of "when" memory, a delay effect caused by forgetting should be evident from the beginning of training, and remain constant across training. Unfortunately, the data are too sparse to support reliable analysis of learning in the first few trials alone, an analysis that might discriminate between these two possibilities. However, further analysis of forgetting can be conducted on visits to unbaited sites.

To determine whether forgetting occurred between the short- and long-delay tests, we examined the probability that monkeys searched in the unbaited site. Forgetting could be of three distinct types: monkeys might forget which locations contained rewards, or they might forget which food was in each of the two rewarded locations, or they might forget both types of information. The first two types of forgetting make distinct predictions about the probability of searches in the unbaited location. If spatial memory failed, monkeys would be forced to guess which locations contained food, and one-third of these guesses would be directed to the unbaited site. By contrast, if monkeys remembered which locations contained food but forgot which specific foods were in the two baited locations they would choose between the two baited locations and still successfully avoid looking in the unbaited location. Because so few errors were made to the unbaited site, the data were collapsed across blocks to reduce the number of '0' values in the analysis. A repeated measures ANOVA with Delay as the within-subjects factor, and Group as the between-subjects factor did not reveal a difference in the probability of searches at the unbaited site after long-compared to the short-delay intervals (Fig. 6; Delay $F_{1,8} = 1.81$; Delay × Group $F_{1,8} = 0.91$). Thus, loss of spatial memory cannot account for the main effect of Delay on searches to the location of the preferred food. However, partial forgetting over the long-delay interval, whereby the location of the baited sites is retained, remains a viable account for these results. Such forgetting would lead to fewer searches directed at the location of the preferred food at the long delay, without a correlated increase in the probability of visits to the unbaited site. Partial forgetting, rather than weak "when" memory, therefore likely accounts for the small reduction in the number of searches to the site of the preferred food on the long- versus the short-delay tests (Fig. 5).

Our analyses also revealed that group Hp made significantly more visits to the unbaited site than did controls at both delays, indicating more forgetting in this group (Group $F_{1,8} = 34.43$, $p < .01$). However, both groups of monkeys visited the unbaited location less often than would be expected by chance (33.3%; Fig. 6) at both the 1-h delay (Con $t_4 = 15.76$, $p < .01$; Hp $t_4 = 6.11$, $p < .01$) and the 25-h delay (Con $t_4 = 7.99$, $p < .01$; Hp $t_4 = 7.08$, $p < .01$). Thus, both groups of monkeys did show significant memory for the locations of both foods even at the 25-h delay, but group Hp
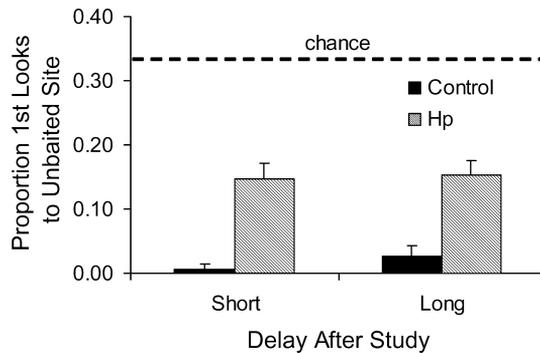
Fig. 6. Probability of visiting the location that did not contain food during study by intact control monkeys (Control) and monkeys with selective hippocampal lesions (Hp) after both the 1- and 25-h delay. Because there were three foraging sites, chance performance is 0.33; values below 0.33 reflect memory for the locations where food was found during study. Error bars are standard errors.

showed more forgetting than group Con, consistent with earlier findings for these monkeys (Hampton, Buckmaster, et al., 2004). Presumably, this accounts for the somewhat poorer (but not significantly so) overall performance of monkeys in group Hp at both delays (Fig. 5).

In these experiments, we adapted the techniques used by Clayton and Dickinson (1998), who demonstrated WWW memory in scrub jays, for use with rhesus monkeys. Although our monkeys were able to rapidly learn and to remember—for at least 25 h—the locations of two foods differing in palatability, they did not learn through training to discriminate between knowledge acquired 1 h versus 25 h earlier. Thus, our monkeys demonstrated memory for what and where, but not when.

The failure to find evidence for knowledge of the time of learning, which is critical to some definitions of episodic memory, could be due to a number of features in our experimental design. Thus, we cannot rule out the possibility that rhesus monkeys would demonstrate WWW memory in other circumstances. For example, we trained monkeys for only 60 days (30 trials) and this may have provided insufficient experience to support learning the discrimination. Alternatively, perhaps macaques would demonstrate WWW memory in contexts in which a larger part of their food ration was procured during foraging, or when tested in a social domain rather than a foraging domain. Yet another possibility involves the number of training runs. In the study phase, we gave monkeys 8 training runs in which to learn the locations of the two foods, and such a procedure may have biased our monkeys away from use of episodic memory. That is, it can be argued that the 8 training runs have the cumulative effect of establishing a semantic memory, rather than an episodic memory referring to a specific discrete episode. We doubt, however, that the difference between episodic and semantic memory hinges so simply on the "discreteness" of the to-be-remembered event. Indeed, real life events often unfold over time and involve a series of related experiences, rather than a specific "snapshot" of an instant. In addition, the scrub jays studied by Clayton and Dickinson (1998) made multiple caches per trial in each side of the ice-cube trays used as the caching substrate in their experiments.

Thus discrete experiences are not a prerequisite for the expression of WWW memory, and the repetition of the study trials therefore seems unlikely to account for our failure to find WWW memory in monkeys.

Unlike the study of Clayton and Dickinson (1998), our procedure used both long and short delay intervals on every trial. It is possible that finding both foods in the locations they occupied during study after the short delay interfered with the ability of the monkeys to learn to avoid the location of the preferred food after the long delay. Given our failure to find "when" memory in this study, it may be worth repeating the experiment with only a single delay used for each trial unique array of food locations.

This pattern of robust memory for the location and type of food reward, without concurrent memory for the time at which this information was acquired is not restricted to the present case. In experiments that also closely parallel the work with scrub jays, rats (*Rattus norvegicus*) carried preferred cheese chunks and less-preferred pretzel pieces to boxes located at the ends of the arms of an eight-arm radial maze, where the rats left the foods. Cheese was made unpalatable by treatment with a quinine solution; for half the rats, cheese was thus degraded after short delays and, for the other half, after long delays. The rats showed reliable memory for the type and location of food, but they did not learn to search pretzel locations selectively after delays associated with quinine treatment of the cheese (Bird et al., 2003). In a related set of experiments, rats also failed to learn to reenter the first arm of the maze visited during a session to receive a large reward (Roberts & Roberts, 2002).

We know of only one additional published attempt to apply the WWW criteria of Clayton and Dickinson to nonhuman animals, reported in this issue (Babb & Crystal, 2005). Rats foraged on a radial maze and encountered rat chow pellets in three arms and a chocolate pellet in a fourth arm. The rats were reintroduced to the maze either 30 min later the same morning, or 4 h later in the afternoon. In morning tests neither pellets nor chocolate was available in the arms visited 30 min earlier; instead, the remaining four arms were baited. Rats confined their visits to the new (i.e., unvisited) arms. In afternoon tests, chocolate was again available in the arm where it had been encountered in the morning, but pellets were only available in arms the rats had yet to visit that day. The rats tracked the temporal pattern of availability of chocolate, making more visits to the "chocolate arm" in the afternoon test (when chocolate was available) than in the morning test (when chocolate was not available). Whereas this result does, in a sense, demonstrate memory for "what, when, and where," we argue that it does not demonstrate "when" memory in the sense required for WWW memory. Because chocolate was available in afternoon tests, but not morning tests, time of day offers a reliable discriminative stimulus for the choice to search or avoid the chocolate-baited arm. The present study with monkeys, Bird et al.'s (2003) study with rats, and Clayton and Dickinson's (1998) study with scrub jays all used procedures that prevent such use of time of day to guide search behavior. Thus, the animals in these other studies are required to know how *long ago* they learned the locations of food, rather than what time of day is associated with the availability of a certain food. Encoding the rule that chocolate is available in the afternoon, but not in the morning, is much more analogous to semantic than episodic memory.

Although there are other published paradigms presented as evidence of episodic memory in nonhumans, none includes a demonstration of memory for the time of learning in the sense specified here (e.g., Agster et al., 2002; Bierley et al., 1983; Eichenbaum & Fortin, 2003; Fortin et al., 2002; Gaffan, 1994; Kesner et al., 2002; Schwartz et al., 2002; Zentall et al., 2001). Thus, to date, there appears to be no evidence for the "when" component of WWW memory in animals other than scrub jays.

The study of memory in food-storing scrub jays is of particular interest because their natural history includes the unusual behavior of caching food and retrieving it later using memory. It is possible that outside of humans, WWW memory has only evolved under the specific selection pressures faced by food-storing birds. Alternatively, it may be that the birds expression of natural caching behavior merely provides a particularly convenient "window" through which to see evidence for WWW memory. Similar evidence may emerge in other species once appropriate paradigms are developed. It will be of interest to determine whether other species of food-storing birds—ones that face the same ecological demands for memory as do scrub jays—demonstrate evidence of WWW memory.

An additional, unresolved issue is whether simultaneous discrimination of what, where, and when is by itself sufficient evidence on which to infer episodic memory, rather than semantic or some other type of memory (Hampton & Schwartz, 2004; Roberts, 2002; Suddendorf & Busby, 2003; Suddendorf & Corballis, 1997; Zentall et al., 2001). At least three issues need to be addressed. First, if animals are repeatedly tested on the same material or according to the same rule, they may encode memories semantically rather than episodically. For example, humans can demonstrate WWW memory about certain autobiographical details, such as those regarding their own birth, despite the fact that humans do not remember the episode of being born. Such autobiographical facts belong to semantic memory rather than episodic memory. By this argument, accurate performance on *novel* tests is required to demonstrate episodic memory. Second, episodic memories are part of long-term, rather than short-term, or working memory (Squire & Zola-Morgan, 1991; Tulving, 1972). By the classic definition of working memory used in animal learning (Honig, 1978), the food-caching and retrieval behavior of scrub jays is a clear example of working memory, despite the long intervals over which these birds remember the location of caches. Furthermore, what constitutes a "short" or "long" delay interval differs widely among species. Development of new criteria may be required to relate human and nonhuman short- and long-term memory systems. Third, episodic memory is a type of explicit memory (Squire & Zola-Morgan, 1991). Whether WWW memory in scrub jays is explicit has not been tested. As indicated in the Introduction, there is presently no means of documenting, in nonhuman animals, the conscious re-experiencing of an event. Nevertheless, recent findings suggest some new functional parallels between human explicit memory and memory in nonhuman animals. This emerging body of work suggests that some nonhuman primates have metamemory, a form of metacognition that likely depends on explicit representation (Call & Carpenter, 2001; Hampton, 2001, 2003; Hampton, Zivin, & Murray, 2004; Smith, Shields, & Washburn, 1998, 2003).

Although many issues remain unresolved regarding the significance of WWW memory, the work of Clayton and Dickinson and their colleagues has stimulated a fruitful reevaluation of the characteristic properties of episodic memory and its distribution among species. By defining episodic memory in a way that is experimentally tractable, yet captures at least some of the critical features of human episodic memory, their work has advanced efforts to test for this type of memory in nonverbal species and to understand the selective pressures that led to the evolution of episodic memory.

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