

Elements of episodic-like memory in animals

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A number of psychologists have suggested that episodic memory is a uniquely human phenomenon and, until recently, there was little evidence that animals could recall a unique past experience and respond appropriately. Experiments on food-caching memory in scrub jays question this assumption. On the basis of a single caching episode, scrub jays can remember when and where they cached a variety of foods that differ in the rate at which they degrade, in a way that is inexplicable by relative familiarity. They can update their memory of the contents of a cache depending on whether or not they have emptied the cache site, and can also remember where another bird has hidden caches, suggesting that they encode rich representations of the caching event. They make temporal generalizations about when perishable items should degrade and also remember the relative time since caching when the same food is cached in distinct sites at different times. These results show that jays form integrated memories for the location, content and time of caching. This memory capability fulfils Tulving's behavioural criteria for episodic memory and is thus termed 'episodic-like'. We suggest that several features of episodic memory may not be unique to humans.

Keywords: episodic memory; food caching birds

1. INTRODUCTION

In the latter half of the nineteenth century, Charles Darwin suggested that mental characteristics are subject to natural selection in much the same way as morphological traits, and that human mental capabilities therefore share many features in common with those of other animals (Darwin 1871). Inspired by Darwin's thesis that we should be able to learn about our mental lives by studying those of other animals, comparative psychologists began to develop animal models of learning and memory and have spent the past hundred years and more in the scientific study of animal memory. Of the many categories of memory that humans possess (e.g. Squire *et al.* 1993; Schacter & Tulving 1994), there is only one form of memory that is thought to differentiate us from other animals—the ability to episodically recall unique past experiences (e.g. Suddendorf & Corballis 1997; Tulving 1983; Tulving & Markowitsch 1998). The argument is derived from the fact that language-based reports of episodic recall suggest that the retrieved experiences are explicitly located in the past ('mental time travel') and are accompanied by the conscious experience of recollection, so-called 'autonoetic consciousness' (Tulving & Markowitsch 1998).

This definition makes it impossible to demonstrate episodic memory in animals because there are no agreed non-linguistic behavioural markers of conscious experience (Griffiths *et al.* 1999). The dilemma can be resolved to some degree by adopting Tulving's (1972) original definition in which he states that episodic memory 'receives

and stores information about temporally dated episodes or events, and temporal-spatial relations among these events' (p. 385). Thus, episodic memory provides information about the 'what' and 'when' of events ('temporally dated experiences') as well as 'where' they happened ('temporal-spatial relations'). The merit of this definition is that the simultaneous retrieval and integration of information about these three features of a single, unique experience may be demonstrated behaviourally in animals without the need for language. We therefore refer to an animal's ability to fulfil the behavioural criteria regardless of autonoetic consciousness as 'episodic-like' memory (Clayton & Dickinson 1998, 1999a).

To date, most studies of animal memory have not distinguished between episodic recall of events from semantic knowledge for facts that can be acquired over multiple trials. Typically, the memory tasks require the animal to retrieve information about only a single feature of the episode as opposed to testing its ability to form an integrated memory of 'temporal-spatial relations'. It is also common for the animal to be given multiple training experiences thereby removing the trial-uniqueness of the task (see Griffiths *et al.* 1999). Furthermore, in many of the tasks that have been used, the animal does not need to recall the 'what, where and when' of an event. Instead, the task may be solved by discriminating on the basis of relative familiarity, a process which is dissociable both psychologically (Mandler 1980; Jacoby & Dallas 1981; Jacoby 1991) and neurobiologically (Aggleton & Brown 1999) from episodic memory recall.

Most of the tasks that have been used to investigate animal memory can be explained in terms other than episodic recall. A different strategy of testing whether or not animals are capable of episodic memory is to adopt

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an ethological perspective and consider cases in nature in which an animal might need simultaneously to retrieve and integrate information about what happened, where and when during a specific previous experience. The ability to remember the 'what, where and when' of individual past episodes is probably met by several behaviours.

When considering the evolutionary history of episodic-like memory in animals, it might seem intuitively logical to focus on the abilities of non-human primates. The study of non-human primate coalition or alliance formation might provide a useful starting point, given that the social partners need to keep track of cognitively complex social relationships. Social status is at the core of monkey and ape society. Males are distinguished from each other on the basis of size, strength, fighting ability, etc., and the greater these attributes, the higher the individual's social status, and the greater their access to resources such as food and mating partners (Tomasello & Call 1997). Alliances are predominantly formed after a number of conflicts, usually between subordinate animals in attempts to gain access to those resources unavailable to them when alone, and are more long-term and more stable than coalitions (Van Schaik & Aureli 2000). Alliance formation may be more reliant on episodic-like memory processes than coalition formation because of the need to keep track of a number of different trial-unique events concerning who did what and to whom. Less certain are the roles of the 'where' and 'when' components of episodic-like memory in alliance formation, as there is still little known about the mechanisms of this behaviour.

An alternative strategy would be to look to the behavioural ecology of an animal that may provide important clues to which species may make use of, or require, an episodic-like memory. One potential candidate may be brood parasitism. Brood parasitic birds, such as cuckoos and cowbirds, deposit eggs in the nests of other species and the young are then cared for by the host species. This is a mechanism by which the parasitic birds may remove the high costs associated with parental care (by getting another bird to pay the costs). There are two types of brood parasite: specialists and generalists (Krebs & Davies 1993). Cuckoos (*Cuculus canorus*) are specialist parasites in that they lay eggs in the nest of one species of host—they observe the host building a nest and then wait for them to begin their clutch, laying their egg during the host's laying period. Secrecy is of the essence, for fear of discovery by the host, and the total time spent at the host nest is thought to be less than 10 s in this species (Davies & Brook 1988). By contrast, brown-headed cowbirds (*Molothrus ater*) are generalist parasites because they lay their eggs in the nests of many species of host birds, each of which will produce clutches at different times. Both generalist and specialist parasites 'must remember where potential victims have started their nests in order to return to them one to several days later when the time is ripe for the cowbird to add her egg to those already laid' (Alcock 1998, pp. 112–113). A successful brood parasite may use information concerning the location of the host nest ('where'), the status of the clutch ('what') and the time of laying ('when'), although the memory load may be greater for generalist parasites in terms of the number of different host nests they visit. Episodic-like memory

would be important for this form of parasitism, not only because the parasite would need to remember the 'what', 'where' and 'when', but also because these events are likely to be trial-unique. The parasite would not be able to keep returning to each host nest to see whether the clutch had been laid through fear of discovery by the host. Thus every discovery of a possible host nest would be a trial-unique event and the calculation of the relative time to parasitize each nest would be essential.

Another potential candidate for a natural use of episodic-like memory may be present in animals that have a polygynous mating system, such as some species of vole. Meadow vole (*Microtus pennsylvanicus*) males mate with multiple females and have larger home range sizes than females of the same species, and of other species of voles that form long-term pair-bonds with only one partner (Jacobs *et al.* 1990). Male meadow voles control a large number of females through mate guarding at the time of oestrus and the females mate exclusively with that male. The females are distributed over a wide area and come into oestrus at different times. One potential mechanism by which the male can keep track of the females' reproductive state, and ensure that the females do not reproduce with other males, may be through the use of episodic-like memory. Again, this form of behaviour could benefit from the ability to remember the 'what' (female identity), 'where' (location of female) and 'when' (changing reproductive state and relative time of states between females) components of episodic-like memory. This form of behaviour would also be trial-unique because every female would be encountered during a particular reproductive state at a particular location.

The final example we will consider in more detail is food caching. The advantage of food caching is that it can be studied in the laboratory as well as in the field, and is easily amenable to experimentation. Scatter hoarding birds hide hundreds of seeds throughout the territory and rely on memory to recover their food caches, weeks or even months later (for a comprehensive review, see Shettleworth 1995). It is well established that food caching species remember cache locations. There are good reasons to believe that they would need to encode much richer representations of the caching event, however. It is known, for example, that some food-caching species do not return to sites from which they have retrieved all the food, which suggests that they can remember whether or not they have emptied a cache site (Clayton & Dickinson 1999b; Shettleworth & Krebs 1986). Some of these species, including scrub jays (*Aphelocoma coerulescens*) cache insects and other perishable items as well as seeds (Vander Wall 1990). It may be adaptive, therefore, for them to encode and recall information about what has been cached when as well as where.

In order to fulfil the behavioural criteria for episodic memory, animals would need to be able to encode the information about the caching or recovery episode based on a specific past experience, and then accurately recall the information about what, where and when a particular past event occurred. In the remainder of this paper, we will describe a series of experiments on episodic-like memory in scrub jays and discuss how these studies may provide a working model for testing episodic-like memory

in animals in the absence of language (Clayton & Dickinson 1998). To test the jays' ability to retrieve and integrate information simultaneously about the 'what, where and when' of a specific caching episode we capitalized on the jays' natural propensity to cache perishable and non-perishable food items, and rely on memory to search for their caches at a later date. In this way, we could test their ability to remember the contents and location of their caches and the relative time of caching in terms of whether or not the cached items should have perished by the time of recovery.

2. EPISODIC-LIKE MEMORY IN FOOD-STORING BIRDS

To test whether scrub jays are capable of episodic-like memory, birds were allowed to cache perishable foods, such as mealworms and crickets, and non-perishable peanuts in sand-filled caching trays on Monday morning. The scrub jays were divided into two groups, 'degrade' and 'replenish', which differed in whether or not they had the opportunity to learn that some foods are perishable and therefore degrade over time. Both groups of birds were given the opportunity to recover their caches on Monday afternoon (i.e. 4 h later), Tuesday afternoon (i.e. following a 28 h retention interval) or on Friday afternoon (i.e. after a 100 h retention interval). The logic is as follows. Jays show a strong preference to cache, recover and eat the perishable foods when they are fresh, and prefer both mealworms and crickets to peanuts, but prefer mealworms to crickets. Both mealworms and crickets degrade rapidly over time, however, so that if they are left for several days they become rotten and unpalatable. If birds in the degrade group can remember when they cached as well as what they cached and where, then they should recover the perishable foods when they were cached just a few hours ago. They should avoid them, however, and instead search for peanut caches, if the mealworms and crickets were cached several days ago and have had time to degrade. To ensure that the perishable items were thoroughly degraded, we coated them in washing up liquid and left them to rot in the sun. A supply of these degraded mealworms and crickets was kept in the refrigerator. We arranged for the mealworms to degrade more quickly than the crickets: mealworms were only fresh 4 h later and had degraded by both the middle and the long retention intervals, whereas the crickets were still fresh after 28 h, but were rotten 100 h after caching (Clayton *et al.* 2001).

To ensure that each episode was unique, the birds cached and recovered from trial-unique plastic, sand-filled ice-cube trays that contained two rows of eight ice cube moulds that served as individual cache sites. Each tray was attached to a wooden board and surrounded by a visuo-spatially distinct Lego Duplo structure that was placed next to one of the long sides of the tray (see Clayton & Dickinson 1998, 1999*a,b*). The jays cached the perishable items in one side of the tray and then cached non-perishable items in the opposite side of the same tray, or vice versa. Birds were given access to only half of a tray at a time by attaching a transparent Perspex cover over one half of the tray with bulldog clips, thereby restricting access to one column of eight cache sites parallel to the Lego structure.

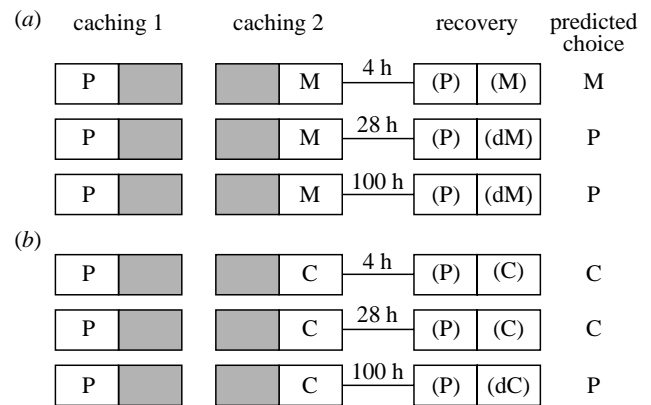


Figure 1. The caching and recovery conditions during each type of training trial for the two sides of the caching tray during the two caching periods and the recovery period for experiment 1; (a) P/M trials, (b) P/C trials. Also shown are the predicted choices for the degrade group at recovery. The shaded areas represent the non-accessible side of the tray and the non-shaded areas the accessible side. P, peanuts; M, fresh mealworms; C, fresh crickets; dM, decayed mealworms; dC, decayed crickets; (), food items present on training trials but absent on test trials. h = hour. Reprinted by permission of Clayton *et al.* (2001, fig. 1).

The 'degrade' group received a series of training trials in which they had the opportunity to learn when the mealworms and crickets degrade. They were allowed to cache two food types and then recover them after retention intervals of 4, 28 and 100 h. They cached peanuts (P) in one side of a caching tray on every trial and then either mealworms (M) or crickets (C) in the other side so that each bird received alternating P/M and P/C trials at each of the three retention intervals. The six different types of training trials are illustrated in figure 1, as are the predicted choices for the 'degrade' group. The birds should selectively recover mealworms on P/M trials and crickets on P/C trials, when those items are fresh. They should switch their preference to peanuts, however, when the mealworms were cached 28 or 100 h ago on P/M trials, and when the crickets were cached 100 h ago on P/C trials.

The birds were given only four P/C and P/M trials at each retention interval because the 'degrade' group birds acquired this information about rates of perishability after just two or three trials of each type. To assess the extent to which their recovery searches depended on memory, the experiment concluded with six test trials (P/M and P/C trials at each retention interval) in which all the food items had been removed prior to recovery. The trays were filled with fresh sand so that no extraneous cues were present and the birds therefore had to rely on their memory of where and when the worms and peanuts had been cached. As predicted, the results of both training and test trials showed that the 'degrade' group jays reversed their search preference when the retention interval was such that the perishable foods would have degraded. The fact that this switch in search preference was observed even on test trials in which no food was present at recovery shows that the jays relied on memory as opposed to visual, olfactory or tactile cues that may emanate directly from the sand covering the hidden food.

Finally, to ensure that the preference profile depended on learning about the perishability of the mealworms and crickets, the performance of the 'degrade' group was compared with that of the 'replenish' group in which both mealworms and crickets were fresh on every trial. As predicted, birds in the 'replenish' group searched preferentially for mealworms and crickets at all retention intervals on both training and test trials. The fact that the 'replenish' group did not show the switch in search preference on P/M and P/C trials rules out a simple explanation in terms of differential rates of forgetting for the different types of food caches. It also rules out the possibility that jays use some intrinsic, unlearned sensory properties of the food, such as texture or shape, to guide their preference to search for perishable foods after the short retention interval but to avoid them when a long time had elapsed between caching and recovery. The results of this first experiment suggest that the 'degrade' group scrub jays can rapidly learn to remember temporal information about when the items were cached relative to recovery, as well as which items were cached where.

Without further training, the birds were given a new caching condition that they had not experienced previously: the birds cached mealworms in one side of the tray and crickets in the other side of the same tray. We gave them a test trial (i.e. no food present during recovery) in which they were allowed to search for these caches either 4 h (when both foods are still fresh) or 28 h later (when the mealworms have decayed but the crickets are still fresh). Since the birds prefer fresh mealworms to crickets, the 'replenish' group should always search preferentially in the sites in which they had cached the mealworms. If birds in the 'degrade' group can apply their knowledge about the relative perishability profiles of mealworms and crickets derived from earlier P/M and P/C trials to this novel M/C trial, then they should search selectively for mealworms when they had been cached 4 h ago but switch to searching for crickets when the mealworms had been cached 28 h previously. The results confirmed these expectations, demonstrating that the birds can remember where and when they hid their caches. The birds also possess sufficient information about the contents of the caches to allow them to distinguish between mealworm and cricket cache sites. Furthermore, the results suggest that the birds can flexibly use the information learned in one context and apply it to a new caching condition.

In order to search preferentially for mealworms during the four-hour test trials and for crickets during the 28-hour test trials, at the time of recovery birds in the 'degrade' group must have been able to recognize the trays in which they had cached mealworms and crickets earlier. Like many other tests of memory, the problem is that this task can be solved either by recollection or by familiarity. Familiarity is an automatic process based on the perceptual characteristics of the stimuli that allow the individual to distinguish previously experienced stimuli from novel ones, but it does not require the birds to remember any of the details of the original presentation of the stimuli (Mandler 1980; Jacoby & Dallas 1981; Jacoby 1991). Thus the jays may have based their decision of when to search for mealworms on the relative familiarity of the two trays as opposed to recalling what they cached where and

when. If this were the case then 'degrade' group birds could have learned to search in mealworm sites on the four-hour trials when the tray was relatively familiar, and learned to search in cricket sites when the tray had not been seen for 28 h and was therefore relatively unfamiliar.

We therefore tested whether the jays could remember what, where and when in the absence of using tray familiarity as a cue. The same birds were given a further pair of test trials in which they cached mealworms in one side of the tray and crickets in the other side of the same tray. On the M/C trial, birds cached mealworms first and then, instead of caching crickets immediately afterwards, there was a retention interval of 24 h between the two caching events followed by a further gap of 4 h before the recovery test phase (in which no food was present, so we could test for memory). Thus, the mealworms were 28 h old and the crickets were only 4 h old at the time of recovery on the M/C trial. The reverse order of caching was enforced on the C/M trial so that the crickets were 28 h old, and the mealworms were still fresh, having been cached only 4 h ago. If the 'degrade' group birds were relying on familiarity to solve the task then they should preferentially search for mealworms on both M/C and C/M trials because on both recovery test trials the tray had been seen only 4 h ago. By contrast, if the birds remembered how long ago each type of food had been cached then they should only search for mealworm cache sites on C/M trials (when the mealworms had been cached 4 h ago) and switch to cricket caches on M/C trials (when the mealworms had been cached 28 h ago and should therefore have degraded). The 'degrade' group birds showed this switch in preference from mealworm sites on C/M trials to cricket sites on M/C trials and, as expected, the 'replenish' group always searched in mealworm sites. We therefore conclude that the 'degrade' group birds must have remembered the time at which they cached the mealworms and in a way that cannot be explained by relative familiarity of the trays (Clayton *et al.* 2001).

Taken together, the results of this series of experiments show that jays can remember the 'what, where and when' of specific past caching episodes. We believe that the specific 'what–where–when' information encoded during each trial-unique caching period is episodic in nature. By contrast, the information about the decay properties of the food that the birds acquired during training can be characterized as non-episodic (semantic-like) declarative memory as opposed to procedural memory because of the flexible way in which the birds use this information about the decay properties of the food. The jays used information about the decay profiles of mealworms and crickets learned during training on P/M and P/C trials in the first experiment to control searching in C/M and M/C trials in which the jays were given a direct choice between mealworm and crickets cache sites for the first time.

3. REMEMBERING THE 'WHAT' OF AN EVENT

The results in the previous section suggest that food-caching scrub jays can remember some information about the contents of their caches, as well as the relative time since caching and the locations in which the items were cached. Stronger support for this claim that birds remember the 'what' of an event comes from a second

study in which we assessed how richly the events that occur during a caching episode are encoded by contrasting memory for caching with that for recovery (Clayton & Dickinson 1999*b*). The fact that some food-caching species do not return to sites from which they have retrieved all the food (e.g. Shettleworth & Krebs 1986) suggests that they can remember whether or not they have emptied a cache site. In order to do so, the birds would need to distinguish between the actions of placing the bill in the sand to cache, and placing the bill in the sand to recover the cache. Of course, these caching and recovery episodes involve memory for the location and content of the same food items. The episodes differ in terms of the type of actions performed, namely caching or recovering caches, and whether the food cache is intact at the end of the episode (after caching) or whether the cache site is now empty (after recovery).

The study consisted of four caching phases and two recovery phases followed by a recovery test phase. Birds cached three peanuts in the left-hand sides, and three dog-food kibbles in the right-hand sides, of two visuo-spatially distinct caching trays. They were then allowed to recover all three peanuts from one tray and all three kibbles from the other tray 3 h later. This meant that at the end of these recovery phases, one tray contained only kibbles and the other tray contained only peanuts. As in the previous experiment, the birds had access to only half a tray at a time during caching and recovery. In a final test, both sides of both trays were presented to the bird simultaneously. The caches were removed prior to this test trial and the trays were filled with fresh sand so that no extraneous cues were present and the birds therefore had to rely on their memory. If they can remember what type of food they had cached in each of the sites, what they had recovered from each site, and can integrate these two sources of information, then during the test trial birds ought to go to the tray that should still contain their preferred food (Clayton & Dickinson 1999*b*).

The relative preference of the foods at recovery was manipulated by pre-feeding the jays with one of the two food types because pre-feeding of a specific food selectively reduces the subsequent value of that food in terms of both eating and caching (Clayton & Dickinson 1999*c*). They were pre-fed peanuts or dog biscuits in powdered form to ensure they could not cache during the pre-feeding phase. Those that had been pre-fed peanuts preferentially searched in the cache sites in which they had cached dog biscuits and selectively searched only in those sites from which the birds had not recovered dog biscuits during the previous recovery phase (i.e. the intact dog biscuit sites). Likewise, those birds that had been pre-fed dog biscuits preferentially searched in the intact peanut sites. This ability to encode what action occurred, and whether the cache site still contains food, enables the animal to keep track of 'what' is cached and 'where' across a series of caching and recovery episodes (Clayton & Dickinson 1999*b*).

The results of this second study confirm the finding described in the previous section that scrub jays encode information about the contents of their caches. Without this knowledge they could not have directed their searches selectively to the tray that should still have contained the non-pre-fed food. The results also show

that the birds can integrate information of the content of a cache at recovery with information about the specific location of the cache. Without the capacity for such integration, the birds could not have directed their searches selectively to the intact sides of the tray, let alone to the particular cache sites in which they had stored the food items. Furthermore, their ability to encode what action occurred, and whether the cache site still contains food, enables the animal to keep track of 'what' is cached and 'where' across a series of caching and recovery episodes (Clayton & Dickinson 1999*b*).

In a third study we tested whether scrub jays can remember where a conspecific has cached and then subsequently recover (pilfer) them more accurately than conspecifics who are not given the opportunity to observe food caching (D. P. Griffiths, A. L. Duarte and N. S. Clayton, unpublished data). Although other studies have suggested that corvids have this ability, this study introduced a novel control for the use of other potential cues that may signal the location of food, thereby limiting the difference between the groups to the opportunity to observe caching. Storer birds cached in a sand-filled caching tray in their home cage. The control and observer birds' cages were equidistant from the storer's cage, but differed in whether or not they could see the storer as well as hear the bird caching. The observer bird had the opportunity to see where the storer cached by observing through a Plexiglas screen that divided the two cages. The control could not see the storer because the divider between the control's and storer's cage was made of aluminium. The control group could therefore listen but not look.

After a retention interval of approximately 4 h, each subject had the opportunity to search in the caching tray in which the storer had cached. During recovery, none of the other birds could observe the subject as a dark cloth was placed between the cages to entirely cover the back of the cage. We then compared accuracy of recovery when each of the three groups of birds had the opportunity to search for the storer's caches. As in the previous studies, there was no food available during the recovery phase of the test trial so the birds had to rely on memory. Although scrub jays that stored food were the most accurate at cache recovery, the results of this experiment also showed that observer birds made fewer searches to discover the cached food, relative to control birds that could hear but not watch the items being stored. These results suggest that observation is an effective mechanism by which a bird can increase its pilfering success.

Taken together, the results of the experiments described in this section demonstrate that the bird's ability to encode and recall 'what' memories is not limited to information about the contents of the caches. Jays can also remember other types of 'what' information such as whether or not the food has been recovered and whether that information has been gained by a personal experience of caching or as a result of observing another individual's food-caching behaviour.

4. KEEPING TRACK OF TIME

The ability to accurately encode and recall trial-unique spatial locations has been well established across a variety of spatial memory tasks, from the performance of rats in

radial arm mazes (e.g. Olton & Samuelson 1976) to the caching behaviour of food-storing birds (e.g. Shettleworth 1995). The results described in the previous sections provide strong evidence for the claim that scrub jays can also remember 'what' occurred during caching: our results suggest the birds can recall information about the type of food item cached and the nature of the behavioural transaction in terms of whether it was cached or recovered. It is also clear that the jays can remember the relative time since caching, in the absence of using tray familiarity as a cue. What is less clear, however, is the mechanism by which the jays keep track of time and the nature of the temporal representation of caching episodes.

In order to characterize the nature of this temporal control, Clayton and colleagues conducted a further experiment to assess the temporal generalization of search preferences for birds that had received the peanut and cricket caching trials (N. S. Clayton, K. Yu and A. D. Dickinson, unpublished data). Having been trained with 4, 28 and 100 h retention interval trials, both 'degrade' and 'replenish' group birds were given probe tests in which no food was present during recovery to test whether the pattern of searching was based upon memory for the caching episode. Birds cached peanuts and crickets as usual but then received these recovery tests at untrained retention intervals of 52, 76 and 124 h, i.e. after two, three and five days. These generalization tests were conducted in pairs. The first pair assessed the recovery preference after two- and three-day retention intervals, whereas the second reassessed recovery after the three-day interval and compared the preference with that observed after a five-day retention interval.

The replenish group showed a consistent preference to search in the cricket cache sites across variations in the retention interval. By contrast, the proportion of searches varied with retention interval for the degrade group. After the one-, two- and three-day intervals, birds in the 'degrade' group also showed a strong preference to search in cricket cache sites. The four- and five-day intervals produced a marked divergence between the groups with the 'degrade' group searching preferentially in the peanut cache sites. This generalization of search preferences across variations in retention interval suggests that the 'degrade' group scrub jays treated the perishability of crickets categorically. Having been trained that crickets are fresh and palatable at 4 h and one-day intervals, but decayed and disgusting after a four-day interval, these birds showed a stable preference for the crickets at intervals shorter than four days but a marked preference for peanuts at intervals of four days or longer.

The fact that the search preferences of the replenish group were independent of the retention interval also provides strong support for the claim that the jays were not simply forgetting the locations of the various food types at different rates. Clearly, the temporal control of searching by the 'degrade' group could not have reflected more rapid forgetting of the perishable caches. This temporal control could have been mediated by the strength of a decaying trace of a 'what-where' memory, however, without any direct encoding of the time of caching. In his review of memory for the time of past events, Friedman (1993) identified the strength of a decaying memory trace for an episode as one of the

possible processes by which humans judge the time of the episode. An account in terms of strength of a memory trace assumes that the jays in the 'degrade' group learn to search mealworm or cricket sites if a retrieved 'what-where' memory is strong and to search for the peanuts sites if the memory trace is weak. This account rests on the implausible assumption that the discriminability of memory traces does not vary with their strength. Using a specific satiety devaluation procedure, Clayton & Dickinson (1999b) reported that the difference between searching for caches of the devalued and non-devalued food was just as strong after a 172 h retention interval as after one of 4 h, thereby demonstrating that the discriminability of the 'what-where' memories for the two foods was just as good after one week as after a few hours. The overall level of searching did not decrease with retention interval in any of the aforementioned jay experiments, as might be expected if the strength of the memory trace for a cache episode determines searching activity.

There is no doubt that animals can time elapsed intervals (Bradshaw & Szababi 1997). Interval timing has been studied mainly using operant conditioning procedures in rats and pigeons and there is now an extensive body of data and theory about the processes underlying interval timing (for a review, see Shettleworth 1998). Essentially, the encoding event is thought to start an internal 'clock' in the form of a pacemaker (e.g. Gibbon *et al.* 1984) or a series of oscillators (e.g. Church & Broadbent 1990). To time events, the animal compares the current state of its clock with a stored reference value that was acquired during training. In evaluating the relevance of such models to the temporal control of cache recovery, it is important to note that these models are based on tests using operant conditioning procedures in which the elapsed intervals are a matter of seconds, minutes and at most a few hours (Gibbon *et al.* 1997), rather than days involved in cache recovery. The fact that jays in the 'degrade' group showed a switch in preference from mealworms to peanuts at both the 28 h and 100 h retention intervals, yet showed a switch from crickets to peanuts after only the 100 h interval, requires the bird to use multiple timers simultaneously, each associated with a particular cache location. Furthermore, the birds could not simply use the passing of a night as a cue for when to switch their search preference because the degrade group birds discriminated between one and four diurnal cycles in their searches for crickets and peanuts. There are, however, a number of other processes that could have mediated the temporal control observed in these caching studies. For example, Gallistel (1990) has argued that animals automatically encode the time of an experience in memory with some form of time tag. In addition to trace strength and automatic time tagging, Friedman (1993) identifies six further processes that could play a role in human temporal memory.

5. THE STRUCTURE OF INTEGRATED 'WHAT, WHERE AND WHEN' MEMORIES

The experiments described in the previous sections suggest that scrub jays form integrated memories of the 'what, where and when' of a caching episode, but they do

not address the structure of this integrated memory. It has been suggested that the retrieval of information about a discrete event, such as a caching episode, depends on multiple, complex mnemonic structures and processes (e.g. Gallistel 1990; McClelland *et al.* 1995; Teylor & DiScenna 1986). The aim of the final experiment was to attempt to specify the minimal memory structure required to support the cache recovery observed in the present studies (see Clayton *et al.* 2001).

One possibility is that the presentation of the caching tray at recovery activates 'where' representations of the cache sites, which in turn retrieves both 'what' representations of the food items cached at those locations and 'when' representations of how long ago the caching event occurred in that location. We shall refer to this memory structure as a 'what-where-when' structure to illustrate that the 'what' and 'when' information is integrated into the memory of the caching episode through the 'where' representation of the cache sites. Figure 2*a* illustrates the structure of such 'what-where-when' memories in the case in which peanuts were cached in the left side of a caching tray and mealworms were cached in the right-hand side relatively recently. Note that there is no direct association between 'what' and 'when'. At retrieval, the bird can recall what type of food it cached in a particular location and when it stored the food in that location, but it has no direct access to temporal information from the content representation or *vice versa*. Only the 'where' information provides access to both 'what' and 'when' memories.

An alternative structure is a 'where-what-when' memory in which binding occurs through the 'what' representation, which retrieves information about where and when those food items were cached but in this case there is no direct association between the 'where' and 'when' representations. Figure 2*b* illustrates the structure of the 'where-what-when' memories for the same caching episode as shown in figure 2*a*, namely when peanuts were cached in the left and mealworms were cached in the right side of a caching tray just a few hours previously.

The final possibility is a 'what-when-where' structure. In this case, the information about 'what' and 'where' are integrated indirectly as a result of both being bound by a 'when' representation of the time of caching. This structure is not illustrated in figure 2 because it cannot support the patterns of recovery already described in the previous studies. Consider the case in which the birds cached crickets and mealworms, and then searched for their caches either 4 h or 28 h later. According to this 'what-when-where' structure, both the recent and remote temporal representations would both retrieve 'what' representations of the two foods. The recent and remote temporal representations would also retrieve 'where' representations of the two sides of the caching tray but, without a direct link between the 'what-where', the bird would be precluded from knowing which type of food item was stored where. Consequently, this memory structure would not allow selective searching for the two food types depending on whether the foods had been cached 4 or 28 h ago. The patterns of recovery observed in those previous experiments can be explained by both a 'what-where-when' (figure 2*a*) and a 'where-what-when' structure (figure 2*b*), however. In the final

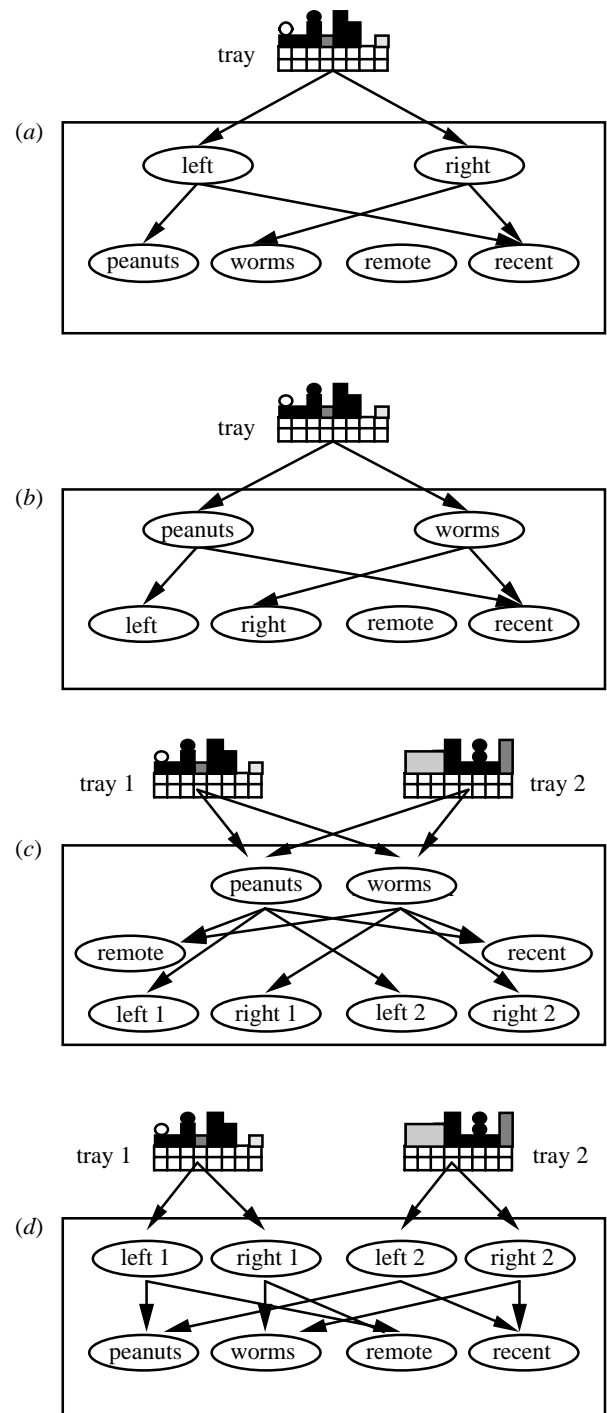


Figure 2. The memory structures for caching episodes (see text). (a) the 'what-where-when' structure for peanuts cached in the left side of the tray and mealworms in the right side of the tray relatively recently. (b) The 'where-what-when' structure for the same caching episodes as in (a). (c) The 'where-what-when' structure for peanuts cached in the left sides of the trays and mealworms in the right sides when caching occurred in tray 1 at a time remote from recovery and in tray 2 more recently. (d) The 'what-where-when' structure for the same caching episodes as in (c). Reprinted from Clayton *et al.* (2001, fig. 7).

experiment we therefore distinguished between the two structures.

The design capitalized on the fact that, under certain circumstances, the 'where-what-when' memory cannot

support appropriate search patterns for a single type of food item depending upon the time since caching. Consider the following scenario in which jays cache mealworms in tray 1 on a Thursday morning, then cache mealworms in tray 2 on a Friday morning and are allowed to search for their caches 4 h later on a Friday afternoon. Whether or not the birds should search for mealworms depends upon which tray is presented at recovery. The birds should avoid mealworm sites when presented with tray 1 because the mealworms were cached 28 h previously and should have already decayed. When tray 2 is presented, however, they should search for the mealworm caches because those mealworm caches are only 4 h old and should still be fresh.

A 'where-what-when' memory cannot support this search pattern, however, because the birds can remember what was cached where, and what was cached when, but there is no direct memory for when and where (figure 2c). According to this memory structure, the bird should retrieve the 'what' representation of mealworms when presented with either tray and this mealworm representation should then retrieve 'when' representations for both the 24 h and the 4 h retention intervals. Consequently, the bird would have conflicting temporal information about when the mealworms had been cached and would not be able to use its knowledge about perishability to search for the relatively fresh mealworms and avoid searching for the older ones. To do so, 'when' and 'where' representations must be bound directly. A 'what-where-when' memory structure (figure 2d) can support the appropriate search pattern, however, because the 'where' representation retrieves information about both the time of caching in that location as well as the contents of those caches.

We therefore allowed the birds in both the 'degrade' and 'replenish' groups to cache peanuts in one side of a tray and mealworms in the other, on two occasions separated by a day. Different trays were used on each day. Four hours after the second caching period, the jays were given two recovery periods in succession, first with the tray in which they cached on the first day and then with the tray in which they cached on the second day. No food was present during recovery in order to test for memory. As expected, birds in the replenish group that always received fresh mealworms irrespective of retention interval consistently searched in the mealworm sites in both trays. It is the birds in the 'degrade' group, however, that provide the critical test concerning the type of memory structure jays might use when encoding a caching episode. As predicted, birds in the 'degrade' group searched preferentially in the peanut side of the first tray but searched mainly in the mealworm side of the second tray. This result is therefore consistent with a 'what-where-when' memory structure in which the animals can remember both the 'what and where' and also the 'when and where' (figure 2d). It should be noted, however, that this structure is only the most parsimonious one warranted by the present studies and that the same performance could, of course, be supported by more complex mnemonic structures and processes. Gallistel (1990), for example, has also argued that feeding-related experiences set up multiple memory records that encode and integrate what, where and when information.

6. CONCLUSIONS

The results of this series of experiments show that jays possess an episodic-like memory of the 'what, where and when' of specific caching events that have occurred in the past. The jays can also remember what they recovered and from where, they can differentiate between memories of caching and recovering, and update information about the current status of their caches, based on whether or not they have already recovered from that particular cache. In addition, they can remember information about the social context of the caching event, based on whether they have a personal experience of food caching or have observed another bird doing so. When integrated, the jay has sufficient information to isolate 'what', 'where' and 'when' and thus is able to recall the episode of caching a specific item (Griffiths *et al.* 1999). These results fulfil Tulving's original behavioural criteria for episodic memory by providing information about 'temporally-dated experiences' and their 'temporal-spatial relations' (Tulving 1972).

There is a large gap between human and animal studies of memory and, in particular, the extent to which non-human animals possess episodic-like memory. This is principally due to the absence of suitable tasks that can isolate episodic memory without the reliance on language for testing episodic recall. We now believe, however, that the food-caching paradigm can test the ability of an animal to recall episodic-like information about a specific past experience and is mediated by an integrated or bound memory with at least a 'what-where-when' structure. A challenge for the future will be to develop other tasks that capture some of the critical features of episodic memory that do not rely on language, which in turn may provide invaluable insights into how space, time and events are represented and remembered in the brain.

Griffiths *et al.* (1999) have argued that unlike the food-caching jay paradigm, previous demonstrations of trial-unique memory in animals could have been mediated by relative familiarity rather than the temporal encoding of the episode and, hence, do not require an integrated memory of the features of the episode. Based on the results of a recent experiment, Menzel (1999) suggests that chimpanzees can remember the location and content of food sources. It remains to be seen whether the chimpanzees can also form integrated 'what-where-when' memories. As we suggested at the outset, the ecological approach to animal cognition (e.g. Real 1993; Healy & Braithwaite 2000) suggests that there may be a number of other naturally occurring situations in which an animal's ability to encode and recall integrated memories of specific past events are of vital importance to its survival. Potential candidates include brood parasitism, mate guarding in polygynous species where females come into oestrus at different times, and possibly social signalling systems such as the ability to form coalitions and maintain alliances in some monkeys and apes. The capacity for episodic-like memory is unlikely to be unique to humans and food-storing birds, and is probably important for survival in a number of animals.

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