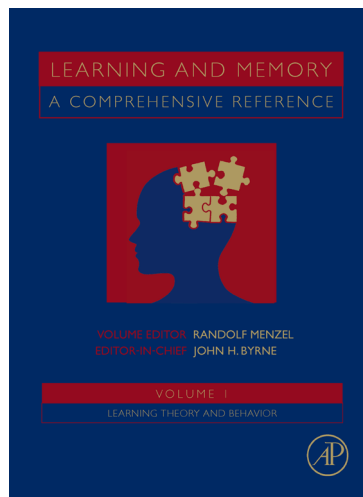


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1.23 What Do Animals Remember about Their Past?

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1.23.1 Introduction

Episodic memory refers to the ability to remember specific personal happenings from the past. Ever since Tulving first made the distinction between episodic memory and other forms of declarative memory in 1972, most cognitive psychologists and neuroscientists have assumed that episodic recall is unique to humans, in part because our reminiscences are accompanied by the subjective awareness of remembering (e.g., Tulving, 1983; Suddendorf and Corballis, 1997; Wheeler, 2000; See also Chapters 1.02, 1.04, and 1.21). Tulving argues that, like many animals, his pet cat can acquire and retrieve all kinds of information about events that have happened in the past, but only in a way that is devoid of any awareness of remembering such events. So while his cat may know that she caught a mouse, what she does not recall is the personal experience of having caught that mouse. To be fair, humans also have many instances of knowledge acquisition in which we do not remember the episode in which we acquired that information. For example, although most of us know when and where we were born, we do not remember the birth itself or the episode in which we were told when our birthday is.

According to Tulving, the retrieval of semantic factual knowledge and episodic memories can be differentiated in terms of the remember-know distinction. To *know* that the Psychological Laboratory was opened in Cambridge in 1912 is semantic knowledge, whereas

remembering having attended a comparative cognition lecture at Cambridge University is an episodic memory. Remembering and knowing are thought to be two separate subjective states of awareness, the former being an awareness of reliving past events in the mind's eye (what he later called mental time travel; Tulving, 2000), whereas the latter only involves an awareness of knowledge without any requirement to travel mentally back in time to reexperience the past (Gardiner and Richardson-Klavehn, 2000).

In humans, these episodic memories are often recalled vividly and contain a rich representation of the past event. Furthermore, the memories may appear quite suddenly, and out of the blue. In his autobiographical novel *Remembrance of Things Past*, Marcel Proust (1922) described such a moment of episodic recall:

And suddenly the memory returns. . . . The taste was that of the little crumb of madeleine which . . . my aunt Léonie used to give me, dipping it first in her own cup of real or of lime-flower tea. And once I had recognized the taste of the crumb of madeleine soaked in her decoction of lime-flowers which my aunt used to give me . . . immediately the old grey house upon the street, where her room was, rose up like the scenery of a theatre to attach itself to the little pavilion, opening on to the garden, which had been built out behind it for my parents (the isolated segment which until that moment had been all that I could see); and with the house the town, from morning to night and in all weathers, the Square where I

used to be sent before lunch, the streets along which I used to run errands, the country roads we took when it was fine.

One of the cardinal features of episodic memory is that it operates in what [Tulving \(2002\)](#) calls “subjective time,” namely that remembering the event is always accompanied by an awareness of traveling back to the past time in which the experiences were recorded (see also [Hampton and Schwartz, 2004](#)). Episodic memory differs from all other kinds of memory in being oriented to the past, and specifically in the past of the owner of that memory. So while some factual memories do involve a datable occurrence, they are fundamentally different from episodic memories. Indeed, as William James so aptly wrote:

Memory requires more than the mere dating of a fact in the past. It must be dated in *my* past. ([James, 1890: 650](#))

[Tulving \(2002\)](#) argues that episodic remembering requires a specific form of self-consciousness, *chronesthesia*, that enables an individual to address her own, personally experienced past, which “does not reside in memory traces as such; it emerges as the phenomenally apprehended product of episodic memory system” ([Tulving, 2000: 17](#)), much like the piece of madeleine dipped in linden tea enabled Proust to consciously relive the past as a simultaneous part of his present. Many cognitive neuropsychologists have argued that this ability to travel back in time in the mind’s eye to reexperience the past is unique to humans; animals, by contrast, are stuck in the seemingly eternal present (e.g., [Tulving, 1983](#); [Suddendorf and Corballis, 1997](#); [Roberts, 2002](#)). So according to [Tulving \(1983\)](#), his pet cat does not recall the personal experience of having caught the mouse, nor is she aware that the event is explicitly located in her past.

Language-based reports of episodic recall suggest not only that the retrieved experiences are explicitly located in the past but that they are also accompanied by the conscious experience of one’s recollections (e.g., [Wheeler, 2000](#)), of feeling that one is the author of the memory, what [Tulving \(1985\)](#) called *autonoetic consciousness*. It is this feature of episodic recollection that William James referred to when describing what he called the “warmth and intimacy” of one’s episodic memories ([James, 1890](#)).

This phenomenological definition makes it impossible to assess the claim that episodic memory is unique to humans, because there are no agreed nonlinguistic behavioral markers of these kinds of conscious

experiences in nonhuman animals ([Griffiths et al., 1999](#)), and therefore we have no way of assessing whether Tulving’s cat, or any other animal, does or does not experience an awareness of the passing of time and of reexperiencing one’s own memories while retrieving information about a specific past event. This dilemma can be resolved to some degree, however, by using Tulving’s original definition of episodic memory ([Tulving, 1972](#)), according to which he identified episodic recall as the retrieval of information about where a unique event occurred, what happened during the episode, and when it took place. The advantage of using this definition is that the simultaneous retrieval and integration of information about these three features of a single, unique experience may be demonstrated behaviorally in animals. We refer to this ability as *episodic-like memory* ([Clayton and Dickinson, 1998](#)) rather than episodic memory, because we have no way of knowing whether or not this form of remembering is accompanied by the various phenomenological aspects that accompany conscious recollection in humans.

1.23.2 Animal Studies

Some of the earliest evidence that animals may be capable of episodic-like recall came from studies of rats foraging in a radial arm maze (See Chapter 1.22). In a paper entitled “Remembrance of places passed: Spatial memory in rats,” [Olton and Samuelson \(1976\)](#) argued their laboratory rats could remember which arms had already been chosen and/or which had not in order to forage efficiently by avoiding those arms they had visited previously. Another potential example of episodic-like memory came from studies of visual short-term memory in which rhesus monkeys (*Macaca mulatto*) had to choose, for example, either the previously presented stimulus or the novel stimulus in a delayed matching or nonmatching to sample task ([Mishkin and Delacour, 1975](#)). In both of these studies, the animals may have solved the task by remembering the specific past event – about which arms had been visited in the case of the rats, and which stimuli had been seen in the case of the monkeys. There is a simpler alternative, however, namely that the animals could have based their decision of where to search in the maze or which stimulus to choose in the matching tasks on familiarity rather than recall; for example, they could simply have learned to avoid stimuli that look familiar, arms in the case of a rat in the radial maze and objects in the

case of the monkey performing the matching task (see Griffiths et al., 1999).

There is growing evidence that familiarity and episodic recall are separate cognitive processes, both psychologically (Mandler 1980; Jacoby and Dallas, 1981; Kelley and Jacoby, 2000) and neurobiologically (Aggleton and Brown, 1999, 2006; Wheeler, 2000), and that they have different retrieval dynamics (e.g., Yonelinas, 2001; Yonelinas et al., 2002, 2005, for humans; Fortin et al., 2004, for rats). For example, Yonelinas (2001) has argued that the receiver operating characteristic (ROC) of human recognition memory consists of two components. The first is a *familiarity* component, which is mediated by a standard signal-detection process, whereas the second is an *episodic recollection* component that reflects a high-threshold process in which recollection only occurs once the strength of the episodic memory trace exceeds a threshold. Given this analysis, there is no need to appeal to anything more than the discriminative control exerted by the familiarity of an arm in the radial maze task or of the sample stimulus in a delayed matching task.

Fortin and colleagues used Yonelinas' analysis to determine whether rats were capable of episodic recollection using an odor recognition paradigm (Fortin et al., 2004). Importantly, the rats produced an asymmetrical ROC curve that is characteristic of the conjoint control of recognition by familiarity and episodic recollection. Moreover, their assessment of the two processes through the ROC analysis allowed the authors to dissociate the two processes, by both brain lesions and retention interval (See Chapter 1.21).

Clayton and Dickinson (1998) adopted a different approach to the question of whether or not animals other than humans are capable of episodic recall. Rather than applying a theoretically derived analysis, they considered cases in nature in which an animal might need to rely on episodic recall as opposed to other forms of memory. They suggested that the food-caching behavior of Western scrub-jays (*Aphelocoma californica*) might be one such example, because this species of bird hides both perishable food items (e.g., insect larvae) and nonperishable food items (e.g., nuts) for later consumption (for other potential candidates, see discussion by Clayton et al., 2001a). A suite of studies have shown that Western scrub-jays, like many other food-caching animals, have highly accurate and long-lasting spatial memories for the locations of their caches (Bednekoff et al. (1997) for Western scrub-jays; see review by Shettleworth (1995) for food-caching

animals in general; See also Chapter 1.22). As these jays rely on their caches for survival in the wild, the selection pressure for remembering which caches were hidden where and how long ago might have been particularly strong (Griffiths et al., 1999), particularly since they cache year round (Curry et al., 2002). Furthermore, the birds also cache reliably in the laboratory, providing both ethological validity and experimental control (Clayton, 1999).

Rather than identifying episodic-like memory by its retrieval characteristic, Clayton and colleagues focused on the behavioral criteria for episodic-like memory, namely that the animal must be capable of remembering what happened where and when on the basis of a single past experience and in a way that cannot be explained in terms of relative familiarity. Clayton et al. (2003a) argued, however, that this criterion was insufficient; rather, an animal's *episodic-like* memory must fulfill three criteria: content, structure, and flexibility. In terms of the content of an episodic-like memory, we have argued that it is the 'when' component that is critical, since episodic memory is the only kind of memory to be explicitly located in the past. Furthermore, the what-where-and-when components form an integrated structure, and this feature of episodic memory is important because it permits discrimination between similar episodes that occurred at different times and possibly different places. Finally, the third criterion is one of flexibility, namely that the information can be represented in memory in a form that allows it to be used in a number of different ways, depending on the context. This flexibility arises from the fact that episodic memories are embedded within a larger declarative system that also encodes factual knowledge (e.g., Tulving and Markowitsch, 1998), and consequently the information can be updated and generalized across situations (See Chapters 1.04 and 1.21).

1.23.3 The Critical Components of Episodic-Like Memory

In the following section we discuss each of these three key features of episodic-like memory in turn in order to assess the evidence that some nonhuman animals do have episodic-like memory and, if so, which ones. We shall start our analysis by reviewing what is known about the memories of food-caching jays and then discuss subsequent studies that have been conducted on other animals, primarily rodents and primates.

1.23.3.1 The Content Criterion: The Importance of Pastness

Episodic memory is the only memory to be oriented in time (Tulving, 2000), and more precisely, in subjective time. Semantic and other memories do contain information that was acquired in the past, but without any notion of when they had been acquired, and thus these memories are timeless. As we argued in the introduction, having an awareness of the passage of time ('pastness') is a critical feature of episodic memory, one that distinguishes it from all other forms of memory, so it is therefore essential that any demonstration of episodic-like memory must show that the animal remembers when a particular event occurred in the past as well as what happened where (Clayton, 2004).

1.23.3.1.1 The what-where-and-when memories of food-caching Western scrub-jays

When investigating food-caching by Western scrub-jays as a natural candidate for episodic-like memory in animals, Clayton and Dickinson reasoned that, as these birds do not eat rotten insects, the recovery of perishable items is only valuable as long as they are still fresh. Consequently, a jay should remember not only the location of a cached food item but also the content (perishable or nonperishable food item), in addition to keeping track of the time since caching. Clayton and Dickinson (1998) gave the jays a series of trials in which they cached both their preferred food wax worms (wax moth larvae), and the less-preferred peanuts in two sand-filled ice cube trays, both of which were made visuospatially distinct and trial-unique by structures of children's building blocks (Lego Duplo) attached to the sides of the trays. Consequently, the jays cached in different pairs of trays on different trials so that each caching episode was unique (Figure 1). Although the birds had no cue predicting whether or not the wax worms were perished other than the passage of time, the birds quickly learnt that wax worms were available and fresh when recovered 4 h after caching, but rotten after 124 h, while peanuts were always fresh (Clayton and Dickinson, 1998).

Having received four pairs of training trials, the birds were given a pair of test trials, in which the caches were removed prior to recovery and the trays were filled with fresh sand to ensure that the birds could not use any cues emanating directly from the hidden food. The birds' search patterns at recovery demonstrated that they did remember which caches they had hidden in which particular trays and when, because they



Figure 1 Sweetie Pie, one of the Western scrub-jays in Clayton's colony, is about to cache one of the wax worms in one of the visuospatially unique caching trays. Photo courtesy of Ian Cannell and Dean Alexis, University of Cambridge, UK, with permission.

looked primarily in the places in which they had hidden the wax worms when the food had been cached 4 h ago, but redirected their search to peanut sites when the food had been cached 124 h ago. Note that the recoveries after both short and long retention intervals (RIs) always occur at the same time of day (4 h after caching on the same day as caching or 5 days after caching), and therefore neither circadian rhythms nor the state of hunger at the time of recovery could provide cues to guide the jays' searching behavior (see de Kort et al. (2005) for further discussion).

At issue, however, is whether the birds really remembered the specific past caching episodes or whether they simply knew what had been cached where and when. In order to search in the correct cache sites that were unique to that specific caching event, the jays had to retain information about which caches they had placed where. However, it is possible that rather than remembering how long ago they had cached, the birds relied on familiarity judgments with the caching trays in order to decide whether to search for worms or peanuts. When caching had occurred just 4 h previously, the trays are presumably much more familiar than when caching occurred 124 h ago, and so the jays might have used a conditional rule, "if the trays look familiar search for worms, but if the trays look relatively unfamiliar search for peanuts."

To investigate this issue, Clayton and Dickinson (1999a) then gave the jays a second test trial (i.e., with no food actually present at recovery to test for memory), using an interleaved trial procedure shown in Figure 2. The jays were allowed to cache one food type on one side of a tray, while the other side of the tray was made inaccessible for caching by attaching a transparent strip of Plexiglas to cover all the caches sites on that side of the tray. The birds then got their trays back in the morning of the fifth day, prepared so that the birds

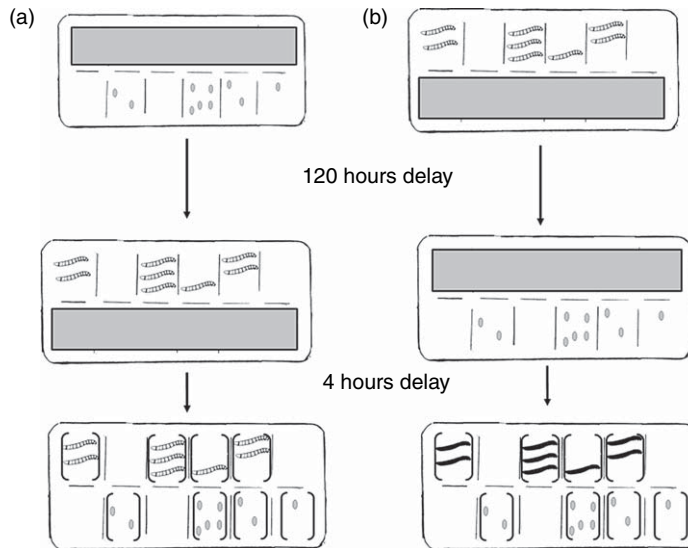


Figure 2 The food caching what-where-when memory paradigm used to test the content criterion of episodic-like memory by Western scrub-jays. Having received a series of training trials in which the birds could cache and recover peanuts and wax worms, the birds received an interleaved trials procedure in which they cached peanuts in one side of a caching tray and then wax worms in the other side of the tray 120 h later (a) or vice versa (b). On test, 4 h later, they then were given the opportunity to search in both sides of the tray. The brackets indicate the fact that the food caches were not present at recovery in order to test for memory. The open symbols represent fresh wax worms, the black symbols illustrate rotten wax worms, and the grey filled circles denote peanuts. The grey bar indicates the side of the tray that was blocked by a Plexiglas strip (the unavailable cache site) during each of the two caching events.

could cache the second food type in the previously inaccessible side of the very same tray, and they were prevented from recovering the previous caches by our attaching the Plexiglas strip to the other side of the caching tray. In the afternoon of this day 5, the jays were allowed to search in both sides of the tray. What is important here is that the interleaved procedure removes the differential relative familiarity of the tray because the temporal pattern of exposures to the tray was the same irrespective of whether or not the worms had been cached first, 124 h ago, or second, just 4 h ago. And since the caches were not present at recovery, the birds would have to rely on their memory of the previous caching episodes in order to search appropriately.

This they did: the jays spontaneously searched for the worms they had cached 4 h earlier, whereas on the trial in which they had cached the worms 5 days ago they ignored searching in the worm sites and instead searched for peanuts. This pattern of recovery searches suggests that the birds were not using tray familiarity as a cue but, rather, that they were remembering specific past caching episodes in terms of where they had hidden the peanuts and worms, and how long ago. Subsequent work established that the jays could also keep track of two perishable foods that decayed at different rates (Clayton et al., 2001b).

Several authors have argued that, as the jays had received a number of training trials in which they could cache and recover the various food items, they may have learned to solve the task by learning semantic factual rules about when to recover the particular foods rather than episodically recalling which foods had been cached where and how long ago (e.g., Zentall et al., 2001; Dere et al., 2005; Hampton et al., 2005). However, such claims misunderstand the theoretical interpretations of the role of semantic and episodic-like memory in the control of caching. Clayton and colleagues have argued that, to search in a particular tray for the perishable caches only when fresh and not when degraded, the birds must integrate a semantic-like rule about how long each food type remains fresh with a specific episodic-like memory of which caches they hid where in a given tray on a specific day (Clayton et al., 2003b).

1.23.3.1.2 Evidence of what-where-and-when memories in other animals

There have been a number of attempts to assess the content criterion of episodic-like memory in other animals (See Chapter 1.22). For example, Hampton and colleagues (Hampton et al., 2005) adopted our scrub-jay paradigm to test what rhesus monkeys

remember about specific foraging events. The test room contained three foraging sites, two baited and one unbaited, and what the monkeys had to learn was that all food was fresh after 1 h, but their preferred food was rotten after 25 h, while the less-preferred food remained fresh. The monkeys rapidly learned to search first for their preferred food, and to avoid the empty foraging location. However, although rhesus monkeys rejected the rotten food much like the jays did, they did not reverse their search patterns after the long delay, but instead they revisited those locations that contained their preferred food irrespective of the length of the delay. Like the jays, the monkeys remembered the what-and-where of trial-unique events; however, unlike the jays, there was no evidence that they encoded temporal information.

Perhaps the foraging paradigm might be less suitable for testing episodic-like memory in rhesus monkeys, given that they do not naturally cache perishable and nonperishable foods, although they do have specialized cheek-pouches that allow them to hoard food and eat it later in safe surroundings. But certainly their survival does not depend on them caching food for later, and their feeding ecology does not require them to keep track of decay rates, as they are primarily herbivorous (Hampton et al., 2005). Given the complexity of their social lives (e.g., Humphrey, 1976; Tomasello and Call,

1997; Whiten and Byrne, 1997), however, tests of episodic-like memory in primates that involve a social component, such as who was present in a particular social setting, may be more salient.

Roberts and colleagues found no evidence that rats could remember when they had cached various food types (Bird et al., 2003; McKenzie et al., 2005). However, most species of rat do not store much food in the wild (Vander Wall, 1990), and like primates, but unlike the jays, they do not rely on their caches for survival (Vander Wall, 1990). When viewed in this light, perhaps it is not so surprising that the rats behaved like the monkeys rather than like the jays, preferentially searching at recovery in those locations in which they had hidden food more often than other locations that had not been associated with food. Yet there was no evidence that they encoded the 'when,' because they did so even when items repeatedly degraded or were pilfered before recovery (Bird et al., 2003; McKenzie et al., 2005).

By contrast, recent work by Babb and Crystal (2005) did provide some evidence that rats could remember the what-where-and-when of specific past events. Instead of hoarding the food items themselves, the rats were trained to remember where they had previously encountered food that they could subsequently recover after either 1 h (the short RI) or after 25 h (the long RI). As shown in Figure 3, using a

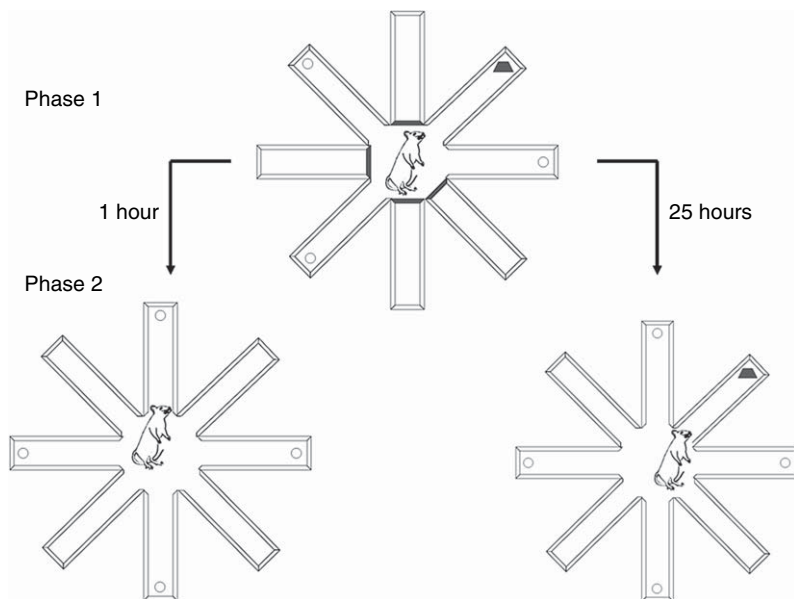


Figure 3 The what-where-when memory paradigm used to test rodents in a radial arm maze. In phase 1 the rats were given the opportunity to explore four of eight arms, three of which contain rat pellets, and one of which contains chocolate. During phase 2, the rats were allowed to explore all eight arms. The delay between phase 1 and phase 2 was either 1 h or 25 h, and rats received training with both the short and the long delay. The black bars show entrances that were inaccessible during phase 1; open circles represent rat pellets, and solid symbols denote chocolate pieces.

standard eight-arm radial maze, the rats were allowed to search during phase 1 for food located at the ends of four arms of the maze (the other four arms were blocked): three of them with regular pellets and one with highly preferred chocolate pellets. During phase 2, the rats were returned to the maze with all eight arms accessible, and the four previously inaccessible arms were baited with regular pellets. In addition the chocolate pellets were replenished if the rats were returned to the maze after a long delay, but not after a short RI. If the rats remembered which arms they had visited and eaten food from in phase 1, then they should selectively search in the previously inaccessible arms, because these are the ones that still contain food. If they also remembered which foods were available where and how long ago they had visited the maze in phase 1 then they should prefer to visit the arm containing the chocolate pellets after the long RI, but avoid that arm after the short RI.

Babb and Crystal found that the rats did learn to avoid the previously baited arms and to revisit the chocolate arm after a long RI only, demonstrating that rats could use the length of the retention interval as a cue to guide their choice of where to search, a finding that has also been replicated by Roberts' group (Naqshbandi et al., 2007). In both studies, however, the issue is whether the rats also remembered the specific contents of the encountered food. Although the rats may have remembered that a particular arm they had visited during phase 1 specifically contained chocolate, it is also possible that they simply encoded that the arm contained something more preferred than rat chow as opposed to encoding the precise type of food. Actually Clayton and Dickinson (1999b) already made a similar argument in the case of the jays' memories for what they had cached where. To establish that the jays did remember the content of their caches, the jays were given the opportunity to cache two equally preferred foods, and then just prior to recovery they were fed one of the two foods until satiated. The jays searched preferentially for the non-preferred food at recovery, even on test trials in which no food items were present during recovery, thereby demonstrating that the jays did remember which particular foods they had cached where.

Babb and Crystal (2006b) addressed this question in an elegant satiation study. In phase 1, rats found three arms baited with regular food, and two of the other arms were each baited with a particular flavored food (grape, raspberry), both of which were equally preferred over regular pellets and both replenished after the long, but not short, RI. The

rats were more likely to revisit the flavored arms and avoid the other previously baited arms after the long delay, just as they had done in the previous study. However, when the rats were satiated on one flavor shortly before phase 2, the rats avoided that arm but revisited the arm containing the other flavored food, suggesting that they remembered not only which arms contained preferred food but that they also recalled the specific food contents of these arms. A transfer experiment using banana chips and chocolate, the latter devaluated by pairing it with a lithium chloride injection after phase 1, produced the same results.

Crystal (2006) argued that these experiments provide evidence of episodic-like memory in rats. Only by remembering what happened where and when could the rats return reliably to the replenishing chocolate arm after the long interval, but avoid this arm when the chocolate was devaluated. However, this experiment does not control for relative familiarity. It is not clear whether the rats really remembered when to visit the chocolate arm or whether the rats could have solved the task by learning a rule that it is only when the arm appears to be relatively unfamiliar that the rats should search for the chocolate, or grape, or raspberry. As the lithium chloride treatment may have caused a general aversion to chocolate, the rats had to return only to the previously blocked arm, and since that arm had not been visited during phase 1, it may have been less familiar to the rat than the arms that had been visited in phase 1.

The results of the satiation study, although more convincing, can still be explained in terms of familiarity. Although rats do not use time of day or state of hunger as cues guiding their behavior (Babb and Crystal, 2006a), the relative familiarity of the maze itself could function as a cue to avoid or to revisit arms with preferred food in just the same way as we argued for the jays and their trays in the first experiment, namely that when the maze cues are highly familiar, then avoid all familiar arms, and when the maze cues are much less familiar, then revisit the arm containing the preferred food. Clearly what is needed to discriminate between these two possibilities is an interleaved trial procedure of the kind described for the jays in Figure 2.

Eichenbaum and colleagues used a different approach when developing their rodent model of episodic-like memory, with a focus on resolving the recollection versus familiarity dispute (See Chapter 1.21 for detailed discussion). Their sequence learning paradigm is based on the assumption that humans

may infer the sequence of events by their relative times of occurrence (Roberts, 2002), because “one event precedes, co-occurs, or succeeds another in time” (Tulving, 1983: 38). For example, Ergorul and Eichenbaum (2004) trained their rats to learn unique sequences of four odors in terms of which odors the rats encountered where and in what order (‘when’). On test, two of the four odors were presented, and the rats were reinforced for choosing the location of the cup containing the odor that had occurred earlier in the sequence. This they did. However, when the rats were given a probe test, in which the cups that had previously contained the odors were placed in the correct locations but the odors had been removed so that they did not provide scent cues, then the rats failed to make the correct choice. Consequently, the rats may have solved this task by remembering which odors they had encountered earliest in the sequence without any recourse to remembering where.

A similar rationale was adopted by Schwartz and Evans (2001), who tested the 31-year-old gorilla, King, for his ability to remember a temporal sequence of specific past feeding events. Specifically, they argued that “the animal’s response should provide information about its past rather than about the current state of knowledge” (Schwartz et al., 2005: 231). King received three types of food in succession, each 5 min after finishing eating the former one. On test, a few minutes later, the experimenter asked King what he had eaten and in what order. Although King was able to answer correctly, he itemized the food in reversed order only, from the most familiar to the least familiar item. Consequently, his performance could be explained in terms of relative familiarity rather than episodic-like recall.

To summarize this section, attempts to establish models of episodic-like memory in nonhuman animals other than Western scrub-jays suggest that the ‘when’ component is by far the most challenging feature. In some studies, the animals failed to show any sensitivity to the temporal relationships between events (Bird et al., 2003; Hampton et al., 2005). Of course, the absence of evidence is not evidence of absence, and the fact that rats do appear to remember what happened where and how long ago when tested for the memory of food they have seen previously (Babb and Crystal, 2005, 2006b; Naqushbandi et al., 2007), but have not cached previously (Bird et al., 2003), suggests that the ecological salience of the task may be critical. One advantage of the caching paradigm when employed with Western scrub-jays is that it taps into this particular species’ natural propensity – if not

obsession – to cache and efficiently recover perishable as well as nonperishable food. That said, an outstanding issue in the rodent memory models is whether the animals may have solved these tasks using relative familiarity or rule learning after intensive training instead of episodic recall (Schwartz and Evans, 2001; Babb and Crystal, 2005, 2006a), and the extent to which an animal’s ability to remember and discriminate between sequences (e.g., Schwartz and Evans, 2001; Agster et al., 2002; Ergorul and Eichenbaum, 2004; *see also* Chapter 1.21) depends on episodic-like recall.

1.23.3.1.3 Challenging the “when” component

Other researchers have questioned whether the encoding of the ‘when’ component is central to the concept of episodic-like memory, or whether in fact it is the context in which the event occurred that is critical. Although human memories are usually rich and detailed in some aspects, the quality of the temporal information may be rather poor (e.g., Friedman, 1993, 2001; Simpson et al., 1998; Eacott and Norman, 2004). This does not remove our own sense of the pastness of a memory, however, just as Proust was fully aware of the concurrence of his present and the mentally relived past. Furthermore, most humans have seemingly little difficulty in discriminating between memories that have the same ‘what’ and ‘where’ contents but different ‘when’ components. For example, most of us find it easy to differentiate between memories of two different meals with the same friend. In this case the ‘when’ component may simply be a temporal form of the occasion setting ‘which,’ and we distinguish between our memories of the two events by binding each episode to the different contexts provided by the two restaurants. Eacott and Norman (2004) therefore suggested that the behavioral criteria for episodic-like memory should not be restricted to what-where-and-when but should also include what-where-and-which, with the ‘which’ component functioning as the occasion-specific context (see also Kart-Teke et al., 2006).

The what-where-and-which concept of episodic memory has been exploited by capitalizing on the rodent’s propensity to seek out novelty (e.g., Eacott and Norman, 2004; Dere et al., 2005; Norman and Eacott, 2005; Kart-Teke et al., 2006). The most convincing example is that conducted by Eacott and her colleagues (2005), because they were able to control for relative familiarity. To do so, they built a maze in the shape of an E so that they could place two different novel objects at the two outside ends of

the E-maze, out of sight of the rats at their starting point, as shown in **Figure 4**. The rats were given the opportunity to explore the two different objects in one specific context before being allowed to investigate them again in a different configuration in a second context that was texturally different from the first (plain grey and smooth to the touch versus wire mesh). Following this episode, the rats were exposed to one of the objects outside the two contexts until they had become habituated to it, an experience that enhanced their propensity to explore the other object when returned to one of the two E-maze contexts. A rat could only do so, however, if it had remembered where the objects were located in the E-maze in a particular context during the initial episode. Their rats' success at this task led Eacott and colleagues to argue that the rats recollected the object (what) and its location (where) in a particular context (which) on the basis of unique what-where-and-which memories. Note that, because the objects were out of sight at the starting point, the rat's choice to turn right or left could not have been based on relative familiarity of the object.

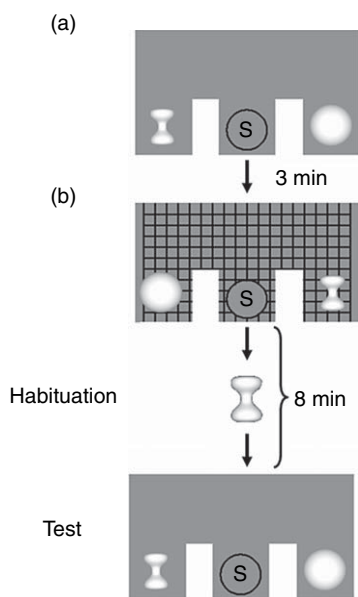


Figure 4 The what-where-which paradigm used to test rodents in the E-maze. The rats explored two different objects placed in a certain spatial configuration in a particular context (a), before investigating them again in a different configuration in a second context (b). Following this episode, the rats were exposed to one of the objects in a different place until they were habituated. On test they were placed back in either context (a) or (b), but the objects were not visible from the starting point (S) in order to test for memory.

1.23.3.1.4 Differential forgetting or remembrance of times past?

Although we have argued strongly for the importance of the 'when' component of an episodic-like memory, several researchers have suggested that demonstrations of an animal's ability to remember the what-where-and-when of a specific past event may not be sufficient to claim that the animal is capable of episodic recall. In the case of our jays, it is argued that, instead of traveling back in time, the birds might have used the strengths or ages of memory traces in order to know when to search for the food items at particular locations.

There are two ways in which a jay could use the strength or vividness of the memory trace to date its memory of a particular caching event: spontaneous forgetting and directed forgetting (for detailed discussion see [de Kort et al., 2005](#)). Consider the case of the jays that learned that if there was a short delay between caching and recovery then their worms would still be fresh at the time of recovery, whereas if a long interval had elapsed between caching and recovery then the worms would have degraded. In terms of spontaneous forgetting, the bird might simply forget the location of degraded worms because the event happened a relatively long time ago. Alternatively, rather than having an all-or-none response (remember–forget), the bird might use forgetting, just like familiarity, as a conditional cue to control its pattern of searches at recovery. The birds learn to search for the worms when they recall a vivid memory of the caching episode, whereas they learn to avoid attempting to recover the worms when they recall a less vivid or partially forgotten memory. [Staddon and Higa \(1999\)](#) have recently proposed an account of interval timing based upon conditional control by the strength of the memory for a time marker.

If the jays use vividness to date the caching episode, we should expect the birds to show some evidence of forgetting for other aspects of the content of the memory, specifically the location and types of caches, at longer delays. Even if the worms did not degrade with time since caching, the time-dependent forgetting of the memory representation should be accompanied by a loss in accuracy for locating the different caches of food. To assess this possibility, [Clayton and colleagues \(Clayton and Dickinson, 1998, 1999a; Clayton et al., 2001b\)](#) tested the cache recovery behavior of a second group of jays, whose potentially perishable caches did not in fact degrade. These birds showed no loss in accuracy of locating the food caches at the retention

intervals for which the putative forgetting should have been controlling the recovery choice of the birds whose caches did degrade. Furthermore, the jays were just as accurate at locating caches after 5 days as they were after 4 h (Clayton and Dickinson, 1999b), even though we should have to assume that the strength of the cache memory after 5 days was significantly weaker than after 4 h if this strength difference is to control a complete reversal in recovery patterns. Consequently we think that it is unlikely that the jays' temporal control of caching was mediated by memory decay.

Although spontaneous forgetting is unlikely to account for the behavior of the jays, perhaps directed forgetting (Roper and Zentall, 1993) may be more plausible. Consider, once again, the case in which jays cache and recover worms and peanuts after a short and a long delay. As the peanuts never perish, the jays always recover fresh peanuts. However, this is not the case for their worm caches, which are found to be degraded at recovery on half of the trials (i.e., those in which recovery occurs after a long delay). According to the directed forgetting account, experience with unpalatable worms on half of the recovery trials causes the jays to forget the location of these caches more rapidly. For example, perhaps having experienced degraded, unpalatable worms at recovery, the jays subsequently devote less processing of the location of these caches on subsequent caching episodes, which in turn leads to more rapid forgetting of those caches.

A test of this hypothesis would be to establish whether the jays could learn the opposite profile for when worms are edible, namely one in which worms ripen rather than degrade over time (de Kort et al., 2005). To do so the jays received a series of trials in which they could cache peanuts and worms as before, but this time the worms were degraded after the short delay but were fresh after the long delay. de Kort and colleagues found that the jays rapidly learned to avoid searching for worms after the short retention interval, while preferentially searching for them after the long one. The fact that jays' performance could not be explained by either spontaneous or directed forgetting strongly suggests that jays encode time specifically within their episodic-like memory of events (de Kort et al., 2005).

As explained in the first section, we can never ascertain whether or not an animal is aware of the past while retrieving a memory. All we know is that animals can discriminate among events which occurred at different times in the past. One way to tackle this issue would be to devise an experiment in

which the animal is given the opportunity to report that it knows whether or not it has remembered using an uncertainty monitoring paradigm (Smith, 2005), just as Hampton (2001) did when testing whether his rhesus monkeys knew what they had and had not remembered.

1.23.3.2 The Structural Criterion of Episodic-Like Memories: An Integrated Representation

In humans, the content of an episodic memory is usually a rich representation of what happened, where, and when. Imagine the moment when handing over a carefully chosen present to a special person. We not only remember where and when we bought this present, and of course what we have chosen, but we may spontaneously remember a number of other details about the event, such as whether it was a rainy or a sunny day, and whether the shop was overcrowded or completely empty, and some of us might remember other seemingly trivial details such as what shoes we were wearing.

One of the cardinal features of human episodic memory is that, when we come to recall the event to mind, we retrieve all these components together as a gestalt image. This reflects the structure of episodic memory, namely that the 'what,' 'where,' and 'when' components are not encoded separately but are bound together in an integrated representation, and consequently the retrieval of one component elicits the retrieval of the others. Contrast this integrated representation with a linear one in which the components are not directly linked. If we were to remember the episode as a series of separate components, then we would not be able to distinguish between episodes that have similar contents and locations but different temporal contexts, such as family Christmas dinners that occurred in different years. It is this feature that led Clayton et al. (2003a) to argue that the criterion of remembering what-where-and-when is not, by itself, sufficient to characterize a memory as episodic-like if, by this term, we mean that the memory has the behavioral properties of human episodic memory.

To illustrate this point, let us consider another food-caching scrub-jay scenario in which the birds cache the same foods in two trays at different times. The design is illustrated in Figure 5. Briefly, the trained jays were allowed to cache peanuts and worms in one tray on one day, and then at a later time they cache the same food types in a second tray, after which the jays are allowed to recover from both

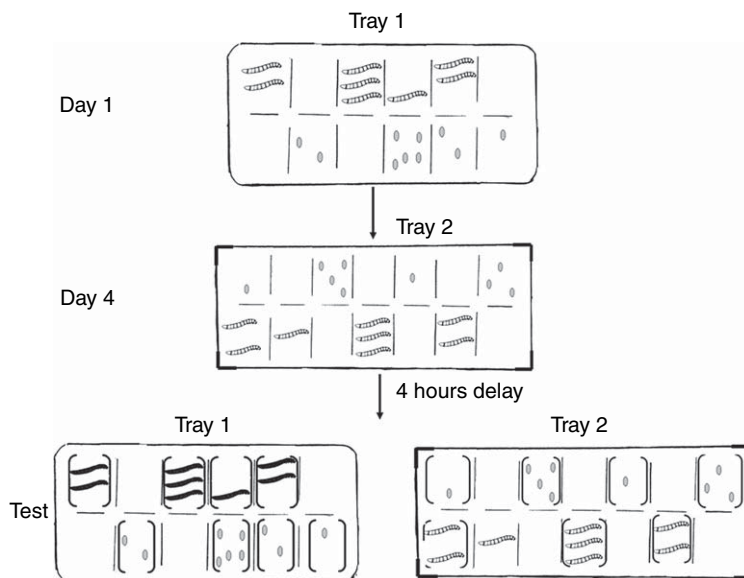


Figure 5 The food caching what-where-when memory paradigm used to test the structure criterion of episodic-like memory by Western scrub-jays. The jays cached peanuts and wax worms in one caching tray on day 1, and then again in a second tray on day 4. On test, 4 h later, the jays were given the opportunity to search in both trays. The brackets indicate the fact that the food caches were not present at recovery in order to test for memory. The open worms represent fresh wax worm caches, the black worm symbols denote rotten wax worm caches, and the grey filled circles illustrate peanut caches.

trays. The retention intervals are such that the worms will be decayed in the first tray while still being fresh in the second tray, and the critical question is whether the jays show the appropriate search pattern for each of the two trays.

If the birds retrieved the ‘when’ component separately, they could not have distinguished between the caching episodes because, by that account, the jays would simply associate caching the worms with a temporal tag, and the memory of caching worms at recovery would retrieve temporal tags for both the long and short RIs. In short, a linear mnemonic structure does not support the appropriate recovery pattern, namely searching for peanuts in the first tray and worms in the second tray. However, the jays do in fact search appropriately (Clayton et al., 2001b), a result that suggests that they do form integrated memories, because they can distinguish in memory between the two caching episodes in terms of their time and location, even though they involved the same food items.

Clayton and colleagues interpreted this finding as evidence that the jays’ behavior met what they called the *structural* criterion for episodic-like memory (Clayton et al., 2003a,b). Not only must a memory have the what-where-when representational *content* to be episodic-like, but that content must be bound in a

form that yields a unique memory for each caching episode. It is this representational binding that allows the jays, like humans, to discriminate between similar episodes that occurred at different times and possibly different places.

What of other animals? So far, the only other study to test the structural criterion of episodic-like memory is that by Shettleworth and colleagues (Skov-Rackett et al., 2006). In a series of delayed matching to sample tasks on a touch screen, they tested their pigeons’ memory of all three features independently: on some trials they had to select the correct ‘what’ in terms of an object’s identity, on other trials they had to select the correct ‘where’ in terms of an item’s location on the screen, and on yet other trials they were tested for their memory of ‘when’ in terms of the time intervals passed since presentation of items. The pigeons performed well above chance on all three types of trials, which suggests that the pigeons could encode all three features during a single presentation. However, further tests established that the pigeons’ memories were stored independently in a linear rather than in an integrated structure. It remains to be seen whether the rodent what-where-when and even what-where-which memories possess an integrated structure like those of jays and humans, or whether they are linear, like those of pigeons.

Further evidence for the integrated structure of scrub-jay episodic-like memories comes from studies of the social context of caching (reviewed by Clayton et al., 2007). These birds readily steal one another's caches (e.g., Clayton and Emery, 2004) and go to great lengths to protect their own caches from being stolen by another bird, hiding them behind barriers (e.g., Dally et al., 2005) and moving those caches another individual has seen them make once that other individual has left the scene (Emery and Clayton, 2001). Of particular relevance to the issue of integrated memories is the finding that these jays recognize particular individuals and remember which particular individual was watching them cache during specific past caching episodes and take protective action accordingly (Dally et al., 2006). It is this integrated structure of their episodic-like memories that allows them to discriminate between caching episodes that differed only in terms of who was watching when.

The only other published study that tested an animal's episodic-like memory with a 'who' component was conducted on the gorilla King (Schwartz et al., 2002), who was trained to associate five food types and their respective English words with five wooden cards carrying a picture of each food in question. In addition, he was trained to associate each of two human trainers who were present during the trials with a card carrying the name of that person. To test King's episodic-like social memory, the "to-be-remembered trainer" handed the gorilla one piece of food through the bars of the cage, while the second trainer was present but did not do anything. On test, either about 10 min later or on the next day, King received five cards for the various food types plus the two cards for the two trainers. In response to the questions "What did you eat?" and "Who gave you the food?" King was expected to hand over the card that corresponded to the food he had eaten and the card with the name of the trainer who had given him the food, which he did for the most part accurately (see also Schwartz et al., 2004). However, the issue remains as to whether King episodically recalled the specific past event or whether King's performance could have been based on relative familiarity, given that he simply needed to select the cards that matched the stimuli he had encountered most recently (for detailed discussion see Schwartz, 2005; Schwartz et al., 2005).

To summarize this section, we have argued in order to demonstrate episodic-like memory in an animal requires not only evidence that the animal

remember the what-where-and-when of a specific past event, and in a way that cannot be explained by relative familiarity, but that the structure of this memory requires an integrated representation. To our knowledge, so far only the jay studies provide evidence for all features. Even less well studied than the structural criterion is the third key feature of episodic-like memory – its flexibility.

1.23.3.3 The Flexibility Criterion

As we argued at the end of the section titled 'Animal studies,' there is a third defining feature of episodic-like memory, namely that it should be capable of flexible deployment (Clayton et al., 2003a). This term refers to the fact that the use of the information encoded in a memory can vary depending on the context. Because episodic memories are embedded within a larger declarative memory system that also encodes factual knowledge (e.g., Tulving and Markowitsch, 1998), the information can not only be generalized across situations but also updated when new information is acquired after the encoding of the original memory.

Evidence for the updating of episodic-like memories comes from a study by Clayton and Dickinson (1999b) in which the jays cached two types of food, peanuts and dog kibble, in both of two trays. They then allowed the jays to recover the peanuts from tray A and the dog kibble from tray B. If the birds could update their original cache memories in light of these recoveries, they should have represented tray A as containing only kibble and tray B only peanuts following the recovery episodes. To test whether this was so, one of the foods was then devalued by allowing the jays to consume it to satiety before they once again searched for their caches. Evidence for mnemonic updating came from the observation that the jays searched the kibble sites when preferred peanuts and peanut sites when preferred kibble, thereby demonstrating that they integrated the memories of the caching and recovery episodes in a way that enabled them to know the identity of the food items remaining in the trays.

This study also illustrated a second form of flexibility. The fact that the jays searched preferentially for the nondevalued food types shows that the deployment of cache memories is sensitive to changes in the incentive values of the caches. There is now good evidence that rats are also capable of this form of mnemonic flexibility. Eacott and colleagues have argued that their rats do show flexibility

because the demonstration of the what-where-and-which depended upon devaluing one of the objects as a target of exploration by habituation. A similar claim was made by [Babb and Crystal \(2006a\)](#) on the basis of the fact that, when their rats acquired taste aversion to chocolate after the memorization phase, they subsequently avoided the chocolate arm.

A final form of flexibility illustrates the fact that episodic memory is embedded with a general declarative system and that episodic information interacts with semantic knowledge in the control of behavior. Again this point can be illustrated with the scrub-jay food-caching paradigm. Across a series of training trials, the jays learned that different types of perishable food decayed at different rates – mealworms were rotten just 1 day later, whereas crickets, like wax worms, took longer to degrade ([Clayton et al., 2001b](#)). Clayton and colleagues argued that, in order to adopt the appropriate recovery strategy of recovering perishable caches while they are still fresh but avoiding them once they have perished, the jays would need to acquire a semantic-like knowledge about the rates at which various cached foods decay and to combine this with an episodic-like memory for each particular caching event ([Clayton et al., 2001b, 2003b](#)). The basic idea is that degrade rates of the different foods are extracted across a number of caching-and-recovery bouts and stored in a semantic-like representation, but that this information needs to be coupled with a particular episodic-like memory of the caching event if the jay is to know what to search for and where. The flexibility of this declarative memory system arises from the fact that the same episodic-like memory can support different recovery strategies depending upon the jay's semantic-like knowledge of when the caches degrade.

A strong test of this declarative flexibility asks whether the deployment of a cache memory is sensitive to new information about perishability, even though this information is not available until after the caching has occurred. [Clayton et al. \(2003b\)](#) assessed this form of flexibility. To do so, the jays first received a series of training trials in which they learned that crickets remain fresh for 1 day but have degraded after 4 days. On the basis of a temporal generalization test, it was then established that the birds behaved as though they expected the crickets to remain fresh for up to 3 days after caching, even though they had not been trained with these retention intervals and had no direct information upon which to base these expectations, merely an interpolation from the differential training at the

1- and 4-day intervals. At issue was whether the birds would change their strategy of where to search at recovery if they obtained subsequent information after they had already cached the food that their expectation about the durability of the cricket caches was, in fact, false.

In order to provide this information, the jays were given the opportunity to cache crickets in three different trays on three successive days. The critical design of this test is illustrated in [Figure 6](#). On the fourth and fifth days the jays recovered the crickets from each of the first two trays, one per day, so that the jays had experienced a 3-day retention interval between each caching and recovery episode. During these two recovery episodes, the jays discovered to their surprise that the crickets were degraded. Note that this information was acquired a long time after the birds had formed the episodic-like memory of caching crickets in a particular tray on a given day.

At issue was whether the birds in this group would integrate this new, semantic-like information with the episodic-like memory of caching in the third tray on day 3. On the sixth day the birds received the final tray back, but no caches were present in order to test for memory. All the birds avoided searching in the cricket sites on test, a result which demonstrates that such integration occurred and attests to the declarative nature of the jay's memory for caching in particular trays. By contrast, a control group whose caches perished at the expected rate showed the same recovery pattern as before, preferentially searching for crickets.

1.23.3.4 Incidental and Automatic Encoding

So far we have argued that there are three key features of the behavioral components of episodic memory. The first – in terms of content – is that the subject recalls a specific event that happened in the past and in a way that cannot be explained in terms of discrimination by relative familiarity. Second, the representation of that past event should contain multiple features (e.g., where, what, who) in addition to 'when,' which are bound in an integrated structure. The third pertains to the flexible deployment of information acquired after encoding of the original memory, which allows memories to be embedded within a broader declarative memory structure and allows the subject to keep track and update information accordingly. However, several

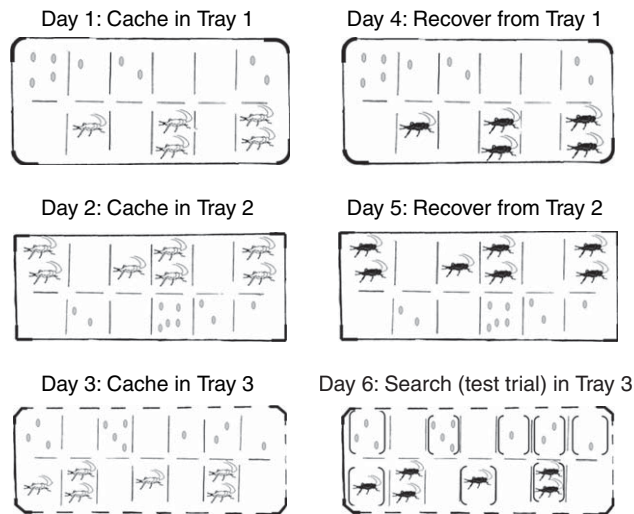


Figure 6 The food caching what-where-when memory paradigm used to test the flexibility criterion of episodic-like memory by Western scrub-jays. The jays cached peanuts and crickets in one caching tray on day 1, and then again in a second tray on day 2, and in a third tray on day 3. The birds were given the opportunity to recover the caches they had hidden in tray 1 on day 4, and in tray 2 on day 5. On test, on day 6, the jays were allowed to search in tray 3. The brackets indicate the fact that the food caches were not present at recovery on day 6 in order to test for memory. The open symbols represent fresh cricket caches, the black symbols represent rotten cricket caches, and the grey filled circles represent peanut caches.

other facts of human episodic memory remain to be explored.

When addressing the issue of an integrated representation, for example, we noted the richness of many episodic representations, of how we typically encode many seemingly incidental features of an event, without any deliberate intent to do so. So what is the origin that causes the flood of memories during episodic recall? In their “automatic recording of attended experience” hypothesis, which they invoked to explain the function of synaptic plasticity in the hippocampus, [Morris and Frey \(1997\)](#) emphasized this feature of episodic memory.

Zentall and colleagues ([Zentall et al., 2001](#)) have made a similar point by noting that, when animals receive a number of training trials, they may come to expect a test of their memory even though the event may be novel. For example, in the case of the jays, the birds may come to expect that their caches will be available for recovery, and that the expectation of this recovery test may lead to a semantic memory rather episodically encoding the unique features of that particular caching event. He argues that it is only when asked an unexpected question that one has to travel mentally back in time to reexperience the event in question and find the correct answer. We remain to be convinced, however, that incidental encoding is a defining feature of episodic memory. While many

features of an event may indeed be encoded automatically, it does not follow that a prior request to remember specific aspects of an event preclude it from being encoded as an episodic memory. Consider a special event, a wedding, for example. Knowing that one may be asked to describe the event to others later does not prevent one from reexperiencing that episode each time one is asked to do so.

Perhaps some of the most convincing work on spontaneous episodic recall comes from [C. Menzel's \(1999, 2005\)](#) studies of Panzee, an 11-year-old female chimpanzee, who was trained to use a lexigram as well as gestures in her daily encounters with her human caretakers ([Figure 7](#)). Panzee could regularly watch from indoors how a human caretaker in the outdoor area kept a particular object in his hand and then hid it under a natural cover before leaving the outdoor area. Later, Panzee would spontaneously initiate contact with the caretaker, showing that person the lexigram of the hidden food type, and subsequently guiding the trainer outdoors, giving the gesture for ‘hide,’ and eventually pointing in the direction where she had observed the object being hidden. Of course Panzee’s own initiative in catching the caretaker’s attention and communicating is not without nonepisodic explanations (for discussion, see [Menzel, 2005](#)), but it may provide a promising avenue for future studies on this issue.

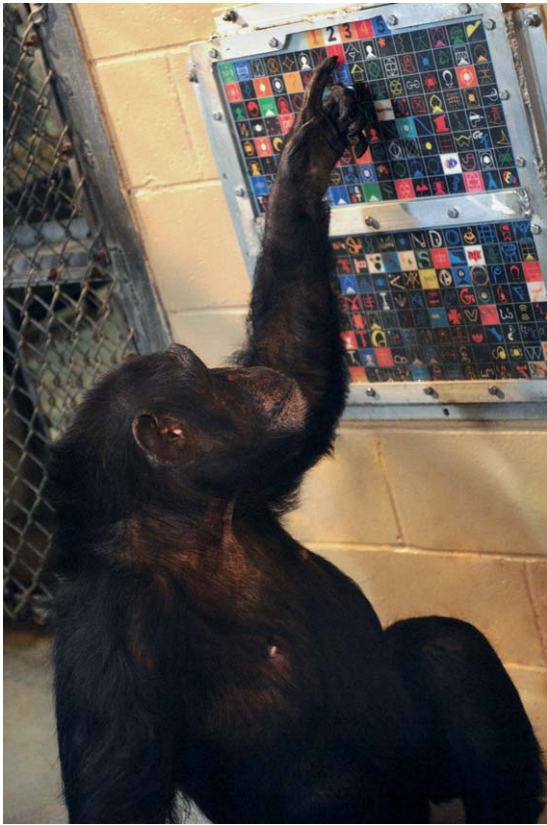


Figure 7 Panzee, the chimpanzee, using the lexigram to communicate with her human caretakers. Photo courtesy of Charles Menzel and Carolyn Richardson, Georgia State University, USA.

1.23.4 The Distribution and Evolution of Episodic Memory

Many people share Nietzsche's view that animals are stuck in the present and thus cannot episodically recall specific events that happened in their past because they have no sense of possessing a personalized past:

they do not know what is meant by yesterday or today, they leap about, eat, rest, digest, leap about again, and so from morn till night and from day to day, fettered to the moment and its pleasure or displeasure, and thus neither melancholy nor bored. (Nietzsche, 1983: 60)

Such an ability to acquire and retrieve information about the world in a seemingly depersonalized timeless zone may have its advantages, for as Nietzsche pointed out:

This is a hard sight for man to see; for, though he thinks himself better than the animals because he is

human, he cannot help envying them in their happiness – what they have, a life neither bored nor painful, is precisely what he wants. (Nietzsche, 1983: 60)

The problem with such an account is that it is essentially untestable. As we pointed out at the start of the introduction, we can probably never know whether any nonhuman animal is capable of episodic recall, at least in the form that we humans experience, with the associated conscious experiences of chronesthesia and auto-noesis.

By turning our focus to the behavioral criteria for episodic memory, we can at least assess which animals possess these elements of episodic memory that, in the absence of any assessment of phenomenological criteria, we call episodic-like memory. This perspective may in turn provide clues as to how and why episodic memory evolved. After all, it seems unlikely that episodic memory evolved in humans *de novo*, without any precursors in the rest of the animal kingdom.

What does an understanding of the distribution of episodic-like memory among animals tell us about the evolution of episodic memory? If we accept that episodic-like memory is present in at least one species of corvid (i.e., the Western scrub-jay) and at least one species of ape (i.e., humans), then it follows that this ability might have arisen through convergent evolution (similarities that arise as a result of adaptation to similar selection pressures in distantly related species) rather than through a shared common ancestor (homology). However, if we were to show that all birds and mammals possess episodic-like memory, then the parsimonious explanation would be that they share a common ancestor who also possessed the same traits. The answer to this question will only be known when studies have been conducted on a wider sample of species.

So far the attempts to establish models of episodic-like memory in nonhuman animals are still in their relative infancy, and perhaps this is not too surprising given that the initial paper on episodic-like memory in jays was published about 10 years ago (Clayton and Dickinson, 1998). Our review of the available evidence to date suggests that a strong case can be made for the scrub-jays, and a promising case for the chimpanzees, yet there is no evidence that rhesus monkeys remember when as well as what and where, and for rats the results are mixed. Rats do appear to remember what happened where and how long ago when tested for the memory of food they have seen previously (Babb and Crystal, 2005, 2006b;

Naqshbandi et al., 2006), but not that they have cached previously (Bird et al., 2003), suggesting that ecological salience may be critical in designing and developing the appropriate tasks.

As we noted earlier in this chapter, an outstanding issue in the rodent memory models is whether the animals may have solved these tasks using relative familiarity or rule learning after intensive training instead of episodic recall (Schwartz and Evans, 2001; Babb and Crystal, 2005, 2006a), and the extent to which an animals' ability to remember and discriminate between sequences (e.g., Schwartz and Evans, 2001; Agster et al., 2002; Ergorul and Eichenbaum, 2004; See also Chapter 1.21) depends on episodic-like recall. Furthermore, with the exception of the scrub-jay studies, most of the experiments have focused on the content criterion for episodic-like memory, rather than on its structure or flexibility of deployment. So clearly there is much more work to be done. A key question for future research will be to make sense of these apparently conflicting results, perhaps by using similar paradigms with different species. But this pattern of mixed results provides a cautionary note that even species that can remember the what, where, and when of a specific past experience may not necessarily express this ability under all conditions (Clayton, 2007).

The other point worthy of mention, and one we alluded to earlier, is that of ecological salience. Perhaps it is no coincidence that the evidence for episodic-like memory in the jays comes from studies of their natural propensity to cache and form rich representations of previous caching events in order to recover their food efficiently in the future. There are a number of features of the food-caching behavior of scrub-jays that might be rather special. The first is that there is no need to train the animals to perform a caching and recovery task, as these are behaviors that the animals do for a living. Moreover, Western scrub-jays are highly motivated to do so and will go to great lengths to protect their caches from being stolen by conspecifics (see review by Clayton et al., 2007), and so presumably there was intense selection pressure on mnemonic processing by jays. McKenzie et al. came to a similar conclusion when arguing that the observed differences in chronesthesia between rats and scrub-jays

favor greater fitness for birds through sooner and greater acquisition of food. . . . Food hoarding and retrieval behaviors inherited by rats from rodent ancestors may not have been fine-tuned by the same demands placed on food-storing birds. (McKenzie et al., 2005: 24)

Perhaps it is not surprising that the scrub-jays show such rapid learning about the fate of their caches over just two or three trials.

Indeed, the jays cache perishable foods in an environment where the rate at which foods decay changes across the year, and from day to day, depending on the weather conditions between caching and recovery, so fast that flexible learning may be essential to their survival. For jays that live in the Central Valley (California, USA), the ambient temperatures rarely fall below 10 °C but may rise to over 40 °C between July and September. At such temperatures, caches that consist of various invertebrates, for example, will degrade rapidly in the heat and more slowly in cold. So the problem for a scrub-jay is not only to learn how quickly a particular food type degrades but also to be capable of updating information in a flexible manner, based on the ecological conditions that occur in the interim between caching the item and recovering it (de Kort et al., 2005).

Not all animals cache food, but there are a number of others that forage for food that degrades, ripens, or replenishes, providing another potential candidate for studying episodic memory that could be investigated experimentally (for suggestions of other candidates, see Clayton et al., 2001a; Griffiths and Clayton, 2001; Clayton and Griffiths, 2002). Nectar-feeding hummingbirds and bats, for example, could increase their food intake by taking into account a given flower's secretion rate to guide an individual's revisiting schedule. Henderson et al. (2006) tested whether free-living, territorial Rufous hummingbirds (*Selasphorus rufus*) could keep track of when the flowers refilled with nectar. The animals quickly learned the different refilling rates of the two types of flowers and roughly adjusted their revisiting schedules accordingly. Furthermore, the birds appeared to remember which particular flower they had emptied recently (Jones and Healy, 2006). Similarly, Gonzalez-Gomez and Vasquez (2006) found that green-backed firecrown hummingbirds (*Sephanoides sephanioides*) remembered not only the location of a particular flower but also the locations of the most rewarding nectar sources among less-rewarding flowers. The flower bats (Phyllostomidae, Glossophaginae), for example, *Glossophaga soricina*, may also be a promising candidate for testing episodic-like memory, especially given that these bats can hold more than 40 feeder visits in working memory without indication of memory decay (Winter and Stich, 2005), and would allow a second test of convergence of episodic-like memory in birds and mammals.

If convergent evolution is the most likely process, then what are the common selective pressures shared between the ape and corvid species (see Emery and Clayton, 2004), or between the hummingbirds and bats? One direction for future research will be to characterize what advantages the possession of episodic memory might have, and this is where comparisons of different behavioral systems may be particularly informative. It is important to note at this point that similarity arising as a result of convergence need not lead to identical solutions (e.g., Salwiczek and Wickler, 2004), and therefore episodic-like memory in different groups may have similar functional properties without necessarily having similar neurobiological structures (de Kort and Clayton, 2006). A second direction for future research will be to ask questions about the brain systems necessary to support the various kinds of memory and the extent to which convergently evolved brain systems are similar in their details. For example, although there is good evidence that the hippocampus plays an important role in spatial memory processing in both birds and mammals, the two types of hippocampi differ in structure, with the avian one being nuclear and the mammalian one being laminar (see Emery and Clayton, 2005).

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