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Animals may not be stuck in time ☆

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Abstract

Humans have the ability to mentally travel forward and back in time. They can retrieve vivid memories of past events (episodic memories) and can imagine the future (planning). Although it has been suggested that this is a uniquely human ability, the evidence for subjective time travel in humans is typically based on verbal report and elaboration. Such evidence cannot be obtained from animals. However, we may have indirect evidence for episodic memory and planning. For example, we can show that animals can ‘report’ about their recent past experience when they are unexpectedly asked to do so—performance that is analogous to episodic memory. We can also show that animals use the anticipation of a future event as the basis for a present action—analogueous to planning. Thus, we have suggestive evidence that animals may not be stuck in time.

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Humans have the ability to retrieve vivid images of past events. They also have the ability to imagine future events. Thus, it can be said that they have the ability to mentally or subjectively travel in time. When humans travel backward in subjective time, it is often referred to as episodic memory because it involves the memory of past episodes. When humans subjectively travel forward in time, it is often referred to as prospective memory or planning because it involves the anticipation of future events.

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Is subjective time travel a uniquely human ability? According to [Gopnik and Graf \(1988\)](#), children younger than 4 years are not able to remember or understand the sources of factual beliefs that they hold. This finding suggests that humans may not be born with the ability to retrieve episodic memories. Furthermore, the ability to travel in subjective time appears to be absent in humans with certain kinds of brain damage ([Tulving, 1989](#)). Such an individual would not consciously remember an event from the day before but, importantly, he or she may be able to make use of those past experiences. That is, such an individual might be able to learn, for example, to play chess but would not remember ever having played chess before.

Episodic memory differs from other kinds of memory in several ways ([Tulving & Markowitsch, 1998](#)). First, it is concerned with remembering experiences rather than facts or rules (which are the content of semantic memory). Second, unlike other kinds of memory, it is oriented toward the past rather than the present (as are semantic and procedural memory). Third, it involves “autonoetic” conscious awareness (remembering) rather than “noetic” awareness (knowing, [Tulving, 1985](#)). Finally, inherent in the idea of autonoetic memory is a concept of self in the past that is dissociated from the present self, a form of meta-representation or perspective taking ([Suddendorf & Corballis, 1997](#)).

Episodic memory also appears to depend on the frontal lobes of the brain in a way that semantic memory does not. Thus, perhaps because of this specificity, it also appears to be more vulnerable to impairment, if those areas of the brain are damaged.

For all of these reasons, it has been proposed that episodic memory may be a uniquely human ability that it is more recently evolved than semantic memory ([Tulving & Markowitsch, 1998](#)). In fact, it may be that that episodic memory developed relatively recently in human cultures. In humans, the ability to imagine a past or future event requires consciousness or the ability to distinguish between internal and external states, and it has been argued that classical Greek writings showed no evidence that Greeks of that time were aware of internal states that were not reflected in external behavior (see, e.g., [Jaynes, 1978](#)). Of course, this lack of evidence also may reflect the style of writing of the classical Greeks rather than their inability to identify internal states.

Given the above discussion, if it is possible that humans can function reasonably well without the consciousness needed for subjective time travel, it is reasonable to ask, as [Roberts \(2002\)](#) has, “Are animals stuck in time?” Although animals can certainly learn from past experience and can anticipate future events, they may not have the ability to retrieve past episodes or make future plans.

The purpose of this article is to ask what would constitute evidence that an animal is not stuck in time. But first, it is important to distinguish between an animal’s ability to keep track of time and its ability to subjectively travel in time.

For many animals, the time of day can serve as a cue to regulate their behavior. If food is made available at locations that vary with the time of day, pigeons, for example, can anticipate where they will get fed ([Saksida & Wilke, 1994](#)). The results of probe trials indicate that the anticipated location does not depend on the location at which food was most recently found.

Animals can also judge the duration of relatively short intervals. In a fixed interval schedule of reinforcement, reinforcement is provided for the first response that occurs after the designated interval has elapsed. When trained on such a schedule, both rats and pigeons show a rate of responding that starts low and increases to a maximum as the designated time approaches. If probe trials are included in which no reinforcement is provided, one can track the response up to and beyond the time when reinforcement should have been provided. This, so-called peak procedure generally results in response–rate functions over time that peak at about the time that reinforcement is expected (Roberts, 1981). Thus, animals appear to be able to judge the passage of time. But the ability to time durations is not the same as the ability to travel back in time to recover memory of a past event. Timing may be controlled by behavioral cues (see e.g., the behavioral theory of timing, Killeen & Fetterman, 1988) or by the strength of a stimulus trace (Roberts, 1972; Staddon & Higa, 1999).

Animals also can choose based on the relative recency of two events. For example, pigeons can acquire a typical delayed conditional discrimination in which they must choose between two comparison stimuli based on which conditional stimulus was most recently presented. It is possible to view this task as one involving episodic memory. For example, at the time the comparison stimuli are presented, the animal could retrieve the experience of having seen the conditional stimulus. However, the repeated training trials required to acquire the associations between the conditional stimuli and the correct comparison stimuli suggest that a simpler, rule-learning account may be responsible for the accurate performance of this task. This distinction between rule learning and episodic memory will be discussed further in the next section.

To better understand the nature of subjective time travel, it may be useful to identify what constitutes evidence for episodic memory and planning for the future in humans and then determine to what extent one can find similar evidence in animals. I will first examine the evidence for backward-looking episodic memory and then the evidence for forward-looking prospective memory.

Looking backward

It is said that humans can travel back in time to recover personal memories because what is retrieved is much more than a fact or a rule. For example, if asked, “What did you have for breakfast this morning?” the human subjective experience is to recreate the morning event in the “mind’s eye.” With an episodic memory, typically, one can not only give a response to the question about a personal experience but one can also provide additional detailed information about that experience (e.g., while eating breakfast, one may be able to remember that one was interrupted by a phone call, one spilled some milk, or one was unable to find a clean spoon). Episodic memories can be readily studied in humans because humans can talk about and elaborate on memories of their experiences.

The implication of being stuck in time is that one would not have the ability to recover personal memories of past events. That is not to say that one who is stuck in

time would be unable to act on past experiences, clearly most organisms can. The distinction between episodic memory and learning from past experience may not be obvious. Although animals can act on past experiences, they may not be able to actively retrieve them. In humans, this distinction is manifest in the difference between episodic memory and semantic memory. Semantic memory or memory for facts or rules is generally not tied to personal experiences. For example, I know that Frankfort is the capital of Kentucky, but I don't usually associate that fact with a personal experience. Thus, I don't remember the conditions under which I learned that fact.

Although it is relatively easy to identify one's own personal examples to distinguish episodic from semantic memories, when it comes to interpreting the verbal response of others, the distinction may not always be clear. Specifically, if the response to the question, "What did you have for breakfast this morning?" was, "Toast and coffee," the likelihood of its being a semantic rather than an episodic memory would increase if the response were followed by, "It must have been toast and coffee because that's all I ever have for breakfast." Thus, in humans, one can sometimes distinguish between episodic and semantic memory by the nature of the elaborative process. The addition of unique details about the event (something that happened at breakfast today) would suggest an episodic memory, whereas a logical reasoned response would suggest a semantic memory. The problem in making such a distinction in nonhuman animals is it is very difficult to get animals to elaborate on their response because of their relatively limited response repertoire.

As a human, it is difficult to envision what it would be like to be an animal without episodic memory. Imagine, for example, a rat that has been trained to press a lever for food. Without episodic memory it would be unable to remember the event of having pressed the lever and having gotten fed. But in the absence of episodic memory, the rat may still have learned that levers that are pressed may produce food (a semantic memory). Thus, if given the opportunity, such an animal would be inclined to press the lever but, hypothetically, if one could converse with this animal, the rat might not be able to explain why it was about to press the lever or even remember ever having pressed the lever. Just as people might not be able to explain how they know that Frankfort is the capital of Kentucky, an animal would not be able to explain how it knew that pressing the lever would lead to food. Thus, an animal without episodic memory would be able to learn from past experience but it would not be conscious of that experience. And therein lies the problem. The notion of episodic memory implies that one is aware of one's experiences. But what would constitute evidence of awareness in an animal?

The contents of episodic memory

There have been two approaches to the study of episodic memory in animals. The first, proposed by Clayton and her colleagues (Clayton & Dickinson, 1998, 1999; Clayton, Yu, & Dickinson, 2001), is based on a seminal article by Tulving (1972) in which it is proposed that a person who has access to episodic memory should be able to identify a past event in terms of three properties of that event: what had happened,

where it had happened, and when it had happened. In other words, one should be able to place an event at a location and in time. Although these three properties of an event often accompany an episodic memory, evidence that these properties have been acquired may be neither sufficient nor necessary support for the ability to retrieve episodic memories (Suddendorf & Busby, 2003).

First, merely knowing what happened, and where and when it took place does not ensure that the memory is episodic. For example, I know that the Declaration of Independence was signed in Philadelphia on July 4th, 1776, but no one alive today can claim that to be an episodic memory. Thus, one can learn to encode the what, where, and when of an event without having a memory for the event itself.

Perhaps a better example of difficulty in separating semantic memories from episodic memories would involve the example given earlier. I proposed that being able to answer the question, “What did you have for breakfast this morning?” might qualify as an episodic memory. But what if one were forewarned at the time of breakfast that the question about breakfast would be asked later? Knowing that the question would be asked, one might prepare an answer in advance. The prepared answer would not require traveling back in time to retrieve the event, and, thus, it would be classified as a semantic rather than an episodic memory.

Second, many quite vivid episodic memories may be missing one of the three presumably necessary components. For example, I may have a vivid memory of the events that occurred the last time I was at the dentist, but I may not be able to recall when I had been there. In fact, it is very likely that I would use my semantic memory as an aide to deduce when it was. I may reason, for example, that it couldn't have been any day last week because I was out of town and that because the only time that I don't teach or have meetings is Wednesday morning, it must have been Wednesday morning, probably two weeks ago. Thus, the “when” may be missing from my episodic memory.

Another example of a missing component from the presumed content of episodic memory comes from an attempt to mentally travel back in time with a colleague. I said, “Remember, we talked about that, over a beer, at last years meeting.” But his reply was, “No, it couldn't have been there because I didn't attend that meeting. It must have been at a different meeting.” In this case, a clear episodic memory was misplaced in both location and time.

The importance of this conclusion is that the ability to recover past memories may not be related to the ability to know when or even where an event occurred. The fact that knowing ‘what,’ ‘where,’ and ‘when’ is neither necessary nor sufficient for the experience of episodic memory has been described as a double dissociation of these phenomena (Suddendorf & Corballis, 1997).

Returning to nonhuman animal research, can evidence of memory for “what,” “where,” and “when” be taken as evidence of episodic memory? Let us consider a thought experiment involving a variant on a delayed conditional discrimination with pigeons, with four response keys laid out in a diamond pattern. A red conditional or initial stimulus signals that choosing the left comparison key is correct, whereas a green initial stimulus signals that choosing the right comparison key is correct (what), but this rule applies only when the initial stimulus appears on the top

response key. When the initial stimulus appears on the bottom key, the contingencies are reversed (where). That is, a red initial stimulus means choose the right comparison key and a green initial stimulus means choose the left comparison key. There is evidence that pigeons can acquire a four-rule biconditional discrimination that was not very different from this hypothetical task (Edwards, Miller, & Zentall, 1985; Edwards, Miller, Zentall, & Jagielo, 1987).

Now let us add one more property, time, to this task. That is, what if the contingencies described above only hold when the delay between initial stimulus offset and comparison onset is short (1 s). When that interval is long (3 s), all of the contingencies are reversed (when). Could pigeons acquire this triconditional discrimination? Given selection of the right parameters, perhaps they could, but whether they can or not is really not the issue. Even if they could, one probably would not argue that such learning provides evidence for episodic memory. The reason is that the pigeons could have acquired this task by learning eight specific ‘semantic’ rules. Although the task would surely be quite difficult, conceptually the kind of memory involved would not be different from that involved in a standard conditional discrimination.

Additional characteristics of episodic memory

Recently, Clayton and her colleagues (Clayton, Bussey, & Dickinson, 2003; Clayton, Bussey, Emery, & Dickinson, 2003) have suggested two additional behavioral criteria that define episodic memory. In addition to the content of episodic memory (the what, where, and when), they propose that episodic memories also have structure and flexibility.

What Clayton et al. (2003) mean by structure is that the what, where, and when of an episode must be integrated into a unified representation, such that if one of the features is retrieved the other features are also retrieved. In humans, episodes are retrieved as a complete integrated event. But how does one decide if an animal retrieves a memory as an integrated whole? In the thought experiment described above, accurate performance of the task requires that the three cues (color, location, and time since presentation) are retrieved together because the failure to retrieve one of them would result in chance performance. Of course one could posit that the three cues were retrieved sequentially rather than together as a complete configuration, but it is not clear how one would test that distinction behaviorally.

According to Clayton et al. (2003), the third criterion for episodic memory is flexibility. An animal with episodic memory should be able to use it in new contexts. But flexibility should be a characteristic of all learning whether semantic or episodic. When exposed to new contexts, animals should be able to use what they have learned. Thus, flexibility may be a necessary criterion but it does not help us to distinguish episodic from semantic memory.

Still, an animal with episodic memory should be able to modify its behavior when, after the target experience, it is provided with new or redefining information. An example of this is provided by Clayton et al. (2003) who report that if Western scrub jays have a worm-caching experience and they then learn that worms deteriorate at a rate faster than they had experienced earlier, they can adjust their search to accom-

moderate that new information. That is, they will stop searching for the wax worms earlier than they would have in the absence of the intervening experience. There is good evidence, however, from instrumental devaluation studies with rats (Adams & Dickinson, 1981; Colwill & Rescorla, 1985; Holland & Straub, 1979) that such flexibility can occur in much simpler contexts. For example, when pellet rewards for bar pressing are later associated with illness (lithium chloride injections), an almost total absence of bar pressing results (Colwill & Rescorla, 1985). The Clayton et al. (2003) finding is more complex, of course, because the devaluation effect found was specific to the new time of cache retrieval. That is, the experience with faster deteriorating wax worms was not a general devaluation effect, as it did not affect retrieval of worms that were recently cached (i.e., the worms were within the new window of freshness). Nevertheless, as impressive as this form of flexibility is, it is not clear how it qualifies as a measure of episodic memory.

But the criterion of flexibility may be critical to a distinction between episodic and semantic memory in a different way. In the example of human episodic memory cited earlier, it was the appropriate answer to the unexpected question, “What did you have for breakfast this morning.” Recall that if the future question could have been anticipated at the time of the target experience, the answer could have been attributed to the retrieval of a semantic memory. Thus, if one wants to isolate episodic memory from semantic memory, it may be necessary that the question (or in the case of nonhuman animals the memory test) be applied in a novel context so it cannot be anticipated.

To present animals with an unanticipated question requires some preparation. First, the animals would have to receive (semantic) training in how to answer a question having to do with a past event. Humans generally come equipped with an over-learned and highly practiced set of language skills with which to answer questions—animals do not. At a minimum, the animals must be trained to report characteristics of a prior event. Then, the animals could be given targeted experiences and later, unexpectedly, asked to report on those experiences.

Zentall, Clement, Bhatt, and Allen (2001) conducted such an experiment. They chose the behavior of pigeons as the characteristic of the prior event to be reported. Specifically, the behavior to be reported was whether the pigeon had recently pecked or had refrained from pecking a response key. To teach them how to report their behavior, the pigeons were trained to choose the red comparison stimulus if they had recently pecked an initial stimulus and to choose the green comparison stimulus if they had recently refrained from pecking the initial stimulus. The appropriate differential behavior (pecking or not pecking), which was signaled by the initial stimulus, was required to produce the comparison stimuli. One can view this phase of training as analogous to training the pigeons to answer the question, “What did you just do?” And the appropriate answer would be, “I just pecked,” if they chose the red comparison or “I just refrained from pecking,” if they chose the green comparison.

In the second phase of the experiment, the pigeons were exposed to a differential autoshaping procedure designed to induce them to peck at one stimulus (a yellow response key that was always followed by food), and to refrain from pecking another stimulus (a blue response key that was never followed by food). With the autoshaping

procedure, food follows presentation of a stimulus noncontingently but, in spite of the fact that pecking is not required, pigeons typically peck at the stimulus. Under these conditions, however, they almost never peck at a stimulus that is never followed by reinforcement. After stable differences in pecking were established, test trials were introduced in which a yellow or blue stimulus was followed by a choice between a red and a green comparison (see design of this experiment in Table 1). The presentation of red and green comparison stimuli can be viewed as asking the unexpected question, “What did you just do?” Zentall et al. (2001) found that the pigeons showed a significant tendency to choose the red comparison stimulus after having pecked the yellow stimulus and to choose the green comparison after having refrained from pecking the blue stimulus.

But it is not clear that these data provide evidence for episodic memory in pigeons because what is missing is the supportive evidence provided so often by human language and used to confirm the basis for the memory in humans. Instead, the design of this experiment is provided as a better analogy to the procedures used to assess episodic memory in humans.

A similar but more sophisticated approach was taken in an experiment reported by Mercado, Murray, Uyeyama, Pack, and Herman (1998). They used dolphins that had been extensively trained to perform a number of complex responses when given arm-gesture commands. Embedded among commands to perform certain specific responses, the dolphins were trained with a command to repeat the response that they had made most recently. In addition, they were trained with a command that required them to ‘do something/anything that they had not recently done’ (i.e., to perform a relatively novel response). Finally, on probe test trials, they were signaled to ‘do something not recently done’ followed by ‘repeat the most recent response’. Thus, after they had performed a relatively novel response, they were asked, in effect, the unexpected question, “What was the relatively novel response that you just made?” To respond correctly, the dolphin must have been using its own behavior as the basis for the current response, rather than using the command from the previous

Table 1
Design of episodic memory experiment (Zentall et al., 2001)

Samples	Required response	Comparisons
<i>Phase 1</i>		
Vertical lines	Pecking	Red ^a /green
Horizontal lines	Not pecking	Red/green ^a
Stimuli	Required response	Outcome
<i>Phase 2</i>		
Yellow	None	Food
Blue	None	No food
Stimuli	Required response	Comparisons
<i>Test</i>		
Yellow	None	Red/green
Blue	None	Red/green

Note. In phase 1, ^a indicates the comparison stimulus to which pecking was reinforced.

trial as the basis for the current response, because the prior gesture indicated only that the dolphin perform a relatively novel response.

The results of experiments by Mercado et al. (1998) and Zentall et al. (2001) can also be viewed from a different perspective. If one were dealing with a nonverbal human, what evidence would one accept that such a person had episodic memory? In other words, is the verbal description of a past event necessary to demonstrate episodic memory? If language is needed to provide the elaboration required to confirm that a memory is episodic rather than semantic, then it may be procedurally impossible to demonstrate episodic memory in most nonhuman animals. However, Suddendorf and Busby (2003) have proposed that language may not be needed to confirm the presence of episodic memory. Instead, evidence for subjective time travel in nonverbal organisms could take the form of the re-enactment of events through pantomime. Interestingly, this would appear to be what the dolphins were doing.

Another capacity that has been proposed to be an integral component of episodic memory is a concept of self that can be projected into the past (Suddendorf & Corballis, 1997). Like language, it is difficult to know how one would go about looking for evidence that an animal had a concept of self. Several species of great apes appear to be able to recognize themselves in a mirror (they pass the mark test), including chimpanzees (Gallup, 1970), orangutans (Suarez & Gallup, 1981), and gorillas (Parker, 1984). Some have proposed that the ability to recognize oneself in a mirror provides a nonverbal test of self concept (Gallup, 1982), but this conclusion is not without its controversy (Suddendorf & Busby, 2003).

Looking forward

The other half of the subjective time travel continuum is the ability to imagine an event in the future or to plan for a future event. Although many animals prepare for the future by storing food or building nests, there is no evidence that these animals understand the relation between their behavior and their future need. In fact, the Bischof-Kohler hypothesis suggests that animals other than humans are not capable of anticipating their future needs (Bischof, 1978). This hypothesis is consistent with the idea that animals may be unable to dissociate their present mental state from their past or future mental state (Suddendorf & Corballis, 1997). Support for the Bischof-Kohler hypothesis comes from research with primates which shows that monkeys and apes have a form of temporal myopia (Roberts, 2002). For example, cebus monkeys that were fed once a day would eat to satiation and then would often throw the remaining food out of their cage (cited by Roberts, 2002). Given that the monkeys were quite hungry by the time they were next fed, why didn't they learn to save their remaining food.

In a more experimental manipulation, macaque monkeys and a chimpanzee showed that they do prefer alternatives that satisfy their current motivational state over those that do not (e.g., they prefer two bananas over one banana), however, they show indifference when both alternatives satisfy their current motivational state (e.g.,

they do not prefer 10 bananas over 5 bananas, Silberberg, Widholm, Bresler, Frujita, & Anderson, 1998).

The problem with research of this kind is it assumes that saving food for later is generally an appropriate strategy. For example, in natural environments, animals that live in social groups may not be able to maintain supplies of food greater than they could immediately consume. Similarly, given that primates typically live in mobile troops, it is unlikely that they would be able carry with them food that they were not able to consume at one sitting.

Similar evidence for the absence of future planning comes from the relative deficiency of self-control behavior in rats and pigeons (Mazur & Logue, 1978; Tobin, Chelonics, & Logue, 1993). Animals often choose small immediate rewards over larger delayed rewards, whereas humans are better able to maximize rewards (King & Logue, 1987). However, humans may have acquired those strategies through social learning (a form of rule learning rather than planning). Furthermore, the poor self control often found in animal experiments may result from the conflict between pre-disposed impulsive behavior and planning for the future. That is, in nature, delayed rewards typically mean uncertain rewards (environments generally do not remain stable over time) and thus, self control may be selected against. Furthermore, humans do not always behavior ‘rationally.’ The argument based on maximizing rewards may have difficulty explaining why humans are willing to incur the sometimes high cost of finance charges for the immediacy of possessions such as houses, cars, or appliances. It may be that the evidence against planning in animals comes largely from the underestimation of the costs associated with delayed rewards. Thus, if one wants to argue that choice of a smaller immediate reward represents the failure to plan ahead, then humans, who clearly are able to plan ahead, often appear to be unable or unwilling to do so. An alternative strategy in assessing the capacity of animals for planning is to use more arbitrary tasks that do not trigger impulsive behaviors that appear to show that animals are stuck in time.

For some time, a distinction has been made in the animal learning literature between memory for past events (retrospective memory) and memory for future events (prospective memory). A clear distinction between the two can be made by considering a conditional discrimination in which an initial shape stimulus (e.g., a circle or a triangle) indicates which of two hue comparison stimuli (e.g., red or green) will be reinforced. Thus, for example, if the initial stimulus is a circle, the red comparison is correct but if the initial stimulus is a triangle, the green comparison is correct. If one now inserts a delay between the offset of the initial stimulus and the onset of the comparisons, working memory is needed to bridge the delay. The question is, what is it that is held in working memory during the delay? The most obvious candidate is a representation of the initial stimulus. For example, a human asked to perform such a task might label the initial stimulus and rehearse the label during the delay. If this were the case, the memory would be considered retrospective because the memory would consist of a representation of the past event. However, an alternative strategy would be to translate the initial stimulus into a response intention and rehearse the response intention during the delay. Thus, after seeing an initial circle stimulus, one might decide to choose the red comparison at the end of the delay. In

this case, it would be the correct comparison that is labeled and its name rehearsed during the delay.

The distinction between retrospective and prospective representations has important theoretical implications. In the case of retrospective representations, the event that is represented was actually presented, and thus, it may be that during the delay the aftereffects of the event are maintained in memory (in the form of neural activity). In the case of prospective representations, however, the event that is represented during the delay has not yet occurred, and, thus, the representation must be created as an anticipation. This means that evidence that an animal is capable of forming a prospective memory code would suggest that it is not stuck in time.

Some years ago, Peter Urcuioli and I asked whether pigeons would prospectively code comparison choices when performing a delayed conditional discrimination (Urcuioli & Zentall, 1986). Our study was based on the finding that identity matching with hues was acquired and remembered better than identity matching with line-orientations (Farthing, Wagner, Gilmour, & Waxman, 1977). We were interested in what was remembered during the delay. Was it the initial hue or the initial line-orientation stimulus, or was it the intention to respond to the hue or the line-orientation comparison? To answer this question, we trained four groups of pigeons. One group matched initial hue stimuli to hue comparisons. The second group matched initial hue stimuli to line-orientation comparisons. The third group matched initial line-orientation stimuli to hue comparisons. And the fourth group matched initial line-orientation stimuli to line-orientation comparisons. We reasoned that if pigeons were remembering the initial stimulus during the delay, the dimension of the initial stimuli would affect the slope of the retention functions but not the dimension of the comparison stimuli. However, if the pigeons were remembering the comparison that they were preparing to choose, the dimension of the comparison stimuli would affect the slope of the retention functions but not the dimension of the initial stimuli. The results of this study indicated that when the initial stimuli were hues, the retention functions were flatter than when they were line-orientations. But the dimension of the comparison stimuli had little effect on the slopes of the retention functions. Thus, in this case, it appears that the pigeons were using retrospective memory codes (see also, Urcuioli, Zentall, Jackson-Smith, & Steirn, 1989).

The conditions under which animals will prospectively code in conditional discriminations is not well understood. It appears that in a typical discrimination with two initial stimuli and two comparison alternatives there is little evidence for prospective coding. However, one can encourage prospective coding by making it a more efficient strategy. For example, if one increases the number of initial stimuli to four (two hues and two line-orientations) but keeps the number of comparison stimuli at two, one can find evidence for prospective coding (Zentall, Urcuioli, Jagielo, & Jackson-Smith, 1989); but, under these conditions, it appears that the pigeons will use prospective codes only when the initial stimuli are relatively difficult to discriminate line-orientations and not when they are relatively easy to discriminate hues.

Perhaps the best evidence for the use of prospective codes by pigeons performing conditional discriminations comes from research that has used differential outcomes for correct choices on trials involving each of the different initial stimuli. In a typical

conditional discrimination, correct responses to each of the comparisons are reinforced with a common outcome (e.g., mixed grain). But when correct responses to each of the comparisons are reinforced with a unique outcome, important effects on matching performance have been found. For example, Brodigan and Peterson (1976) found that if pigeons were trained on a conditional discrimination with hues as initial stimuli and line-orientations as comparisons, reinforcing correct responses to one comparison with food and responses to the other comparison with water led to better delayed conditional discrimination performance than was found for a control group for which the outcomes were uncorrelated with the correct comparison chosen. The implication of this finding is that, on a given trial, the anticipation of the outcome associated with choice of the correct comparison is elicited by the initial stimulus and that anticipation augments or perhaps even replaces the memory for the initial stimulus. The anticipation then serves, at least in part, as the basis for comparison choice (see also Urciuoli & DeMarse, 1996). The importance of this finding is that a stimulus (outcome) that has not yet occurred on that trial can serve as a discriminative stimulus for comparison choice. Thus, the differential outcomes effect provides evidence for the ability to form and use prospective memory codes.

More direct evidence for prospective memory codes comes from the use of transfer designs. For example, Edwards, Jagielo, Zentall, and Hogan (1982) trained pigeons on two matching tasks using differential outcomes. One task involved hue-identity matching, and the other used line-orientation-identity matching. In each task, the outcome following a correct response to one comparison was one kind of food (e.g., corn) and the outcome following a correct response to the other comparison was a different kind of food (e.g., peas). On transfer trials, the pigeons were given initial stimuli from one task (e.g., hues) and comparisons from the other (i.e., line-orientations), and the presumed outcome expectancy elicited by presenting one initial stimulus either signaled the correct response (for the consistent group) or signaled the incorrect response (for the inconsistent group) (see design of this experiment in Table 2). When the outcome elicited by the initial stimulus correctly signaled which comparison to choose, the pigeons performed significantly better

Table 2
Design of differential outcomes experiment (Edwards et al., 1982)

Training	Samples	Comparisons	Outcome
Task 1	Vertical	Vertical ^a /horizontal	Peas
	Horizontal	Vertical/horizontal ^a	Corn
Task 2	Red	Red ^a /green	Peas
	Green	Red/green ^a	Corn
		Consistent group	Inconsistent group
Test	Vertical	Red ^a /green	Red/green ^a
	Horizontal	Red/green ^a	Red ^a /green
	Red	Vertical ^a /horizontal	Vertical/horizontal ^a
	Green	Vertical/horizontal ^a	Vertical ^a /horizontal

^a Indicates the reinforced comparison response.

than when the outcome elicited by the initial stimulus incorrectly signaled which comparison to choose.

More recently, we have investigated whether it is the outcome expectancies themselves that are used by the pigeons to choose the correct comparison, or whether the outcome expectancies cause the pigeon to treat the initial stimuli differently, and the differential sample behavior mediates choice of the comparisons. For example, if a pigeon pecked at one sample stimulus but not at the other, feedback from these different behaviors could serve as cues for comparison choice. We used a differential outcomes procedure but trained the pigeons to treat the initial stimuli similarly, and we still found a significant differential outcomes effect (Sherburne & Zentall, 1995; Zentall & Sherburne, 1994). Thus, the facilitation of performance produced by differential outcomes does not appear to depend on differential behavior in the presence of the initial stimuli.

It might be argued that the two outcomes used in differential outcomes research typically differ in ways that may represent differential hedonic value (e.g., food and water, food and no food, peas and corn). Although this possibility does not imply the absence of prospective cues at the time of comparison choice, it does leave open the possibility that those cues may be motivational in nature. Thus, it is possible that initial stimulus presentation generates an anticipation of the outcome in the form of a differential incentive (e.g., “good” vs. “better”) rather than a more specific event (e.g., food or water). However, there is research that indicates that outcomes without differential hedonic value, such as different colored lights (Kelly & Grant, 2001) and differential feeder location (Williams, Butler, & Overmier, 1990) can facilitate both acquisition and delay performance. The implication of facilitation with differential outcomes that do not have differential hedonic value is that the central representation of the outcome is arbitrary and symbolic rather than differentially emotional.

Thus, in a typical conditional discrimination, it appears that although pigeons tend to code the initial stimuli retrospectively, they can be encouraged to use prospective codes either by increasing the number of initial stimuli that would have to be coded (especially when the initial stimuli are hard to remember) or by using differential outcomes. Therefore, there appears to be evidence that pigeons have some flexibility in their use of retrospective and prospective codes.

Another approach to the study of the development of prospective codes was first reported by Cook, Brown, and Riley (1985) using a radial maze. A radial maze involves a central platform with arms radiating in all directions, each one containing a small amount of food. It is typically elevated and has no side walls or top. The rat starts on the central platform and visits each arm in succession (see, Olton & Samuelson, 1976). A visit to an empty arm prior to visiting all of the baited arms (i.e., a revisit) is counted as an error.

Rats are typically very good at this task. After some experience on a 12-arm maze, they can often collect all of the food without making an error. Although the rats could adopt a rule such as, always make a sharp left turn when exiting an arm, they do not appear to do so. In fact, they do not appear to make any systematic pattern of choices on a trial and do not appear to use olfactory cues. Instead, they appear to

remember either all of the locations that they have already visited (retrospectively) or all of the locations that remain to be visited (prospectively).

Cook et al. (1985) reasoned that they could induce a rat to make errors by introducing a delay during which they removed it from the maze for several minutes at some point in the trial. Where in the trial the delay was placed (or was interpolated) varied from trial to trial. The purpose of this manipulation was to determine the effect of the point of delay interpolation on the probability of making an error (corrected for opportunity). That is, Cook et al. asked if the probability of making an error (corrected for opportunity) would change with an interpolated delay as the rat progressed through the trial. Assuming that the probability of making an error would increase as the memory load (or number of arms to be remembered) increased, the logic of this manipulation was as follows: If the rats remembered their choices already made (retrospectively), the probability of making an error should increase as the point of delay interpolation increased. However, if the rats remembered their choices yet to be made (prospectively), the probability of making an error should decrease as the point of delay interpolation increased.

Cook et al. (1985) found that as the point of delay interpolation increased, the probability of an error first increased, until the point of delay interpolation occurred at the midpoint of the trial (i.e., following six choices), and then it decreased (see Fig. 1). There are two important implications of these results. First, it appears that the rats could remember either choices already made (retrospectively) or choices yet to be made (prospectively). The finding that memory load may consist of places yet to be chosen suggests that rats appear to be able to plan their post-delay choice behavior. But more important, the rats appear to be able to learn which strategy is most efficient at each point of delay interpolation. That is, by retrospectively coding choices made up to the midpoint in the trial and then prospectively encoding choices yet to be made, the rats minimized the number of choices that they would have to remember (as compared to either strategy by itself). This implies that, at the time of the delay interpolation, the rats were able to remember both the choices already

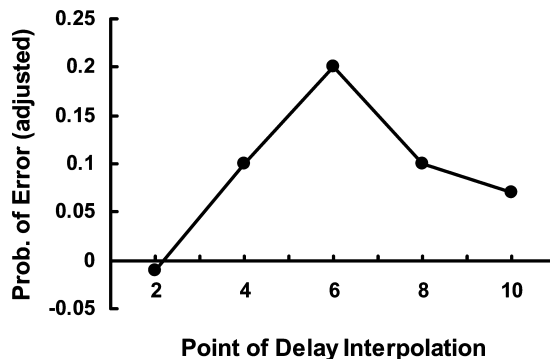


Fig. 1. Probability of making an error by rats' on the radial maze following a within-trial delay (adjusted for opportunity, relative to trials without a delay) as a function of the point of delay interpolation (after Cook et al., 1985).

made and the choices yet to be made. The implication of the inverted V-shaped error functions that were found is that the rats are able to choose to remember either class of responses based on the relative current memory load of each. This finding suggests that the rats exhibited the capacity for some form of meta-memory (or memory strategy), a capacity that has been proposed to be an important component of episodic memory (Suddendorf & Corballis, 1997).

Rats are known for their spatial foraging ability and they have a natural tendency to visit locations not recently visited (Timberlake & White, 1990). That is, rats have a natural win-shift foraging strategy that is well suited for learning not to make revisits to arms in the radial maze. Pigeons, however, have a natural win-stay foraging strategy that is not well suited for this task. They tend to return to places where they have once found food. For this reason, pigeons have a more difficult time acquiring even a simplified operant version of this task (Zentall, Steirn, & Jackson-Smith, 1990). In this study, on each trial, five response keys were lit and choice of any response key was reinforced the first time it was chosen—until each response key was chosen at least once. Pigeons typically begin performing this task by making errors at a rate greater than chance (chance is defined as random choice, that is, no memory for past choices), but they do eventually acquire the task to a reasonable level. In spite of the unnatural nature of this task for pigeons, when they were tested with interpolated delays, and the point of delay interpolation was varied, the pigeons showed an inverted U-shaped error function that was quite similar to that found for rats (see Fig. 2).

The data from these outcome expectancy and radial maze experiments provide the best evidence for the use of response intentions by animals (see also Hampton, 2001). The ability to use the anticipation of future events as the basis for one's behavior suggests the ability to develop meta-representations of those events and thus show the ability to plan for future behavior. Evidence for prospective coding of alternatives not yet chosen suggests that animals are able to represent future

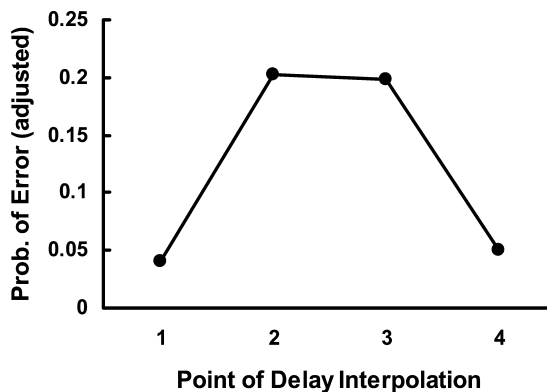


Fig. 2. Probability of making an error by pigeons on a 5-choice, radial-maze-analog task following a within-trial delay (adjusted for opportunity, relative to trials without a delay) as a function of the point of delay interpolation (after Zentall et al., 1990).

events. Such an internal list of future events is analogous to the mental shopping list that humans might prepare when planning a trip to the store.

Conclusions

Animals show some evidence of being able to retrieve information about past personal experiences (episodic memory). Research with differential outcomes and with the radial maze suggests that under the appropriate conditions, animals also show evidence of being able to plan ahead. Thus, animals may not be completely stuck in time. Ultimately, however, the best evidence for subjective time travel comes from the human ability to elaborate on behavior by answering questions such as, “Why did you do that?” and “What are you planning to do?” questions that may not be possible to ask of animals.

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