Are Animals Stuck in Time?

William A. Roberts
University of Western Ontario

People can time travel cognitively because they can remember events having occurred at particular times in the past (episodic memory) and because they can anticipate new events occurring at particular times in the future. The ability to assign points in time to events arises from human development of a sense of time and its accompanying time-keeping technology. The hypothesis is advanced that animals are cognitively stuck in time; that is, they have no sense of time and thus have no episodic memory or ability to anticipate long-range future events. Research on animals' abilities to detect time of day, track short time intervals, remember the order of a sequence of events, and anticipate future events are considered, and it is concluded that the stuck-in-time hypothesis is largely supported by the current evidence.

It has been argued that people cognitively time travel (Friedman, 1993; Suddendorf & Corballis, 1997; Tulving, 1984). In one direction from the present moment, people travel backward in subjective time to remember specific events from their personal pasts. This ability is referred to as *episodic memory* and has been linked to *autonoetic consciousness*, or personal awareness (Tulving, 1985, 1993). Tulving contrasted episodic memory and autonoetic consciousness with *semantic memory* and *noetic consciousness*; these refer to awareness of general information people know but have no specific awareness of experiencing at a particular point in time. In memory experiments, subjects shown a list of items later recognized some items as *remembered* and others as *known* (Gardiner & Java, 1993). Remembered items involve episodic memory and time travel because they are remembered as having occurred in a particular past context, whereas known items are identified only through a feeling of familiarity.

In the opposite direction from the present moment, people cognitively travel forward in time. People plan out their activities over the coming days, months, or even years. Often forward time travel is coordinated with backward time travel; if I remember having potatoes for dinner last night, I will plan to have rice tonight.

Not all humans have episodic memory. Recent research suggests that this may be the case for young children. Gopnik's studies of the beliefs of children younger than 4 years suggest that these children do not remember or understand the sources of factual beliefs they hold (Gopnik & Graf, 1988; Gopnik & Slaughter, 1991; O'Neill & Gopnik, 1991). Perner and Ruffman (1995) found that the ability to free recall pictures in children 3–6 years old was directly correlated with their ability to understand the origin of their own memories. It is important, however, that this correlation was not found when cued recall ability was measured. On the basis of assumption that free recall, but not cued recall, requires episodic memory, they concluded that children under 4 years of age do not have the cognitive structures necessary to form episodic memories. Nelson (1992) suggested that until age 4 years, children have not sufficiently mastered language as a representational system to

form autobiographical memory. Children younger than 4 years may not have the linguistic representational skills to conceive of time as a dimension going backward and forward from the present moment (Barsalou, 1988). Indeed, Friedman reported that children 4 years of age and younger have no knowledge of time scales (Friedman, 1991; Friedman, Gardner, & Zubin, 1995). Thus, episodic memories, autonoetic consciousness, and cognitive time travel may only emerge as children 4–6 years of age develop an understanding of how information is acquired and of a sense of time.

As another example, Tulving (1989, 1993) described the psychology of a patient identified as K. C., who had suffered brain damage to the left frontal-parietal and right parietal-occipital lobes of his cortex. As a consequence, K. C. had a complete loss of episodic memory; he could remember no personal events from his past, although he certainly retained language and other forms of semantic or reference memory. Of further importance, K. C. was completely unable to plan any event he would carry out in the future. K. C. was completely rooted in the present, with no ability to move backward or forward cognitively in time. It appears, then, that the cognitive ability to time travel requires the development of a sense of time in early development and may be lost with damage to certain brain structures.

The question of cognitive time travel in animals has been periodically addressed by several prominent philosophers or psychologists. Aristotle suggested that "many animals have memory and are capable of instruction, but no other animal except man can recall the past at will" (as cited by Winograd, 1971, p. 259). In considering the breadth of the mental time window within which a chimpanzee lives, Kohler (1925) argued that "besides in the lack of speech, it is in the extremely narrow limits in this direction that the chief difference is to be found between anthropoids and even the most primitive human beings" (p. 238). More recently, Suddendorf and Corballis (1997) concluded that cognitive time travel in non-human primates was very limited in comparison with that performed by humans, and Tulving (1983) has explicitly suggested that episodic memory and time travel are not to be found in animals: "Remembering past events is a universally familiar experience. It is also a uniquely human one" (p. 1).

The purpose of this article is to examine the questions raised by these statements in light of the animal cognition literature. Do animals have a sense of time, episodic memory, and an ability to

Correspondence concerning this article should be addressed to William A. Roberts, Department of Psychology, University of Western Ontario, London, Ontario N6A 5C2, Canada. E-mail: roberts@uwo.ca

cognitively project activities into the future, or are animals permanently similar to K. C. and to children under 4 years of age? Could animals be largely stuck in a permanent present, with little ability to remember past personal episodes or to plan activities for the future or might they have either full or limited capacity to cognitively time travel?

Before addressing the evidence on this question, some conceptual issues about time travel and episodic memory will be addressed. What gives us a sense or concept of time? How do we use a sense of time to create episodic memories? What is the importance of succession for episodic memory? Why should we suspect that animals are missing episodic memory and a sense of succession?

Conceptual Issues

The Concept of Time

The human concept of time did not arise de novo. It arose from a need to mark the cyclicity of natural events. The most dramatic natural event we on this planet observe is the light–dark cycle caused by the earth's rotation. In addition, the tides vary, the moon goes through a regular cycle of illumination, and we experience changes in the seasons of the year. Thus, humans mark time on a gross scale in days, months, and years. Early societies observed these cycles and used them as people now do to plan construction, travel, and the planting of crops (Waugh, 1999). Upon these natural phenomena, people impose time reckoned in number of annual cycles from significant human events. Thus, most people keep track of the number of years before or after the birth of Jesus Christ. The Gregorian Calendar keeps track of time since important discoveries, such as years since Columbus's arrival in the New World or years since major wars such as the United States Civil War or either of the world wars. Closely related to people's sense of time is their concept of number. The system of cardinal numbers allows one to count virtually any set of objects or events, including abstract quantities of time. Technology has provided people with calendars and clocks that do this counting for them, allowing them to keep track of time in days, hours, minutes, and very small fractions of a second. The point here is that all of these factors are learned about by a contemporary person and contribute to a sophisticated concept of time.

Time and Episodic Memory

Episodic memories are memories of personal experiences or activities. Although different people share much in common in their semantic or reference memories, their sets of episodic memories vary considerably and are unique to each person. Episodic memory gives each person a *personal history*, or a record of the experiences he or she has had up to the present.

The conception of episodic memory as a personal history necessarily ties these memories to representations of time. Memory for the time of personal events may take at least three different forms (Friedman, 1993). An individual might remember the distance back in time or how long ago an event occurred, the location or when an event occurred within a time scale, or the order in which two or more events occurred over time. These types of time information are not completely independent of one another. For example, given the location of a past event and the present time,

one could infer the distance of the event, or given the locations of two past events on a time scale, one could infer their order.

How is memory for the time of episodic memories encoded? Although it has been suggested that memories of experienced events are time dated or assigned time tags (Flexer & Bower, 1974; Glenberg, 1987; Tulving, 1984, 1985, 1993; Yntema & Trask, 1963), recent theory and research suggests that human memories of past events are not commonly time dated and that the notion of a linear representation of time is a "chronological illusion" (Friedman, 1993, p. 44). Friedman (1993, 1996) pointed out a number of findings that are inconsistent with the notion that personal memories contain time markers that place them on a linear time scale. First, when people are asked about the methods they use to retrieve personal memories, they rarely report retrieving the date on which an event occurred. Conversely, the date of a past event is a very poor retrieval cue for memory of the event (Barsalou, 1988; Brewer, 1988; Wagenaar, 1986). Second, memory for the time of events often shows systematic distortions. One such distortion is *forward telescoping*, or a tendency to move the memory of more distant events toward the present. Finally, memory for the time of events shows scale effects that are paradoxical from the point of view of a linear time line. Most dramatic is the finding that people can often remember rather precisely the time of day on which something occurred but be quite inaccurate about the day, month, or year in which it occurred (Friedman & Wilkins, 1985).

These findings suggest that personal memories do not carry time location tags or information that specifies their distance from the present in time units or number of intervening events. Friedman (1993, 1996) argued that, to the contrary, memory for the time of past events is reconstructive and inferential. Thus, people develop rich reference memories for the structure of time, in which some salient events or periods of time are dated. When a person recalls or is reminded of a personal past event, they relate that event to this time information by finding associations between reference memory time markers or blocks of time and the remembered event. Thus, human memory only roughly but not precisely specifies the location in time when a personal event occurred because events often can only be inferred to have happened within a period or block of time. The time of personal memories is then inferred, and it is this inferred time that gives these memories their episodic or historical quality.

One exception to these conclusions has been found in research with young children. School classes of children 4–12 years of age were tested for their memory of when two events occurred during the past year. These events were a videotaping demonstration and a toothbrushing demonstration in one study (Friedman, 1991) and the more salient events of a child's birthday and Christmas in another study (Friedman et al., 1995). Children were asked which of these events occurred more recently and which occurred a longer time ago. Even the youngest children were able to specify the most recent event significantly above chance. In the Friedman et al. study, a clear distance effect appeared. Children accurately specified that their birthday was most recent when their birthday had occurred within the last 2 months and Christmas had occurred earlier, but accuracy declined as the distance of their birthday increased toward the time of Christmas. The ability of the youngest children to identify the most recent event could not be based on reconstruction of the locations of these events because interviews with these children indicated no knowledge of calendar dates. It was concluded that these children made judgments based on dis-

tance information perhaps obtained from the strength of a decaying memory trace.

What are the implications of this discussion for memory of time in animals? Because animals have no access to information about calendars or clocks, any representation of extended time in reference memory should be limited. Therefore, memories of previous events may not have an episodic quality because they cannot be reconstructed to have occurred at some point in past time. However, some memory of the relative recency of past events might be available to an animal, as it is to a young child, through the relative strengths of memories.

Succession in Episodic Memory

Memory for the time at which events occurred is closely related to memory for order. If the location of two or more events in time can be remembered, their order can be inferred. Conversely, memory for the order of events allows us to specify their relative times of occurrence. Laboratory studies have shown that people can remember the order of two items presented within a list and that memory for order improves as the temporal separation between the items increases (Fozard & Weinert, 1972; Guenther & Linton, 1975; Tzeng, Lee, & Wetzel, 1979). In everyday memory, people remember not only the activities they performed yesterday but the order in which they performed them. People can plan the exact times at which they will hold meetings, take place in recreational activities, and eat meals tomorrow, and they can make long-range travel plans months ahead of time. The ability to remember order of events in time is a critical property of episodic memory, and evidence for this ability in animals will be examined.

Episodic Memory in Animals

Tulving (1972, 1983, 1984) defined *episodic memory* as autobiographical in nature because it contains time-dated personal episodes that are unique to the individual and suggested that animals do not remember personal episodes. In a response to Tulving's ideas, Olton (1984) argued that Tulving was wrong and that there was clear evidence for episodic memory in animals. Olton pointed out that there is considerable evidence that animals remember specific past events. He focused on the delayed matching-to-sample procedure. A pigeon, for example, can be trained to match a red or green sample stimulus, even though there is a memory interval between the sample and the matching test. The pigeon might initially be shown a central green key for a few seconds and then have to choose between green and red side keys after spending 10 s in the dark. The pigeon chooses the matching green key (or red key, if the sample was red) significantly more often than the chance level of 50%, showing memory for the sample stimulus (Grant, 1976). Olton saw this finding as crucial evidence for episodic memory in animals, saying, "thus, the only way the individual can determine which of the responses is correct at the end of the trial is to travel back in time to the beginning of the trial and remember which stimulus was presented then" (p. 250).

These positions taken by Tulving (1972, 1983, 1984) and Olton (1984) clearly delineate the issue of episodic memory in animals. However, the crucial assumption of Olton's argument, that animals travel back in time, is not necessary to explain accurate performance on the delayed matching-to-sample procedure. Although a pigeon may have a memory of a green sample stimulus, it may have no memory of that sample having occurred 10 s in the past or at any time in the past; pigeons could have no concept of a past or a future and still accurately match the green sample because memory of green is currently the strongest memory available to the pigeon.

The human concept of time involves a rich appreciation of time related to natural events, events performed by people, and time-keeping technology. If animals do not have the benefit of this acquired temporal framework, they may be "stuck in time" and thus unable to experience episodic memories, form memories for the succession of events, and plan future activities. This hypothesis should not be assumed to be correct, however, without an examination of the relevant findings. What do we know about animals' ability to keep track of time, to place events in a temporal order, and to anticipate future events? Does the available evidence support the hypothesis that animals have no sense of a time dimension, or are there findings that suggest they do appreciate past and future points in time?

The Evidence

Time Tracking by Animals

Animals are not insensitive to time. In some ways, they are highly sensitive to time, and I review these here. The question of further interest here is whether their sensitivity to time means that they have a concept of time that allows them to view their memories of past events as having occurred at different points over an extended duration.

Time of day tracking. Anecdotal accounts suggest that animals are highly sensitive to the time of day. Dogs are often seen to wait in anticipation at the time of day when the mail delivery person will arrive or to go to the food dish at supper time. In field studies, animals have been observed to wait for prey at the precise time of day when it usually arrives. For example, birds called oystercatchers prey on mollusks that are available on mud flats only for a brief window of time at low tide. Birds were observed to visit the mussel beds at precisely this time each day (Daan & Koene, 1981). Wilkie et al. (1996) found that wild pigeons gathered daily at a location on a university campus just before people arrived to eat lunch in the area; control observations at a nonluncheon site showed no concentration of birds.

Recently, laboratory studies have examined time–place learning under more controlled circumstances. In a study performed by Biebach, Gordijn, and Krebs (1989), garden warblers were placed in an apparatus that consisted of a central living room and four feeding rooms placed around it. During different periods of the day, food was available in different rooms. For example, Room 1 contained food from 0600 to 0900; a bird could fly to Room 1 during this time, open a feeder, and eat for 20 s. It then had to return to the living room for 280 s before it could again visit a feeding room. Feeding Rooms 2, 3, and 4 successively contained food between 0900 to 1200, 1200 to 1500, and 1500 to 1800, respectively. Each of 5 birds learned to go to the appropriate room at the appropriate time of day to obtain food. To control for the possibility that the warblers just sampled rooms until they found the one that yielded reward, test days were run in which all four rooms contained food throughout the day. As shown in Figure 1, birds continued to go predominantly to the room that had contained food during each time period in training.
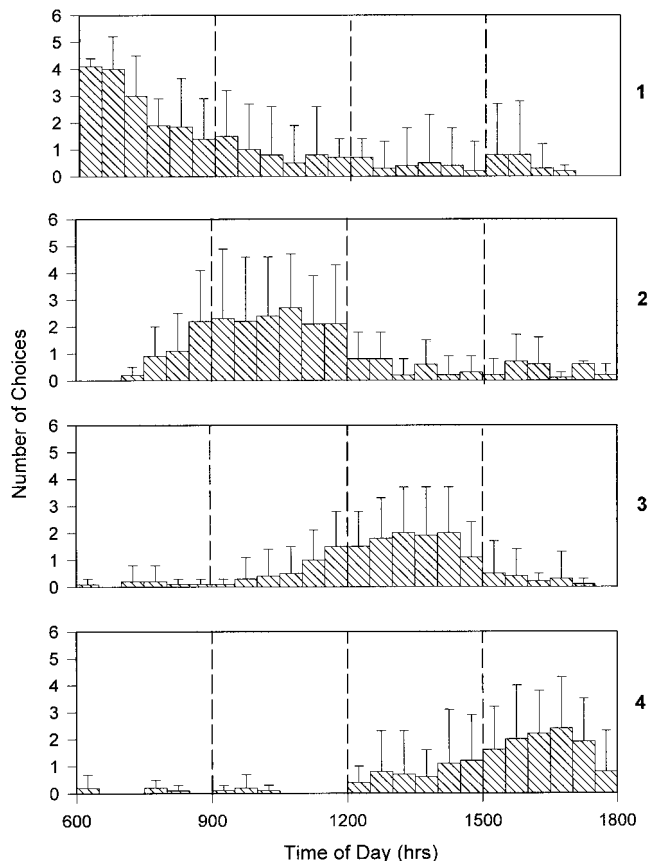
Figure 1. Bars show the number of choices of Rooms 1, 2, 3, and 4 by garden warblers at different times of day. Adapted from *Animal Behaviour, 37*(3), H. Biebach, M. Gordijn, and J. R. Krebs, "Time-and-Place Learning by Garden Warblers, *Sylvia borin*," pp. 353–360, 1989, by permission of the publisher Academic Press/Elsevier Science.

Saksida and Wilkie (1994) performed similar experiments with pigeons. Pigeons were placed in an operant chamber with a pecking key on each of four walls. Pecks on Key 1 always yielded reward when pigeons were placed in the chamber at 0930, but pecks on Key 3 always were rewarded when birds were placed in the chamber at 1600. As had been the case with garden warblers, pigeons learned to peck the appropriate key at each time of day, even during the first minute of a session, when no reward for pecking was delivered. Although these findings suggest that pigeons used time of day to identify the correct key, two alternative explanations were tested. One possibility is that pigeons had learned ordinal rules: If Key 1 was correct last session, peck Key 3 this session, or if Key 3 was correct last session, peck Key 1 this session. To test this possibility, Saksida and Wilkie occasionally skipped a morning or afternoon session and then tested birds at the next scheduled session. The pigeons continued to peck the key indicated by the time of day and not by the most recent test. Another possibility is that pigeons time the intervals from the onset of light in the morning to the times when each key would be rewarded. This explanation was tested by moving the normal time of light onset back from 0600 to 1200. Now, the test given at 0930 occurred after lights had been on for about the same time they had previously been on at the 1600 test. Pigeons continued to peck

Key 1 at 0930 and Key 3 at 1600. It appears that pigeons were associating rewarded keys with time of day.

How does a bird know what the time of day is? Most species of animals, certainly including birds, are equipped with circadian oscillators. A number of internal processes, such as temperature, rates of neural firing, and hormone concentrations, rise and fall through daily cycles. States of sleep and wakefulness are particularly noticeable circadian cycles. It has been suggested that a particular state (phase angle) in a circadian cycle becomes associated with a particular place where food is available (Carr & Wilkie, 1997). The cycles of an oscillator are often controlled by light onset and offset. Animals can be phase shifted by changing these times. In the Saksida and Wilkie (1994) experiments, turning the light on 6 hr earlier than usual should have shifted circadian oscillators back 6 hr. Because phase shifting takes place gradually over several days, pigeons continued to respond correctly when tested because their circadian rhythms had not yet shifted. After several days of the new light regime, however, their accuracy would have diminished.

The important point to be made here is that animals appear to do certain things or go to certain places at given times of day because internal circadian cues prompt them to do so. Nothing in these time–behavior associations suggests that animals have a concept of time or that they time-date events. Thus, a pigeon does not remember that it pecked a key at 0930 yesterday morning or anticipate that it will peck another key at 1600 this afternoon. Beling (1929, as described in Gallistel, 1990) allowed bees to consume sugar water at a feeding station at 19-hr intervals over a period of 10 days. If bees could remember the specific times of previous feedings, they could compute a 19-hr interval between feedings and anticipate food at the feeding station 19 hr after the last feeding. This behavior was not found on a test day; instead, bees showed a small but significant increase in food-seeking behavior at the same time of day as their feeding on the previous day.

An examination of Figure 1 suggests that garden warblers "anticipated" switches between rooms in the location of food. For example, visits to Room 2 began to increase during the final minutes of reward for visits to Room 1. In fact, the anticipatory nature of time–place learning has often been noticed (Gallistel, 1990). Both in nature and in the laboratory, animals appear early at the location that will deliver food. This should not be surprising, however, if animals are responding to circadian cues. The phase changes of many circadian oscillators are sufficiently slow such that the internal cues present some time before feeding are highly similar to those present during feeding. Apparent anticipation of food at a place, then, can be readily explained as stimulus generalization.

There are at least two mechanisms by which circadian cues may control food-seeking behavior. One is that the phase states of oscillators act as retrieval cues that arouse memory of the place–food association (Holloway & Wansley, 1973; W. A. Roberts, 1998; Spear, 1978). The second possibility is that circadian cues act as occasion setters. Occasion setters have been studied in classical conditioning as cues that do not directly elicit behavior but rather tell an animal that the occasion has arisen for a conditioned stimulus (CS) to be followed by a particular unconditioned stimulus (US; Holland, 1992). A circadian cue therefore may quite literally indicate that this is the time or occasion at which food will be found at a given place. In fact, the retrieval cue and occasion

setter mechanisms seem highly similar and may be describing the same process (Bouton, 1993, 1994a, 1994b).

Interval timing. Pavlov (1927) performed an experiment in which a dog was given food at successive points in time separated by a constant interval of 30 min. It was found that the dog learned to salivate at or only a few moments before the scheduled delivery of food. A similar finding was seen in operant training when pigeons and rats were reinforced on a fixed interval (FI) schedule. If a bar press or a key peck delivered food only a fixed time since the last food delivery, a scalloped pattern of responding developed in which an animal would withhold response until only a few moments before the opportunity to earn food arrived. These observations clearly suggested that animals were timing the intervals between food deliveries. A method called the *peak procedure* was used by S. Roberts (1981) to pinpoint the moment in time at which reward was expected. Animals first were trained with discrete FI trials. Each trial began with the onset of a light or tone signal, with each signal indicating a different FI. Thus, a light might indicate that the first response after 20 s would yield reward, and the tone would indicate that the first response after 40 s would yield reward. On test trials randomly intermixed with the FI training trials, either the light or tone was presented for an extended period over twice as long as the FI, and no reward was given for responding. The average rate of responding on test trials was computed for successive time bins and plotted as shown in Figure 2. The peak time curves shown for rats in the top panel and for pigeons in the bottom panel indicate that the peak of each curve is very near the FI. In the top panel, rats trained on FI 20-s and FI 40-s schedules show peaks very near 20 and 40 s. Similar results are seen in the bottom panel for pigeons trained with FI 15-s and FI 30-s schedules.

Animals thus can learn to time intervals marked by specific events very precisely. Several theories have been advanced to account for interval timing in animals. One popular information-processing theory, scalar timing theory, proposes that interval timing arises from the accumulation of pulses emitted from a pacemaker and collected in an accumulator (Church, Meck, & Gibbon, 1994; Gibbon, 1977, 1991). A switch closes when an external signal (light or tone) begins and only opens when reward is delivered. The number of accumulated pulses is permanently stored in a reference memory as a measure of the length of time that elapsed. It may be retrieved into a comparator on a subsequent trial to serve as a criterion for response to a new signal presentation. In a quite different theory, the behavioral theory of timing, a pacemaker is assumed to drive an animal through a sequence of behaviors (Killeen & Fetterman, 1988, 1993). If the animal is reinforced for performing a response while in the midst of a particular behavior, that behavior will establish operant control over the response. If the signal that begins an interval to be timed repeatedly initiates the same sequence of behaviors, the animal's own behavioral state acts as a timing device. Recently, Staddon, Higa, and Chelaru (1999) have challenged scalar timing theory by offering a multiple time scale model. This model suggests that interval timing is accomplished by discriminating the strengths of memory traces that were formed and began to decay at the moment a timing stimulus terminated. When a decaying trace reaches a criterion value, the initiation of responding is triggered. In a fourth theory, a connectionist theory of timing (Church & Broadbent, 1990), it is assumed that interval timing is accomplished by sets of internal oscillators that go in and out of phase at different rates. In
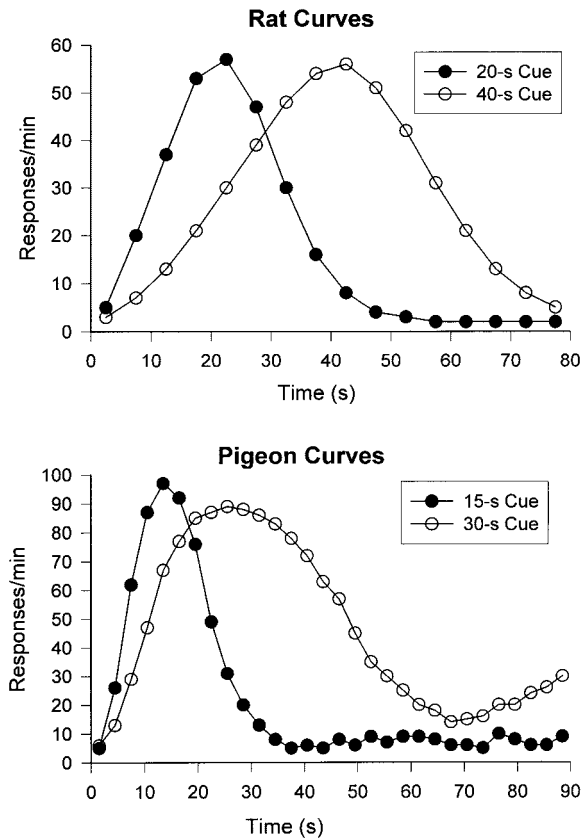

Figure 2. Peak time curves for rats trained on fixed interval (FI) 20-s and FI 40-s schedules in the upper panel and for pigeons trained on FI 15-s and FI 30-s schedules in the lower panel. Adapted from "Isolation of an Internal Clock," by S. Roberts, 1981, *Journal of Experimental Psychology: Animal Behavior Processes, 7,* p. 245. Copyright 1981 by the American Psychological Association. Adapted with permission from the author. Also adapted from "Timing Light and Tone Signals in Pigeons," by W. A. Roberts, K. Cheng, and J. S. Cohen, 1989, *Journal of Experimental Psychology: Animal Behavior Processes, 15,* p. 27. Copyright 1989 by the American Psychological Association.

all of these theories, it is assumed that an interval is timed when some event sets a sequence of activities into motion. These may be the accumulation of pulses, a sequence of behaviors, memory decay, or the monitoring of the status of oscillators. In each case, a response begins as some property of these activities approaches a criterion. Thus, accumulated pulses cross a threshold ratio, a controlling behavior is initiated, a memory trace decays to a criterion level, or storage and retrieval vectors become sufficiently similar. The response is usually initiated before the FI has been reached, giving FI responding the same anticipatory character seen in time-of-day timing. There is nothing in these mechanisms, however, that suggests long-term anticipation of an event at a particular time. Time elapsed since the beginning of a signal started at any time of day is being tracked, and the intervals tracked are usually no longer than a few minutes.

Ample evidence therefore indicates that animals are sensitive to time. They can learn to go to a particular place for food at a particular time of day, and they can learn to precisely time short intervals upon the presentation of an external stimulus. Although

impressive, these abilities do not require a concept of time as a continuous dimension with a present, past, and future. Internal cues supplied by circadian oscillators set the occasion for food-seeking behavior at a particular place within a day, and short-term changes in an internal state allow short intervals to be tracked. These mechanisms do not represent personal experiences backward into an extended past or forward into an extended future.

Memory for Succession of Events

A hallmark of human episodic memory is the ability to remember the sequence in which many past events occurred. Can animals remember sequences of events? This question has been addressed in two ways in animal cognition experiments. In working memory experiments, an animal may be presented with stimuli in orders that vary from trial to trial; in the test phase of each trial, the animal is required to identify the stimulus order for reward. In other experiments, an animal is trained to respond to different stimuli in a fixed order for reward. Because the required order remains constant across trials, these experiments require reference memory.

Working memory experiments. Shimp and Moffitt (1974) trained pigeons to peck three successive keys that lit up on either the left or right side of a panel in a Skinner box. The first lit key was red, the second was blue, and the third was white, and the left-to-right position of each key changed randomly between trials. On a retention test, given after a pigeon had pecked three keys, a red, blue, or white color appeared on the center key. A peck on the center key turned it off and led to the presentation of both side keys illuminated with the same color as the center key had been illuminated. The pigeon could now earn a reward by pecking the same side key it had pecked previously when illuminated with the probe color; pecks to the incorrect side key were nonreinforced. Pigeons learned to choose the correct side key with a high degree of accuracy at a short delay interval between the sequence of side-key pecks and the retention test. This performance can be explained by the formation of an association between the side key pecked and the key color. The color of the probe key may have retrieved memory of the side key pecked. In an important set of further experiments, Shimp (1976) modified this procedure by presenting the same stimulus (a white *X*) on each of the three successive side keys pecked at the beginning of a trial. The probe stimuli continued to be red, blue, and white, signaling the first, second, or third side key pecked, respectively. Notice that the probe stimulus can no longer directly cue a color–side key association. The probe color only tells the pigeon to peck the first, second, or third side key pecked. Pigeons again were highly accurate on this task with a 0.1 s delay between the final side-key peck and presentation of the probe stimulus. As this retention interval increased to 1 and 4 s, retention dropped substantially. There was also a marked recency effect, with accuracy declining steeply from the last side key pecked to the first. Although Shimp argued that these data indicated memory for order or temporal organization in pigeons, they could also be explained as a learned association between key color and memory strength. That is, red would cue response based on the weakest trace—because the first key pecked would have the longest time to decay—blue would cue response to the trace of intermediate strength, and white would cue response to the strongest side key trace.

Weisman and his colleagues presented pigeons with sequences of two successive stimuli (either key lights or overhead colored lights) that can be designated as orders AA, AB, BB, and BA (Weisman & DiFranco, 1981; Weisman, Duder, & von Konigslow, 1985; Weisman, Wasserman, Dodd, & Larew, 1980). Only one sequence, AB, was rewarded for pecking after its presentation, whereas the other three sequences were nonrewarded. Pigeons learned to peck more vigorously after the AB sequence than after the AA, BB, and BA orders. On the basis of several experimental manipulations, Weisman and DiFranco (1981) concluded that pigeons did not respond accurately by remembering positive and negative orders of stimuli and then making a response decision. Rather, pigeons learned to use a two-stage process in which the memory of the first stimulus was kept in working memory while a decision to peck or not to peck was made on the basis of the appearance of the second stimulus. Thus, given recent memory of A, the appearance of B triggered a decision to peck, but the appearance of A triggered a decision not to peck. An initial presentation of B led to an immediate decision not to peck.

In other working-memory experiments, animals were presented with a sequence of stimuli and were then required to reproduce the sequence. Devine, Burke, and Rohack (1979) presented rhesus monkeys with sequences of two stimuli on a single response disk that consisted of black and white shapes or colored fields. Different sequences of two colors, two shapes, a color followed by a shape, or a shape followed by a color were used on different trials. After this presentation, the monkeys were presented with the two stimuli simultaneously on different response disks, and reward was delivered only if a monkey pressed the stimuli in the same order as they were presented. The monkeys learned to do this with considerable accuracy immediately after the sequence had been presented but showed a decline in accuracy as a delay interval before test was lengthened. Parker (1984) required pigeons to peck left (L) and right (R) keys in four different orders (LL, LR, RR, and RL) by illuminating only one key at a time. Both keys then were illuminated, and pigeons were rewarded only for reproducing the order in which the keys had just been pecked. At an immediate retention interval, pigeons were able to reproduce the order at about 75% accuracy, a level considerably better than the 25% chance baseline.

MacDonald (1993) performed an experiment with pigeons that was similar in method to the monkey experiment of Devine et al. (1979). Three colors of stimuli were used: red, green, and yellow. Pigeons saw two of these colors appear in succession on a single key. Following this presentation, all three colors appeared on separate keys. Thus, two of the test stimuli were samples, and the third was a distractor. To be rewarded, a pigeon had to respond to the sample stimuli only, but in the reverse order of their presentation. Thus, if a pigeon was presented with red followed by green and then given a choice between red, green, and yellow, it had to peck green first and red second to earn a reinforcer. An initial peck on red was an order error and led to immediate termination of the trial. A peck on the yellow distractor as the first or second choice also immediately terminated a trial. After 92 sessions (over 6,000 trials) of training, pigeons learned to peck the sample stimuli in the correct order above the chance level of accuracy.

In subsequent experiments, the relative presentation durations of the first sample (S1) and the second sample (S2) were varied. Accuracy was significantly affected by these manipulations. As the length of S1 increased, order errors went up as S1 was incorrectly pecked first. Order errors dropped, however, as the length of S2

increased and the tendency to choose S2 first increased. These findings suggest that pigeons may have been using memory strength instead of order information as a basis for stimulus choice. If memory strength is increased by presentation time and decreased by delay until test, subjects should have a stronger memory of S2 than of S1 when both stimuli are presented for equal durations (W. A. Roberts & Grant, 1976). Thus, pigeons could have learned to base their responses on the stronger memory first and the weaker memory second. The observation that varying the exposure times (memory strengths) of S1 and S2 led to predictable changes in accuracy supports this hypothesis. The monkeys tested by Devine et al. (1979) and the pigeons studied by Parker (1984) also could have learned to respond on the basis of memory strength, if they learned to choose the stimulus indicated by the weaker memory before the stimulus indicated by the stronger memory.

Reference memory experiments. Although evidence for reference memory of serial order is found in animals (W. A. Roberts, 1998), this ability is quite limited compared with human serial memory. In particularly impressive demonstrations with pigeons, Terrace and his colleagues (Straub & Terrace, 1981; Terrace, 1983, 1987, 1991) trained birds to peck as many as five colored keys in a predetermined order. A pigeon was confronted with differently colored keys and might have to peck these keys in the order green → red → blue → white → yellow to obtain a reward. Because the colors of individual keys changed from trial to trial, pigeons could not earn reward by pecking keys in a sequence of spatial locations. Pigeons learned to peck keys in the correct sequence on about 70% of the trials within a session, a level of accuracy far above that expected by chance alone.

Some details of these experiments (Straub & Terrace, 1981; Terrace, 1983, 1987, 1991) are important for the hypothesis considered here. First, pigeons were trained in stages to perform this task. If the sequence of keys learned was designated A → B → C → D → E, a pigeon first was trained to complete the A→B segment for reward. After successfully learning A → B, the pigeon then was trained to complete A → B → C and so on, until it could correctly peck the five-key sequence. That pigeons did not easily acquire this task is shown by the fact that it typically took pigeons 100 or more sessions of training to learn to peck all five keys in the correct sequence. Further tests given with subsequences of keys were highly revealing. On these tests, any combination of two key colors from the list of five were presented to see if the pigeon could peck them in their order on the list. If pigeons were given a pair that contained either A or E, such as AB, AC, AD, AE, BE, CE, or DE, they pecked them in the correct order with high accuracy. When confronted with interior pairs, such as BC, BD, and CD, pigeons did little better than chance. Terrace (1991) explained this interesting pattern of results by suggesting that pigeons had learned certain rules that allowed them to get through the five-item list but that would not lead them to accurate performance on all pairs of list members. He suggested that pigeons had learned the rules "peck A first" and "peck E last." The first rule meant peck A before any other keys, and last rule meant peck E after all other keys had been pecked. These rules would allow the pigeon to correctly order any pair that contained A or E. In addition, pigeons had learned interitem association rules, such as "peck B after A," "peck C after B," and "peck D after C." Although pigeons could then complete the entire list of five items correctly, they would have trouble on an interior pair such as BC

because no response to an A key was made that could then cue a response to the B key. The important message of this analysis is that pigeons did not learn an integrated representation of the entire sequence; rather, they had learned some "if then" rules that told them what to do at each point in the list. Given a stimulus at one point in the list, a pigeon could not anticipate further stimuli in the list other than the stimulus that immediately succeeded the present one.

D'Amato and Colombo (1988, 1989) performed similar experiments with cebus monkeys and found that the monkeys also could learn to respond to a series of five stimuli in a predetermined order for reward. It took the monkeys just over 90 sessions of training to acquire the five-item sequence. When these monkeys were tested with pairs of items taken from the list, they were able to complete interior pairs as accurately as those containing the beginning and end items. These data suggested that the cebus monkeys, unlike the pigeons, may have used a representation of the entire sequence that allowed the order of any pair of items to be determined. In support of such a possibility, it was found that the latency of response to items presented on tests with subsequences varied with an item's position in the list. The first item to be chosen in a pair could be A, B, C, or D. It was found that the latency to respond increased monotonically from A to D. The latency to respond to the second member of a pair was examined as a function of the number of items missing between the members of a pair. For example, the pairs AB, AC, AD, and AE would have 0, 1, 2, and 3 items missing, respectively. Latency to respond to the second item increased monotonically with the number of missing items. Swartz, Chen, and Terrace (1991) reported similar latency data for rhesus monkeys required to complete serial lists of video images. These observations are consistent with the notion that monkeys scanned a representation of list items to determine the position of test items.

Further evidence that rhesus monkeys learn the order of serial lists was found in a derived-lists experiment performed by Chen, Swartz, and Terrace (1997). Monkeys learned to respond in the correct order to four video images on four different lists. They were tested on four-item derived lists that were formed by taking one item from each of the training lists. On maintained derived lists, items maintained the same ordinal position they had had on the training lists; thus, a maintained derived list might be A2 → B4 → C1 → D3, where each number indicates a different training list. Changed derived lists placed items in ordinal positions different from those held in training; an example of a changed derived list is B3 → A1 → D4 → C2. Monkeys completed maintained derived lists immediately with virtually no errors but required substantial new training to master the changed derived lists. These findings indicate that monkeys had formed a strong association between each list item and its ordinal position in the list. Chen et al. concluded that

> In the absence of any evidence that monkeys use numerals to represent ordinal position, a spatial representation of ordinality is the most likely candidate. The traditional method of loci (Yates, 1966), which assumes that list items are coded with respect to a spatial map, provides a plausible match between an animal's nonverbal cognitive abilities and its ability to represent knowledge of an item's ordinal position. (p. 85)

Still another possibility is that the monkeys used a temporal code; that is, they remembered that each item was associated with a point

in a subjective time scale. No current evidence allows us to distinguish between the spatial and temporal code possibilities.

Although these findings suggest that animals can learn to complete an arbitrary sequence as long as five items, three points should be kept in mind. First, it took both pigeons and monkeys considerable training to learn these sequences, and the sequences had to be built up gradually, suggesting that temporal sequencing was not a natural ability for them. Second, pigeons showed no evidence of forming a spatial or temporal representation of the succession of all list items, but monkeys did. Thus, a clear species difference in the representation of a serial list was found. Monkeys might remember the temporal order of response to stimuli. Third, it took a pigeon or a monkey only a few seconds to complete these sequences. The ability to learn more temporally extended sequences that might show a representation of extended time has not been revealed in animals.

Extinction and Spontaneous Recovery

The experiments just considered involved memory of brief events that immediately followed one another. It is difficult to examine animals' memory for the order of temporally extended events because humans have no way of instructing them to tell us what happened first or second or third. Situations can be considered, however, in which successive training regimens require different behaviors. Over successive trials, an animal learns to consistently perform the most recently trained behavior. If some interval of time then is introduced before another trial, the most logical behavior to perform would be the one trained last. If an animal could not locate memory of training episodes along a time scale, however, it would have no memory for the order of these events and thus would not know which was last.

The phenomenon of spontaneous recovery, originally discovered by Pavlov (1927), is highly instructive. After classically conditioning a dog to salivate to a CS by pairing it with delivery of food, the salivary conditioned response (CR) was extinguished by presenting the CS and withholding food delivery. At the completion of extinction, the dog failed to salivate when the CS was presented. Surprisingly, however, if the CS was presented some time later, the dog then made a conditioned salivary response in the presence of the CS. The salivary CR appeared to have spontaneously recovered with the passage of time.

Although many theories of acquisition of Pavlovian conditioning hold that an association is formed between a representation of the CS and a representation of the US, any account of extinction that assumes this association is canceled or unlearned during extinction runs into immediate difficulties with the phenomenon of spontaneous recovery. An unlearned association cannot give rise to a CR with the passage of time. Pavlov suggested that withholding the US (food) led to the growth of an inhibitory process that blocked the CR. This inhibition was temporary, however, and dissipated sufficiently to allow reexpression of the CR after some time elapsed. More contemporary theories (Bouton, 1993, 1994a, 1994b; Kraemer & Golding, 1997; Kraemer & Spear, 1993) suggest that conditioning and extinction give rise to two different memories, one in which the US follows the CS and one in which the US does not follow the CS. Spontaneous recovery, then, can be based on memory of the occasion during which the US followed the CS. Why, though, does spontaneous recovery appear only after some period of time since the end of extinction? By way of several

alternative assumptions, it is held that memory for the reinforced response is more easily retrieved some time after extinction than immediately after extinction. Bouton (1993, 1994a, 1994b) suggested that time acts as a context within which both acquisition and extinction occur. Change in context with the passage of time leads to forgetting through retrieval failure. Spontaneous recovery of the reinforced response occurs because extinction is more affected by the temporal change in context than is acquisition. Kraemer and colleagues (Kraemer & Golding, 1997; Kraemer & Spear, 1993) argued that forgetting or retrieval failure may be more profound for less biologically important memories than for more biologically important memories. If memory of reinforcement is more retrievable or has a lower threshold for retrieval by the training context than memory of nonreinforcement, spontaneous recovery arises from this difference in access to acquisition and extinction memories.

As yet another account of spontaneous recovery, consider what might happen if an animal cannot represent the times at which reinforced and nonreinforced responding occurred. Immediately after extinction, memory of extinction is more salient than memory of acquisition because the contents of working memory are devoted to extinction events. With the passage of some time, these events in working memory are lost, and a return to the learning context will retrieve memories of both acquisition and extinction (Bolles, 1985). Because these memories were not associated with a point in time, the animal has no memory of their order. It only remembers that on one occasion reinforcement occurred and on another occasion reinforcement did not occur. An ambiguous situation exists, and how an animal responds depends on its behavioral strategy for dealing with this ambiguity. Most commonly, animals show spontaneous recovery by responding at some level below that seen at the end of acquisition. If an animal weighs the two memories of reinforcement and nonreinforcement, it may respond in a way corresponding to a computed probability of reinforcement less than 1. On the other hand, the optimal default foraging strategy in such an ambiguous situation may sometimes be a full strength or complete response. If some external cue arises, such as reinforcement or nonreinforcement of an initial response, the ambiguity is quickly removed, and the animal will behave in the manner dictated by the appropriate memory.

Experiments recently performed by Devenport and colleagues even more dramatically show these effects (Devenport, 1998; Devenport, Hill, Wilson, & Ogden, 1997). In one experiment (Devenport et al., 1997, Experiment 1), rats were allowed to forage in two patches, A and B, each of which consisted of a food cup placed in different areas on a platform. Two groups of rats foraged in Patches A and B during two training phases of the experiment. The two groups were referred to as Group A = B and Group A > B, with equality or inequality referring to the relative amounts of food in Patches A and B in Phases 1 and 2. In Phase 1, rats in Group A = B collected 24 food pellets in Patch A and no food pellets in Patch B. They were then given Phase 2 training, in which no pellets were given in Patch A and 24 pellets were collected in Patch B. For rats in Group A > B, 40 pellets were collected in Patch A and no pellets were found in Patch B in Phase 1. In Phase 2, no pellets were collected in Patch A and 8 pellets were collected in Patch B. Independent subgroups of rats then were given the opportunity to forage in Patches A and B 1 min, or 4, 6, or 24 hr after the end of training Phase 2.

The data shown in Figure 3 are the proportions of rats in testing showing first choice of Patch B. The rats in Group A = B showed complete preference for Patch B 1 min after training but then dropped to equal choice of Patches A and B by 6 and 24 hr. Even more dramatically, the rats in Group A > B also showed strong immediate preference for Patch B but then switched to complete preference for Patch A after 6 and 24 hr. These findings indicate that patch choice was controlled by patch differences in Phase 2 shortly after training. After a few hours, the worth of each patch in both Phases 1 and 2 controlled choice behavior.

Devenport et al. (1997) offered a dynamic averaging theory to account for these findings. The value of a patch is based on an average of an animal's experiences with the patch, each discounted by time since the experience. Thus, very recent experiences will be weighted heavily over earlier ones, but as time goes by, the weights of these experiences will approach parity, and earlier experiences will have as much weight as later experiences. Thus, a rich patch visited earlier will come to be preferred over a lean patch visited later. Although the findings seen in Figure 3 clearly support the dynamic averaging model, they also support the position that rats failed to remember the temporal order of the events experienced in Phases 1 and 2. After a few hours, rats no longer remembered which set of conditions, Phase 1 or Phase 2, was in effect most recently. Rats in Group A > B did remember that Patch A yielded 40 pellets on one occasion and nothing on another occasion, whereas Patch B yielded 8 pellets on one occasion and nothing on another occasion. Given these memories, it is obvious that the best foraging strategy was to visit Patch A before Patch B.

Can Animals Anticipate Future Events?

Michael D'Amato (personal communication, October 1974) some years ago related to me a puzzling observation he made of the cebus monkeys in his laboratory. The monkeys were fed
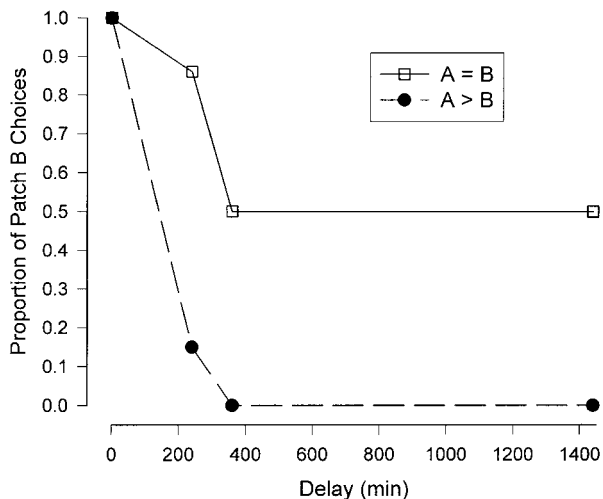

Figure 3. Curves show rats' preference for Patch B in groups A = B and A > B after delays of 1 min or 4, 6, or 24 hr. Adapted from "Tracking and Averaging in Variable Environments: A Transition Rule," by L. Devenport, T. Hill, M. Wilson, and E. Ogden, 1997, *Journal of Experimental Psychology: Animal Behavior Processes, 23,* p. 454. Copyright 1997 by the American Psychological Association. Adapted with permission from the authors.

monkey chow biscuits once a day and hungrily ate the biscuits when they were delivered. The number of biscuits given were sufficiently ample that the monkeys still had some left after eating to satiation. The monkeys then indulged in food-throwing behavior, often hurling pellets out of their cage. The thing that puzzled D'Amato was the illogical nature of this behavior. The monkeys were fed only once a day and developed considerable hunger before each daily feeding. If the monkeys could anticipate that they would be hungry before the next day's feeding, why did they not conserve unwanted biscuits for a later time when they could be eaten? Some problems studied in animal behavior address this question experimentally. I discuss five of these: delayed reinforcement, differential reinforcement of low rates of responding, self-control, temporal myopia, and the time horizon.

Delayed reinforcement. A classic variable in early theories of learning was the delay of reinforcement. In these associative theories, the question was how long a reinforcer could be delayed and still strengthen an association between a stimulus and response. From the standpoint of this article, however, the question may be seen as how long a reinforcer can be delayed and still be viewed as relevant to the preceding behavior. Put another way, How far forward in time can an animal learn to anticipate the consequence of its response? Although some early studies have suggested that reward could be delayed for 30 s or more and still lead to learning (Perin, 1943; Perkins, 1947; Watson, 1917; Wolfe, 1934), these studies were plagued with the confounding effects of secondary reinforcement. That is, cues present at the time a reinforcer was consumed were also present immediately after the target response and thus could have acted as a source of immediate reinforcement.

In a classic experiment performed by Grice (1948), rats discriminated between black and white cues, with different groups trained with varying delays between the choice response and the rewarded or nonrewarded outcome. The possibility of secondary reinforcement from either external visual cues or internal proprioceptive cues was completely controlled. At the 0-s delay, rats learned the discrimination readily. With a 5-s delay of reinforcement, however, it took rats hundreds of trials to learn, and at a 10-s delay, rats failed to learn after more than 1,000 trials of training. The delay of reinforcement gradient appeared to be quite steep.

In more recent experiments, it has been discovered by Lieberman and Thomas and their colleagues that animals can learn a correct discriminative response with as long as 60 s intervening between a choice response and reward. Rats were allowed to choose white or black compartments in a visual discrimination apparatus and were then kept for 60 s in a neutral delay box before being allowed to enter a goal compartment where reward was delivered for choice of the correct visual stimulus. Under these conditions alone, rats showed no evidence of learning over many trials of training. In an alternate procedure, the rat's initial response was marked either by the animal being briefly picked up by the experimenter (Lieberman, McIntosh, & Thomas, 1979) or by the brief presentation of a tone or light (Thomas, Lieberman, McIntosh, & Ronaldson, 1983), which occurred immediately after the response. In this case, rats did learn to choose the rewarded stimulus with a 60-s delay of reinforcement. Why should marking the rat's response lead to long delay-of-reward learning? Although no explanation of the marking effect has been proven yet, one possibility is that a surprising event (handling or a sudden noise or light) produces rehearsal or sustained processing of information in

working memory for the marking event and the behavior that just preceded it (Wagner, Rudy, & Whitlow, 1973). In this case, learning may have been promoted by contiguity between reinforcement and memory of the correct response and not by anticipation of future reward.

Differential reinforcement of low rates of responding. In a differential reinforcement of low rates of responding (DRL) schedule of reinforcement, an animal's response is reinforced only if it is delayed for a fixed time interval since the last response (Reynolds, 1968). Thus, in a DRL 10-s schedule, a subject would be reinforced for responding 10 s or more after the last response, but a response made at any time less than 10 s since the last response would yield no reinforcement and would set the timer back to zero. An animal thus must anticipate the consequences of an early response and inhibit its tendency to respond for at least 10 s. In general, it is difficult to establish a high level of accurate responding on DRL schedules. Pigeons may initially respond frequently and thus get little reinforcement. As responding then begins to extinguish, occasional responses that exceed the time limit are reinforced. These reinforced responses then lead to a higher rate of responding and fewer reinforcements. After considerable training, an animal's rate of responding will be low, but more than half of the responses will still be too early and thus nonreinforced (Richards, Sabol, & Seiden, 1993). Successful responses often are preceded by a chain of other responses, suggesting that delayed response may be learned as a sequence of other behaviors that occupy the interresponse intervals (Mazur, 1998).

Self-control. In self-control experiments with animals, an animal is typically given a choice between two responses, one that will lead to a relatively immediate small reward and one that will lead to a delayed large reward (Logue, 1988; Rachlin & Green, 1972). A common choice is between 2-s access to food (small amount), delayed for 0.1 s, versus 6-s access to food (large amount), delayed for 6 s. The common finding in experiments with rats and pigeons is that they respond impulsively and fail to show self-control by preferring the immediate small reward (Mazur & Logue, 1978; Tobin, Chelonis, & Logue, 1993). Pigeons only demonstrated self-control when training began with long delays for both small and large rewards, and the short delay for the small reward then was faded in gradually over more than 11,000 trials (Mazur & Logue, 1978). When human subjects have been tested in the self-control paradigm, they clearly have shown self-control by choosing the response that leads to the large delayed reward (King & Logue, 1987; Logue, Pena-Correal, Rodriguez, & Kabela, 1986). It is interesting, though, that tests with a cynomolgus monkey also showed strong preference for the larger, more delayed reinforcer (Tobin, Logue, Chelonis, Ackerman, & May, 1996).

Logue et al. (1986) described the self-control behavior of humans as arising "because adult humans, unlike pigeons, are sensitive to events as integrated over whole sessions and tend to maximize total reinforcement over whole sessions" (p. 172). If pigeons and rats have difficulty anticipating the delayed consequences of one response alternative, it is not surprising that they would choose the immediate small reward. Logue (1988) suggested that these animals may have a very small *time window* over which they can integrate events. She further suggested that "if the time window is indeed very short in nonhuman subjects then, functionally, such a subject's choice in a self-control paradigm is between a smaller reinforcer now or no reinforcer at all" (p. 676).

The recent findings of Tobin et al. (1996) with a cynomolgus monkey suggest that a larger time window may have to be extended to nonhuman primates.

Temporal myopia. In experiments with macaque monkeys and a chimpanzee, Silberberg, Widholm, Bresler, Fujita, and Anderson (1998) used the procedure of measuring these animals' preferences between two alternative food arrays. These primates showed clear food preferences, for example, preferring a banana over an apple. When given a choice between one and two bananas, they showed a clear preference for two bananas. When given a choice between a banana and a banana plus an apple, however, they showed indifference, choosing the banana alone as often as the banana plus apple combination. On other choices between 5 bananas and 10 bananas, the monkeys and ape again showed indifference, choosing 5 bananas as often as 10 bananas. Silberberg et al. suggested these effects are based on *selective value* and *temporal myopia.* The choice between a banana and banana plus apple yields indifference because the animals focus on only the most favored food, the banana. When given a choice between 5 and 10 bananas, 5 bananas is sufficient to satiate the current hunger for bananas. In both cases, the animal fails to realize that an apple or 5 extra bananas could be eaten later when the single banana has been consumed or when the satiation produced by eating 5 bananas is replaced by hunger for more bananas. Both the monkeys and the chimpanzee were temporally myopic in the sense that they did not anticipate that the extra food could be consumed at a later time. The concept of temporal myopia also nicely accounts for the M. R. D'Amato (personal communication, October 1974) observations previously described.

The time horizon. The time horizon refers to a time limit over which an animal is able to anticipate a future event. Some experiments have been designed in such a way that an animal should behave differently at a certain moment if it can anticipate a future event from the way it should behave if it cannot anticipate a future event. Flaherty and Checke (1982) allowed rats to drink from a tube that yielded 0.15% saccharin for 3 min. Different groups of rats were then allowed to consume a 32% sucrose solution (a preferred solution) either 1, 5, or 30 min later. A control group was allowed to consume only saccharin, with no subsequent solution offered. These cycles of events were repeated in each group over 11 days of testing. The question of interest is whether the animals' consumption of saccharin would be modified by the subsequent availability of sucrose. Would animals learn to avoid the less preferred saccharin because the more preferred sucrose would appear in the near future? By the final days of testing, animals in all three sucrose groups drank significantly less saccharin than the control group. The amount of saccharin drunk decreased as the interval between saccharin and sucrose decreased from 30 min to 1 min. These findings suggest that rats could anticipate a future reward as long as 30 min into the future and that the strength of the anticipation weakened the longer the time interval.

Timberlake and colleagues have pointed out that theories of optimal foraging often assume that a forager can anticipate the availability of food at considerable time into the future (G. A. Lucas, Timberlake, Gawley, & Drew, 1990; Timberlake, 1984; Timberlake, Gawley, & Lucas, 1987, 1988). For example, the well-known marginal value theorem (Charnov, 1976) suggests that a forager should only forage in a patch until its intake of resources falls below the average of resources in other patches throughout

the habitat. To apply this principle, an animal would have to be able to anticipate the availability of food in other patches, many of which might take some time to reach after giving up searching in the current patch.

As a test for time horizons in the rat, Timberlake (1984) and his colleagues (Timberlake et al., 1987, 1988) set up an experimental situation in which a rat was allowed to forage for food in either of two patches, each of which consisted of a bar placed in a different location within an apparatus. At the beginning of a session, only one bar yielded food reward when pressed, and it did so on a progressive ratio (PR) schedule that increased the number of presses required to earn a reward by one each time a reward was obtained. The PR schedule was designed to simulate foraging in a patch with limited resources that requires progressively more work to find food as the patch is depleted. The alternate bar yielded reward on a consistent reinforcement schedule (CRF) that paid off each time it was pressed. Presses on the CRF bar were rewarded, however, only after some period of time had elapsed since the beginning of the session. An optimal forager then should maximize its food intake for energy expended by refraining from pressing on the increasingly expensive PR bar and waiting for the low-cost CRF bar to become operative. Invoking this strategy, of course, requires the animal to anticipate the future availability of food in the CRF patch.

Timberlake et al. (1987) carried out an experiment in which the CRF bar began to pay off either 4, 8, 16, 32, 64, or 120 min after the session began. The 120-min delay was used as a control or reference delay with which the other delays were compared. The extent to which rats were influenced by these delays was measured by the number of food pellets they earned in the PR patch; if they anticipated low-cost food in the CRF patch, little food should be worked for in the PR patch. Figure 4 shows the pellets earned in the PR patch at different delays up to 64 min, compared with those consumed over comparable time periods during the 120-min delay.
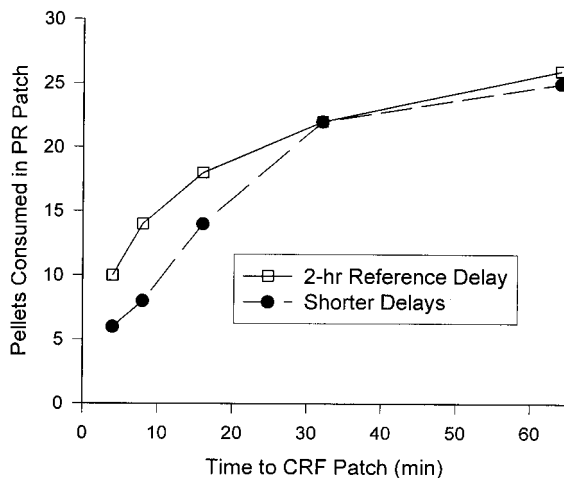

Figure 4. Pellets consumed by rats in the progressive ratio (PR) patch as a function of the delay to access to the continuous reinforcement (CRF) patch. Adapted from "Time Horizons in Rats Foraging for Food in Temporally Separated Patches," by W. Timberlake, D. J. Gawley, and G. A. Lucas, 1987, *Journal of Experimental Psychology: Animal Behavior Processes, 13,* p. 305. Copyright 1987 by the American Psychological Association. Adapted with permission from the authors.

Notice that the intake of pellets was suppressed somewhat at 4, 8, and 16 min but not at 32 or 64 min. However, the degree of suppression was relatively small; even at the shortest 4-min delay, rats worked at a rate that was seven times higher than the price necessary for reward in the CRF patch. Timberlake et al. concluded that "the laboratory data most strongly support the view that animals have a rather short time period over which they behave effectively with respect to temporally separated feeding alternatives" (p. 307). The fact that animal foraging behavior often does approach a computed optimum (W. A. Roberts, 1991; W. A. Roberts & Ilersich, 1989) may result from the use of fairly simple "rules of thumb" applied to the current situation rather than from the computation of future reward.

Challenges to the Hypothesis That Animals Are Stuck in Time

Do Apes Plan for the Future?

Examples of apes apparently carrying out acts that anticipate future consequences can be found in the primate literature (Beck, 1980). Lawick-Goodall (1971) observed chimpanzees in the Gombe Reserve preparing sticks by stripping them of their leaves to use as a tool for termite fishing in holes. Boesch and Boesch (1984) described chimpanzees carrying stones over long distances to be used as tools for cracking nuts found in an area where no stones were available. The bonobo, Kanzi, learned the locations of numerous foods in a wooded area. He would then select the picture of a particular food and lead a naive human companion to the location of that food (Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986).

Although each of these examples suggests that apes can anticipate a future event, their ability to do so may be limited. In each case, the goal prepared for may correspond to the current motivational state of the animal. Suddendorf and Corballis (1997) advanced the Bischof-Kohler hypothesis, based on the common ideas of Wolfgang Kohler (1925), Norbert Bischof (1978, 1985), and Doris Bischof-Kohler (1985). According to this hypothesis, "animals other than humans cannot anticipate future needs or drive states and are therefore bound to a present that is defined by their current motivational state" (Suddendorf & Corballis, 1997, p. 150). Thus, the preparation of a tool to catch termites or crack nuts may be largely bound up in the act of consuming that motivational object only a short time into the future. Would an animal that is not hungry prepare its tools for food it will seek tomorrow? There appears to be little evidence for such behavior in either captive or wild animals. As the monkey report from M. R. D'Amato's lab (personal communication, October 1974) and the data on temporal myopia (Silberberg et al., 1998) suggest, animals appear little interested in performing acts that will provide for a future need not currently experienced.

Ape language studies might be a fertile ground for testing the stuck-in-time hypothesis. In impressive studies carried out with Kanzi, Savage-Rumbaugh et al. (1993) showed that this bonobo could respond accurately to a number of imperative sentences. Kanzi was given such novel instructions as "take the ball to the bedroom" and "put the doggie on the vacuum" and accurately carried out most of these propositional commands. Although these findings may demonstrate some degree of language comprehension, they all involve responses to objects in the immediate

present. Could Kanzi learn to respond accurately to the instruction "get jello out of the refrigerater tommorow at lunch time" or the instruction "do the same thing you did yesterday at this time"? Notice that these requests involve an understanding of the words *tomorrow* and *yesterday* and thus would require Kanzi to travel backward mentally in time or to encode an instruction for behavior to be carried out in the future. The discovery that Kanzi could carry out such instructions would provide a convincing refutation of the stuck-in-time hypothesis, at least in a bonobo.

Hoarding

One well-known type of behavior that immediately springs to mind as evidence that animals plan for the future is hoarding. Many rodents bury nuts or seeds and later retrieve them. Recent prominent work with food-hoarding birds has shown that they bury food items or hide them in openings in trees and use memory to retrieve these food items many hours later (Kamil & Balda, 1983, 1990; Sherry, 1987; Shettleworth, 1983). Although hoarding and recovery behavior suggest that animals are planning for future need, an alternative explanation is possible. Hoarding may be driven not by an intent to provide for the future but rather by genetically programmed, species-specific behavioral tendencies. A distinction between functional or evolutionary causes of behavior versus proximal mechanisms is important here. An animal that hoarded food with the intention of recovering it for later consumption would be using a proximal cognitive mechanism. The evolutionary explanation suggests that animals with acquired genes that control a tendency to hoard and recover food have a survival advantage, causing their genes and this behavior to spread throughout their species and descendant species. The functional explanation suggests that animals hoard food with no awareness of why they do it.

How can these two explanations of hoarding be tested? One possibility is to observe the effects of pilfering on hoarding behavior. Suppose that an animal is allowed repeatedly to hoard food items. After each bout of hoarding, an experimenter removes all of the food items from their hiding places. The animal then returns to recover its food and finds it has all been taken. If an animal hoards with the intention of recovering the food later, it should learn that hoarding is futile, and hoarding behavior should extinguish or decline. On the other hand, if hoarding is driven by species-specific behavior tendencies that involve no anticipation of the future, hoarding should be little affected by pilfering.

Hampton and Sherry (1994) allowed black-capped chickadees to cache seeds in holes in laboratory trees. Red and blue bands marked different holes. After birds had cached seeds, the experimenters pilfered seeds on one side of the aviary and in holes marked by one color. Over 24 caching and retrieval sessions, birds decreased caching on the side of the aviary where seeds were pilfered but did not decrease caching in holes where seeds were pilfered according to color. It appeared then that chickadees had learned to avoid caching in locations that were consistently pilfered. Hampton and Sherry pointed out that although this finding could be explained by an association between caching at a location and the subsequent discovery of no food at that location, it could also be that birds had learned to develop cache-site criteria based on the frequency with which food was found at different locations.

J. R. Lucas and Zielinski (1998) kept Carolina chickadees in an aviary where they could hoard seeds found in a feeder in holes

made in plastic trees. Under a pilferage condition, seeds hoarded were removed from the trees by the experimenters, whereas under a nonpilferage condition, chickadees were allowed to retrieve hoarded seeds. Contrary to the predictions of the researchers, birds in the pilfered condition actually continued to cache seeds at a higher rate than birds in the nonpilfered condition.

Clayton and Dickinson (1999) carried out an experiment in which scrub jays were allowed to hoard two kinds of food, nuts and wax worms, in different locations. The birds were allowed to recover these food items 124 hr later. Although the nut caches were not changed, the worm caches varied between three groups. The worms were either degraded by placing decayed worms in cache locations, replenished by placing fresh worms in cache locations, or pilfered leaving no worms in cache locations. Figure 5 shows the number of items cached over four successive trials. The worm curves show that there was no decline in the rate of caching worms, regardless of whether worms were degraded, replenished, or pilfered. Scrub jays showed an increase in hoarding worms when caches were degraded, and Clayton, Yu, and Dickinson (2001) reported a similar finding that birds who find degraded worms hoard more worms on subsequent hoarding opportunities than birds who have their caches replenished.

The argument made here that animals should discontinue hoarding when food is repeatedly pilfered is based on the common
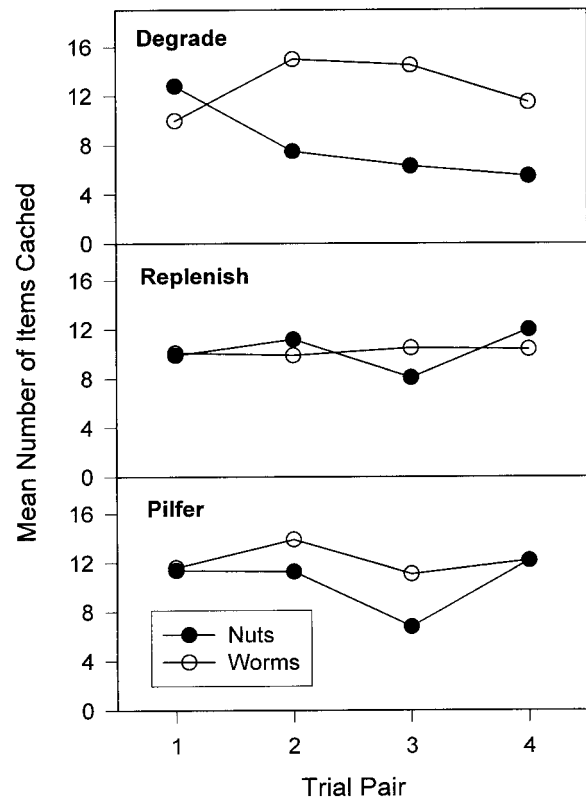

Figure 5. Number of worms and nuts cached by scrub jays over successive trials on which the worm caches were degraded, replenished, or pilfered. Adapted from "Scrub Jays (*Aphelocoma coerulescens*) Remember the Relative Time of Caching as Well as the Location and Content of Their Caches," by N. S. Clayton and A. Dickinson, 1999, *Journal of Comparative Psychology, 113,* p. 406. Copyright 1999 by the American Psychological Association. Adapted with permission from the authors.

laboratory observation that animals extinguish responses that are no longer rewarded. Thus, if food is intentionally hoarded with the anticipation of future retrieval, the failure to find hoarded food on repeated bouts of hoarding and pilfering should lead to extinction of hoarding behavior. Contrary to this argument, Clayton et al. (2001) argued that increased hoarding may represent a response to the challenge of finding decayed or pilfered caches. Such an account might also explain the increased hoarding found in chickadees by J. R. Lucas and Zielinski (1998) when food was pilfered. The Clayton et al. argument therefore preserves the idea that animals hoard with the anticipation of retrieving food at a later point in time, but it requires the assumption that different learning rules operate in hoarding and retrieval behavior than operate in standard operant learning situations in which extinction is typically seen. Future research directed at this question will be of considerable interest.

The Clayton and Dickinson Experiments

The primary purpose of Clayton and Dickinson's (1998, 1999) experiments was to examine scrub jays' memory for foods that did and did not perish over a retention interval. After several training trials on which birds learned that worms but not nuts decayed over a 124-hr retention interval, birds were given a choice between locations where they had hoarded worms and locations where they had hoarded nuts. Figure 6 shows the number of searches directed toward nut and worm locations when retention tests were given at 4 and 124 hr. When worms were degraded, birds preferred worms (their favored food) over nuts at 4 hr but strongly preferred nuts over worms at 124 hr.

Clayton et al. (2001) have recently extended these observations to memory for two perishable food types, meal worms and crickets (Experiment 1). On some trials, scrub jays cached meal worms in sites on one side of a caching tray and peanuts in sites on the other side of the tray. On other trials, crickets and peanuts were cached in different locations. Birds were allowed to recover foods at intervals of 4, 28, or 100 hr after caching. After 4 hr, both fresh meal worms and crickets were found at the caching locations. After 28 hr, however, meal worm sites contained decayed worms, but cricket sites contained fresh crickets. After 100 hr, decayed worms and crickets were found at both caching sites. When scrub jays were tested with unbaited sites to control for odor cues 4 hr after caching, they preferentially searched at locations where worms and crickets had been cached over locations where peanuts had been cached. After 28 hr, they preferred cricket locations over peanut locations but preferred peanut locations over worm locations. When the retention interval was 100 hr, jays preferred to visit peanut locations over both worm and cricket locations. In Experiment 4, birds cached meal worms and peanuts at different sites on one tray on one day and 24 hr later cached other meal worms and peanuts in different locations on a second visually distinguishable tray. When given recovery tests with both trays 4 hr later, the birds searched in the peanut locations on the tray they had cached food on the previous day (28 hr ago) but searched in worm locations on the tray they had cached on only 4 hr ago.

On the basis of these experiments, Clayton et al. (2001) argued that scrub jays remember both the types of food available and where they have hidden each type as long as 5 days earlier. Most important for the issues raised in this article, they argued that scrub jays remember when they have hoarded each type of food. Thus,
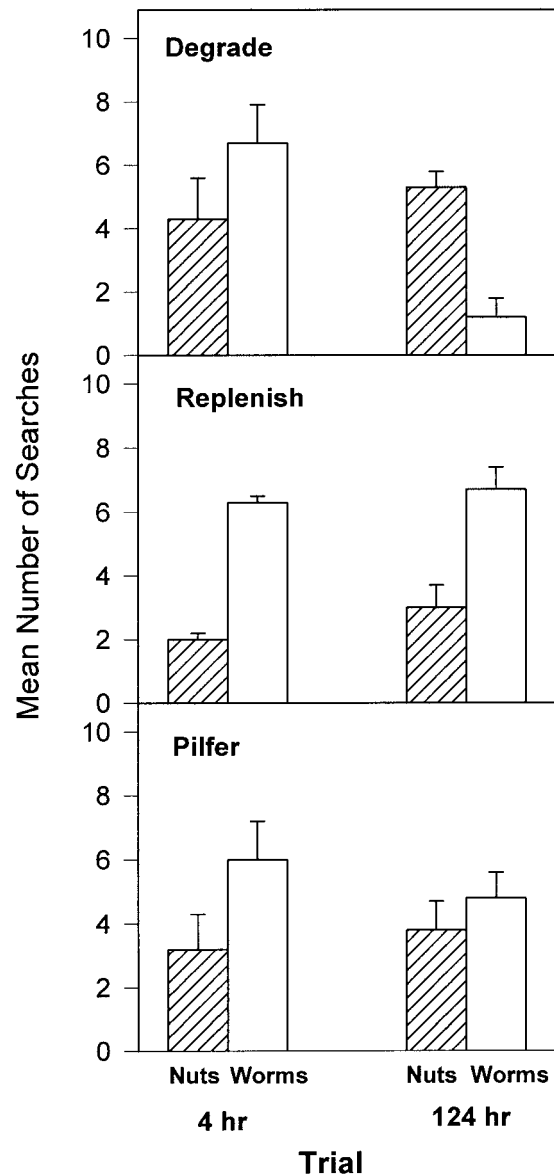

Figure 6. Number of searches made in nuts and worms areas after 4- or 124-hr delays since caching by groups of scrub jays that had been trained with worms degraded, replenished, or pilfered after 124 hr. Adapted from "Scrub Jays (*Aphelocoma coerulescens*) Remember the Relative Time of Caching as Well as the Location and Content of Their Caches," by N. S. Clayton and A. Dickinson, 1999, *Journal of Comparative Psychology, 113,* p. 408. Copyright 1999 by the American Psychological Association. Adapted with permission from the authors.

jays searched for worms after 4 hr because they had learned that worms were still good after that length of time, but they avoided worms after 124 hr because they remembered caching worms that long ago and knew that the worms decayed over that longer period. They concluded that these results show an "episodic-like memory" in scrub jays (Clayton et al., 2001; Griffiths, Dickinson, & Clayton, 1999).

These carefully planned and controlled experiments provide perhaps the best available evidence for a sense of time and episodic memory in animals. If scrub jays can remember when they

cached food, as well as what type of food and where, it would suggest that they can recollect the times of occurrence of past experiences. In their discussion of this question, Clayton, Dickinson, and colleagues alternatively describe scrub jays as remembering "when" a food was cached and "how long ago it was since they stored the item" (Griffiths et al., 1999, p. 79) or "the time that has elapsed since caching" (Clayton et al., 2001, p. 18). These types of memory for time are different. Memory for *when* implies a temporal structure for past time within which events can be located, but memory for *how long ago* could be based only on elapsed time or temporal distance since an event (Friedman, 1993). Just as Friedman et al. (1995) found that young children with no memory or understanding of dates could indicate whether their birthday or Christmas was most recent, scrub jays might be using some correlate of elapsed time to discriminate recent from more distant bouts of food caching. The state of a decaying memory trace would seem to be a possibility. Scrub jays might have learned that a weaker memory trace of meal worm locations meant decayed worms and that a stronger memory trace of meal worms meant nondecayed worms.

Recall that in the discussion of experiments on working memory for stimulus order, memory strength was used as an explanatory mechanism. For example, the findings of MacDonald (1993) were nicely explained by variations in trace strength because relative recency judgments by pigeons could be biased in predicted directions by varying the length of time the first or second sample stimulus was presented and, presumably, its trace strength. Another possiblity is that scrub jays keep track of the number of diurnal cycles that pass between caching and recovery of food. Thus, birds in the Clayton et al. (2001) study might have learned that worms do not decay in the absence of a diurnal cycle but decay after four diurnal cycles. In addition, they might have learned that crickets do not decay over one diurnal cycle but do decay over four diurnal cycles. If scrub jays used one of these mechanisms to keep track of elapsed time or distance from a bout of hoarding a particular food, then time-dependent food searching is not in disagreement with the hypothesis that animals do not cognitively time travel because birds would not be remembering a point within a time scale. On the other hand, if birds do remember a specific location in time when a particular food was hoarded, it would indicate both a sense of time and episodic memory. Experiments that explore these alternatives would seem to be of major importance.

Conclusions

Research from several different areas has been reviewed to explore the extent to which animals have a sense of time that extends from the present into the past and into the future. The evidence reviewed is somewhat mixed. The bulk of it suggests that animals have a very limited sense of past and future time. Thus, experiments on working or short-term memory for the order of two or three events were successful but could largely be explained by the use of trace strength as a discriminative stimulus. Pigeons could peck up to five stimuli in the correct order, but only after a vast amount of specialized training, and tests with nonadjacent pairs of stimuli from the list indicated that pigeons did not have a temporally ordered representation of the the entire list. Research on spontaneous recovery and related phenomena suggest that rats forget the order of reinforced and nonreinforced behaviors within

a few hours. When animals' ability to anticipate future rewards was tested, self-control experiments with birds and rats indicated that they typically responded as if a delayed consequence did not exist. Time horizon experiments with rats indicated that at best they could anticipate a larger reward only 15–30 min into the future. Although some observations of nonhuman primates suggest they make preparations that will allow them to obtain a currently desired reward in the immediate future, research on temporal myopia with monkeys and a chimpanzee suggests that they do not anticipate future needs that are different from those currently experienced.

On the other hand, some evidence presented here does hint at the possibility that some animals have shown evidence of a sense of time. The cebus monkeys studied by D'Amato and Colombo (1988, 1989) learned to correctly respond to stimuli in serial order and showed evidence that they had a representation of the entire list. Whether the list was remembered as a time-based sequence was unclear, however, because monkeys could have used a spatial code. In another example, Tobin et al. (1996) found self-control in cynomolgus monkeys, suggesting that these primates could learn about a delayed consequence. These two examples suggest that perhaps researchers should look for evidence of time travel and episodic memory in nonhuman primates. This suggestion may be belied, however, by the recent discoveries of Clayton and Dickinson (1998, 1999) and Clayton et al. (2001). On the basis of their experiments, they argued for memory in scrub jays of when a particular food was hoarded. The exciting possibility raised by their experiments is that scrub jays remember when they hoarded food not just for a few minutes but for as long as 5 days. The issue raised here of whether scrub jays are remembering when or how long ago food was cached appears to be critical for the question of episodic memory in animals and should be pursued experimentally.

What are the implications of this review for comparative psychology? Macphail (1982, 1987) has argued that aside from language, there are no fundamental cognitive differences between humans and animals. If animals are largely stuck in the present moment, a profound difference would seem to exist between people and animals. Animals may be aware of only a permanent present, whereas people readily see the world from numerous time perspectives. Not only can humans travel backward and forward in time mentally from the present moment, but they can also contemplate what their cognitions about past and present were or will be at different times in the past or future. This temporal flexibility of cognition is vastly different from that of a creature that has no sense of time. If future research finds better evidence for a sense of time in animals, however, Macphail's position may be supported by evidence that the difference between people and animals is only quantitative and not qualitative. In that case, it might be concluded that animals time travel cognitively over shorter times than people.

Finally, one can consider what the basis of cognitive time travel might be. It might simply be argued that human brains have evolved cognitive time displacement and that animal brains have not. That answer may be too simple; both evolutionary and cultural factors should be considered (Tomasello, 2000). An evolved ability to cognitively manipulate memories of events and symbols may have led early *Homo sapiens* to develop a sense of time by noticing and labeling the cyclical nature of natural phenomena. Eventually, these cycles were measured by time technology devices such as

calendars and clocks. With the advent of time-tracking technology, people may have become increasingly aware of and sensitive to the passage of time and the use of time to date events in their lives. Thus, time dating, episodic memory, and planning into the future may have arisen culturally with the development of time technology. An interesting question then arises: Could a cognitively advanced animal be taught a sense of time? If a chimpanzee or bonobo was raised in the presence of calendars and clocks that continually marked when important events in its life had occurred or will occur, might it learn to use these devices to keep track of time? If it could learn this, would it then use time indicators to time date its memories and to anticipate future occurrences? A cultural theory of cognitive time travel suggests that it might be possible to free an ape from the cognitive present and to allow it to learn to time travel as people do.

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