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Animals Represent the Past and the Future

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Abstract: It has been proposed by some that only humans have the ability to mentally travel back in time (i.e., have episodic memory) and forward in time (i.e., have the ability to simulate the future). However, there is evidence from a variety of nonhuman animals (e.g., primates, dolphins, scrub jays, rats, and pigeons) that they have some ability to recover personal memories of what-where-when an event occurred (an earlier requirement of the ability to recover an episodic memory) and answer unexpected questions (another requirement to distinguish between semantic and episodic memory). Also, perhaps more critically, according to Tulving's more recent definition of mental time-travel, several animals (primates and scrub jays) have been shown to be able to pass the *spoon test*. That is, they are able to plan for the future. Thus, although humans show an advanced ability to mentally travel backward and forward in time, there is growing evidence that nonhuman animals have some of this capacity as well.

Keywords: Episodic memory, auto-noetic memory, future planning, what-where-when, unanswered question

Introduction

Historically, research on human memory dealt with the distinction between *reference memory*, once called long-term memory, and *working memory*, once called short-term memory. Although the distinction is not always easy to make, reference memory generally refers to memories to which one is no longer attending. More recently, a distinction has been made between two kinds of reference memory. Memory for well practiced motor skills (e.g., riding a bicycle) have been referred to as *procedural memory*, whereas memory for facts, rules, and events have been referred to as *declarative memory*. A further distinction has been made between two forms of declarative memory. The first is *semantic memory*, which deals with general knowledge of one's environment such as facts and rules. The second is *episodic memory*, which deals with memory for personal events or for specific episodes in one's life. The term "semantic memory" was chosen because of its relation to knowledge or meaning, but it typically refers to language, and when considering

animal memory it is unfortunate because animals typically do not have what we think of as language. Thus, when discussing the memory of nonhuman animals, the concept of memory for knowledge or rules would be preferable.

Distinctions that appear to be relatively simple when applied to human memory are more difficult to make when referring to memory in animals. It is quite obvious that many animals have both working memory and reference memory. Procedural memory is certainly present in animals, as well. In humans, declarative memory is typically assessed by means of some form of language response (either verbal or written). However, a reasonable case can be made for the claim that animals too have some form of declarative memory. Perhaps the best examples come from transfer of training experiments, in which emergent stimulus relations are found (see Roberts, 1998). Although many examples can be cited, perhaps the easiest to describe comes from evidence that animals can form cognitive maps. For example, rats that have learned a particular path to obtain food are able to take a novel path when the acquired path to food is blocked (e.g., Singer, Abroms, and Zentall, 2007). The choice of a novel path that leads to food requires more than a well-practiced motor response. It requires what sometimes has been called a *cognitive map*, or the more general knowledge of where objects are in space.

Human Episodic Memory and Future Planning

Whether animals are capable of episodic memory has been more controversial. Furthermore, because episodic memory generally depends on self report, it would be difficult to demonstrate that animals have such memory in the absence of language. Tulving (1985) has suggested one can distinguish among three kinds of reference memory in humans: *anoetic* consciousness involving implicit memory that does not require awareness, *noetic* consciousness involving explicit memory that requires awareness, and *autonoetic* consciousness involving a form of explicit memory that requires self-awareness. Tulving proposes that anoetic consciousness is all one needs for procedural memory, whereas noetic consciousness is needed for semantic memory. According to Tulving, autonoetic consciousness is needed for episodic memory and only humans have this capacity.

Suddendorf, Addis, and Corballis (2009) proposed that episodic memory evolved specifically to enhance fitness by enabling action in preparation of different possible scenarios and that language may have evolved for the sharing of past and planned future events. Suddendorf and Corballis (1997) expanded on Tulving's view of episodic memory. For them, the capacity for episodic memory requires that one has several phenomenological abilities, including a sense of subjective time, a sense of self or self knowledge that can be dissociated from a concept of self in the present, the capacity to retrieve a representation from memory, and the ability to attribute an event to an earlier or future self (see also Suddendorf and Corballis, 2010).

Evidence of memory for personal experiences would not be easy to obtain in animals. In fact, it is even difficult to obtain in humans who have proficient language with which to respond. However, a different approach would be to ask what it would mean if animals did not have any form of episodic memory. If one trained a rat to press a lever one

day and then placed the rat in the operant box the next day, one might wonder if semantic or rule-based memory would be sufficient to allow the rat to remember what to do. The rat would not have to remember the specific episode of having pressed the lever for food. All it would have to remember is the fact or rule that pressing the lever should lead to the delivery of food. That is, the rat doesn't need to *remember* what it did; it can just *know* that pressing the lever will produce food. In fact, a good working definition of the distinction between semantic memory and episodic memory is the difference between knowing and remembering. For those who hold that animals do not have episodic memory, past experience allows them to *know* what to do but it does not allow them to *remember* that they did it. And for most purposes, knowing works as well as remembering. If so, what is the advantage of episodic memory, of being able to remember?

Fortunately, we can answer this question through several patients who have had damage to their hippocampus that resulted in the loss of episodic memory. The case of K.C. provides a good example (Hayman, Macdonald, and Tulving, 1993). K.C. appears to be normal in many ways. He has knowledge of the subject matter that he learned in school. He knows how to play the organ and various card games. He also knows a lot of things about himself that he has learned. Also, his working memory is intact such that he can remember very recent events. But he cannot remember anything that happened to him in the past. Thus, although he knows how to play cards, he does not remember ever having played cards. According to Tulving (2005), K.C. is not only conscious but he is self-reflectively conscious; however, he does not have normal self-awareness. That is, he is not autoethically conscious. The deficits that K.C. suffers are subtle but quite clear upon examination. He might recognize who someone is, but he would not remember ever having seen them before. It is also interesting, and of some theoretical importance, to note that K.C. is equally impaired in his ability to think about his personal future, as he is in his personal past, suggesting that past and future mental time travel are likely to involve a single neurocognitive capacity (Tulving, 2005).

Two conclusions can be drawn from people with this kind of brain damage. First, it is possible for a human to maintain a relatively normal existence without an episodic memory. Second, the idea that animals may not have episodic memory but may still be able to learn and know what they had learned does not seem unreasonable. That is, episodic memory does not appear to be necessary for the normal survival of animals. In fact, not only do animals not need to have episodic memory, but even in humans it has been argued that autoethic consciousness may be a relatively recent acquisition (perhaps as recently as 3000 years ago; Jaynes, 1976). However, the evidence for the relatively recent development of episodic memory is based largely on indirect evidence, namely an informal analysis of the writings of earlier times.

Less controversial is the hypothesis that humans are not born with episodic memory. However, because young children are considerably less verbal than adults, it should be acknowledged that assessing episodic memory in young children encounters many of the same problems that one has in assessing episodic memory in nonhuman animals; nevertheless, suggestive evidence comes from several sources. For example, to have episodic memory one must have a concept of time (McCormack and Atance, 2011), and children below the age of 4 years do not appear to have a useful concept of time

(Friedman, 1991). Also, they do not appear to remember or understand the sources of factual beliefs they hold (Gopnik and Graf, 1988). Furthermore, although a bit less direct, based on the assumption that the ability to recall pictures requires episodic memory, whereas the ability to recognize words does not, there is evidence that in children 3–6 years old, the ability to recall pictures is directly correlated with their ability to understand the origin of their own memories, whereas the correlation was not found when recall of memory was cued with words (Perner and Ruffman, 1995).

Interestingly, the absence of episodic memory may account for infantile amnesia, the inability of most people to recall early, preverbal memories (Richmond and Nelson, 2007). According to Nelson and Fivush (2004), episodic memory develops gradually in children and is correlated with the emergence of basic memory abilities, language and narrative, memory of adults talking about past and future events, understanding the concept of time, and having a concept of self and others (see also Atance and Jackson, 2009).

Given that human adults do not appear to be greatly impaired without episodic memory and nonhuman animals may not have it at all, one might ask what the function of episodic memory is. At an intuitive level, one might imagine that episodic memory could provide confirmation of knowledge obtained about the environment. For example, it may be quite adequate to know that food can be obtained from a particular location, but it might have additional value to remember that “I found food there yesterday.” Although this view of the value of episodic memory may seem reasonable, it is not very convincing. A more convincing proposal has been suggested by Suddendorf and Corballis (1997; see also Tulving, 2005) and is hinted at by the fact that K.C. is not able to think about his future. The function of episodic memory may be not so much in being able to mentally travel back in time but to mentally travel forward in time. That is, the importance of episodic memory may be that it can be used to simulate the future.

The value of being able to mentally travel forward in time cannot be overestimated. Being able to simulate the future allows one to plan for conditions that are not currently present. Although a nonhuman animal may be able to store food for the winter because it is genetically programmed to do so, it is not likely that the animal understands why it is doing so. On the other hand, a human has the capacity to simulate the future and understand that although it is not hungry now, it will be hungry in the future and it would be a good idea to store food for later use. According to Tulving (2005), the ability to simulate the future allows for the development of culture, and the development of culture allows humans to modify their environment “to create a world to fit them, rather than live in a world into which they had to fit” (p. 22).

Consider how the ability to plan for the future has allowed humans to leave the relatively constant climate of the equatorial zone of central Africa to the more seasonal zones of Europe and Asia. At a time of year when most plants died or went dormant and many animals either migrated away or hibernated for the winter, humans learned to build shelters, store food, and make fire. This ability to plan for the future, together with the ability to communicate (verbally and by imitation), has had what Tomasello (1999) refers to as a ratcheting effect - the ability to develop social culture (Laland and Galef, 2009) based on individual trial and error advances in survival.

At this point, it should not be surprising to learn that the ability of humans to

imagine events that have occurred in the past (episodic memory) and plan for events in the future has been viewed by some as uniquely human (Suddendorf and Corballis, 1997; Tulving, 2005). But it is also the case that the evidence we accept from humans is often much less rigorous than what we require of other animals. For example, if I ask someone about a personal experience I will usually accept the description that they give as evidence of episodic memory. Take the question, “what did you have for breakfast this morning?” If the answer is “toast and coffee,” how do I know the report to be accurate? And even if it is accurate, how do I know that it is sufficient evidence for episodic memory? Although the answer may have been the result of traveling back in time to recover the breakfast memory, it also may be that toast and coffee is what the person always has for breakfast and the response was actually based on semantic memory – knowing what one generally has for breakfast rather than remembering. Thus, even in humans it is not always easy to confirm that a particular memory is episodic rather than semantic.

Episodic Memory in Animals

In an early paper on episodic memory, Tulving (1972) suggested that a person who has episodic memory should be able to recover the *what*, *where* and *when* of a personal event. This definition focuses on the contents of an episodic memory and ignores the, perhaps more important, experience of the memory. For this reason, Tulving (1985, 2005) later expanded on the evidence needed to demonstrate episodic memory to include the *subjective experience* of mentally traveling back in time to recover the memory. However, animal researchers focused primarily on the earlier definition of episodic memory that assessed the content of memory because that definition was more tractable in dealing with nonverbal organisms. One can see the critical elements of the early definition in being able to answer the question, “What did you have for breakfast this morning?” To answer the question, presumably, one must travel back the appropriate amount of time (*when*) to recover the appropriate memory (*what*) and one generally does so by recalling the context in which the event took place (*where*). Of course the most critical element of this mental time travel is time because *what* and *where* can be thought of as an integral part of any acquisition of knowledge or rule (learning). That is, animals routinely learn about the meaning of stimuli (*what*) in a particular context (*where*). Although what-where-when has provided a reasonable working definition of episodic memory, it is clearly insufficient. For example, I *know* that the Declaration of Independence (*what*) was approved in Philadelphia (*where*) on July 4, 1776 (*when*) but clearly, I do not *remember* that event. Furthermore, at a personal level, what-where-when is not necessary for one to have an episodic memory. For example, I vividly remember a conversation that I had with a colleague at a conference (*what*) and I may even be able to remember the context in which it took place (in a coffee shop; *where*), yet I may not remember which conference it was and thus, I may have no idea of when the conversation took place. Thus, because what-where-when may be neither sufficient nor necessary as evidence of episodic memory, most of the research on episodic memory in nonhuman animals has been referred to as *episodic-like memory*.

In animals, it is relatively easy to demonstrate memory for what and where but memory for when an event took place appears to be relatively difficult to demonstrate (e.g.,

Bird, Roberts, Abroms, Kit, and Crupi, 2003; Roberts and Roberts, 2002). And even if one can show that an animal has the ability to respond based on a temporal discrimination, it has been argued that one must distinguish between *how long ago* an event occurred and *when* (e.g., the date or hour) the event occurred. How long ago an event occurred presumably can be judged based on the *strength* of the memory trace (e.g., see Staddon, Higa, and Chelaru, 1999), which does not require episodic memory, as compared with remembering when the event occurred which, presumably, does.

What-where-when experiments with animals

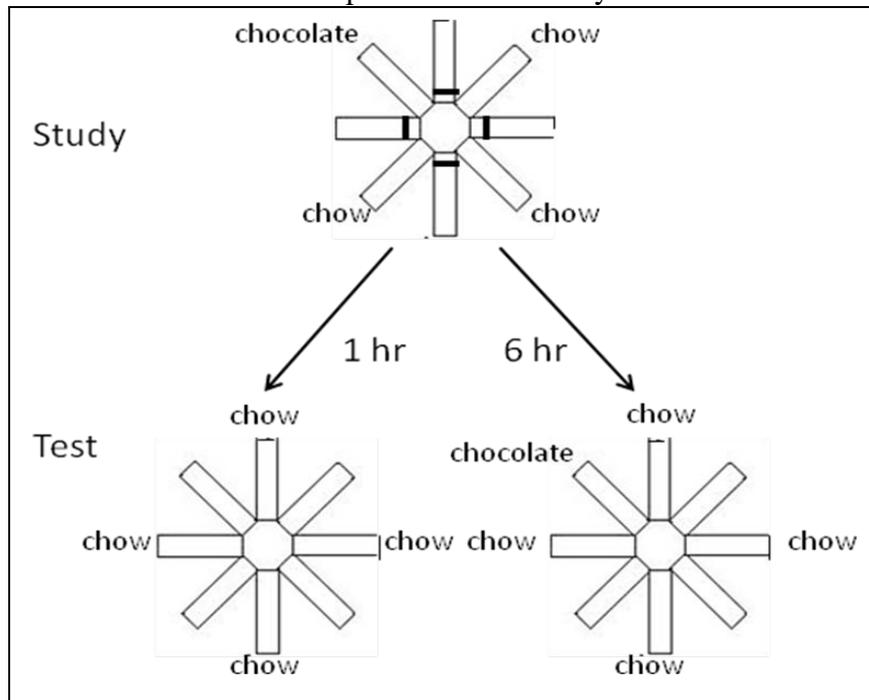
Perhaps the most extensive research into the ability of animals to remember what-where-when has been carried out by Clayton and her colleagues (e.g., Clayton and Dickinson, 1998, 1999; Clayton, Yu, and Dickinson, 2003). This research takes advantage of natural caching behavior of certain birds and their remarkable memory for the location of their caches. The basic procedure is to provide caching birds, such as scrub jays, with two kinds of food: one that is preferred but perishes with time (worms), and another that is less preferred but does not perish with time (peanuts). The birds are allowed to access both kinds of food and to cache them in distinctive locations. After several training trials, the birds learn that worms, but not nuts, decay over a 124-hour retention interval. On test trials, the birds are given a choice between locations where they had cached worms and where they had cached nuts (the food had been removed to avoid possible cuing at the time of choice). If only 4 hours had passed after caching, the birds preferred to search in the locations where they had cached the worms. However, if 124 hours had passed after caching, the birds preferred to search in the locations where they had cached the peanuts. Similar results have been found with other bird species (Feeney, Roberts, and Sherry, 2009; Zinkivskay, Nazir, and Smulders, 2009).

Interestingly, these birds remembered not only the what-where-when of their past experience but they also showed sensitivity to the social aspects of their experience. If another bird had been present when the target bird cached, the caching bird would often re-cache the food when the other bird was no longer present (Dally, Emery, and Clayton, 2006). But re-caching occurred only for birds that had had experience pilfering the caches of other birds. The implication is “it takes a thief to know a thief.”

Related experiments have been conducted with rats by Babb and Crystal (2005, 2006). This research took advantage of the rats’ excellent memory for spatial location. On a study trial, rats obtained food from four arms of an eight-arm radial maze (three arms had standard chow, one had preferred chocolate). The other four arms were blocked. After a retention interval, the rats received a test trial with all arms open and they could find standard chow in the four previously unbaited arms. Furthermore, if the retention interval had been long (4 hours), chocolate was also in the arm it had been in earlier, but if the retention interval had been short (30 minutes), chocolate was absent (see figure 1). The measure of what-where-when was the order of entry into the arms on the retention test. If the retention interval was short, the rats entered the empty chocolate arm later than if the retention interval was long and there was now chocolate there. To respond differently after the 1 and 6 hour-retention intervals, the rats would have had to remember which arms were distinctively flavored (what and where) and when they had visited those arms. However,

their ability to remember when they had experienced the study trial could have relied on the *strength* of the memory trace rather than on their memory for the time of the study trial.

Figure 1. What-where-when test for episodic-like memory



Notes: On a study trial rats received chow in three arms and chocolate in a fourth arm (the other four arms were blocked). On the test trial all arms were open and they received chow in the remaining four arms. If 6 hours had passed the chocolate arm was replenished, but not if only 1 hour had passed (after Babb and Crystal, 2005).

In a follow up study, Zhou and Crystal (2009) demonstrated that the rats could use the time of day of the study trial relative to the time of day of the test trial as a cue independent of the time that had passed between them. Thus, these rats appeared to satisfy the what-where-when criterion because - based on a single, brief encoding episode at the time of memory assessment - the rats remembered when the study episode occurred, in addition to what happened and where it took place.

The unexpected question

Events that one considers important are often encoded purposefully as a semantic memory. For example, one may attempt to encode the name of a person one has just met because one may want to recall that memory at a later time. However, it is unlikely that other, incidental aspects of that encounter (e.g., what they were wearing) would be purposefully committed to memory. Yet it is possible that such a memory could be recovered retrospectively based on episodic memory. The difference between those two memory processes is suggested by the following story: A student comes into the lab one morning and is asked what she had for breakfast that morning. After a few seconds to think,

she answers “Toast and coffee.” The next morning she is asked the same question. Again she pauses to think and answers “Cereal and coffee.” The next morning as she sits down to have her yogurt and coffee, she thinks, when I am asked what I had for breakfast, I should answer “Yogurt and coffee.” The first morning, and in all likelihood the second morning, one can assume that the student used episodic memory to retrieve the memory for what she had for breakfast because those events are generally incidental and would not typically be committed to memory on purpose. However, on the third morning it is more likely that semantic memory was involved because she didn’t have to mentally travel back in time to recover the memory. What this story illustrates is that whenever multiple trials are involved, it is possible for the test subject to prepare a response at the time of the to-be-remembered event. But the prepared response would be much like learning a fact, without having to remember the episode itself. Thus, to rule out the possible use of memory for factual knowledge, the test of episodic memory should be unexpected, especially at the time the event occurs.

It should be noted here that in response to research on the unexpected question, Tulving (2005) has indicated that the requirement that tests of episodic memory must be surprising or unexpected should not be a necessary condition for episodic memory because one can have an episodic memory even if one expects to be asked about it. That is, knowing that one will be asked about one’s memory for an episode does not preclude having such a memory. However, it is not that the absence of expectation is a necessary condition for the recovery of an episodic memory, only that if the request for the memory is expected, it makes it difficult to distinguish between an episodic and a semantic memory. In other words, one cannot eliminate the possibility that the event was encoded as a semantic memory or a rule rather than as an episodic memory.

To design an experiment involving an unexpected question, recall the breakfast question. The example of the unexpected question asked of the student on the first morning assumes both that the student understands the question and can answer it (i.e., that she has receptive and productive language) and that the student’s response is accurate (i.e., that the student is not inventing a response or basing it on semantic memory). Although these assumptions are reasonable for the breakfast example, when it comes to tests of episodic memory in a nonhuman animal, one cannot take them for granted.

In a series of experiments with pigeons, we proposed to establish the conditions for testing animals with an unexpected question (Singer and Zentall, 2007; Zentall, Clement, Bhatt, and Allen, 2001; Zentall, Singer, and Stagner, 2008). In general, the procedure involves three phases (see figure 2 for the design used by Zentall et al., 2001). In the first phase, we had to establish a rudimentary form of *communication* to be able to provide the pigeon with the means of answering a question. To do this, we first trained the pigeons to peck when vertical lines were presented and to refrain from pecking when the lines were horizontal. We then trained the pigeons to choose one of two comparison stimuli depending on whether they had just pecked at the lines or not (e.g., the rules were, choose red if pecking had just occurred, choose green if pecking had not occurred). One can think of this phase as pretraining in how to report the answer to the question “what did you just do?”

In the second phase, we gave the pigeons an experience that we could monitor, to be able to verify the memory that later we would ask them to report. For this phase we

There is also evidence that when unexpectedly asked, pigeons can remember the locations that they most recently pecked (Singer and Zentall, 2007; Zentall et al., 2008) and whether or not they recently had been fed (Maki, 1979). More recently, Zhou, Hohmann, and Crystal (2012) have developed a clever way to demonstrate that rats too can answer an unexpected question about having been fed or not.

One concern that has been raised with regard to research that has used the unexpected question procedure is that episodic memory is generally classified as reference memory rather than working memory, and one typically thinks of reference memory as more than a few seconds old. However, episodic memories do not have to be older memories. Imagine the following scenario: I am about to leave for work and arrive at the front door without my keys. In my mind's eye, I retrace my steps to the kitchen where I try to remember if I put my keys down on the table when I went to answer the phone that rang just before I was leaving. That would certainly qualify as an episodic memory even if it was only a few seconds old. Furthermore, with the procedure used by Zentall et al. (2008) involving the question "where did you most recently peck?", in order to ensure that the pigeons could not use currently available spatial cues, we forced the pigeons to move away from the key just pecked and peck the center key, before being asked the question with presentation of the comparison stimuli. Thus, the time between making the spatial response and responding to the question was typically several seconds.

In the spirit of compiling a more complete picture of the various lines of research, Crystal (2010) has suggested it would be valuable to develop a converging line of evidence that rats can answer an unexpected question, using operant methods, following Zentall et al. (2001), or integrated into tests of what–where–when memory on the radial maze. This appeal to complementary lines of research is likely to promote the development of a more complete picture of the representational abilities of the past events of animals.

Integration

When we think of episodic memory in humans it is typically of the integrated representation of a past event. The where-what-when is bound together as a whole. To what extent can it be shown that animals demonstrate this sort of integration of representation? Iordanova, Good, and Honey (2008) tested the integration hypothesis by presenting rats with one of two auditory stimuli (what, X or Y) in one of two contexts (where, A or B) at one of two different times (when, morning or afternoon). In the morning, X was presented in context A and Y was presented in context B but in the afternoon, X was presented in context B and Y was presented in context A. One of the auditory stimuli X (but not Y) was then paired with foot shock at midday. When the rats were tested for contextual fear, they showed more fear in A than in B in the morning but more fear in B than in A in the afternoon. Thus, the fear that had been acquired to A (what) was transferred to the appropriate context (where) and time (when).

Episodic memory without language

Language provides an accepted means of testing for episodic memory. Not only can humans answer a question about a past experience, but they can often elaborate on that question and use the elaboration as an aide in recovering the event. For example, if asked

what I had for breakfast this morning, my most vivid memory of this morning may have been the failure to awaken when the alarm sounded. But remembering that event may help me to remember that I did not have time to have breakfast and I had to settle on having a quick cup of coffee.

Suddendorf and Busby (2003) recognized the difficulty in assessing episodic memory in animals and proposed that there may be a way to confirm the presence of episodic memory without the need for language. They suggest that evidence for subjective time travel in nonverbal organisms could take the form of the re-enactment of events through pantomime. In that regard, there is evidence that dolphins may have that ability (Mercado, Murray, Uyeyama, Pack, and Herman, 1998). As part of a more general program to train dolphins to recognize syntax, the order of arm-gesture representations of objects and verbs, the dolphins were trained with a particular arm gesture to repeat the action that they had most recently made. To do that, one might assume that they would have to be able to remember what they had most recently done, but Mercado et al. (1998) proposed that the dolphins could have remembered the arm gesture most recently demonstrated and responded to the trace of the trained gesture. To avoid that problem, Mercado et al. (1998) trained the dolphins with a new arm gesture to make any *novel* response (any response that had not been made recently). Then, on a test trial and for the first time, they gave the gesture for the novel response followed by the gesture to repeat the response. They found that the dolphins were able to perform that sequence correctly. Had the dolphins been responding to the repeat gesture by remembering the gesture just before that one, they would not have repeated the specific novel response that they had made. Thus, nonverbal animals may be able to satisfy the criterion proposed by Suddendorf and Busby by using a form of pantomime to demonstrate an event from their recent past.

Future planning

Most of the research on mental time travel in animals has been directed to the assessment of episodic memory. However, if the function of episodic memory is to be able to simulate the future, then animals that have episodic memory should also have the ability to plan for the future. Certainly, learning experiments indicate that animals can anticipate the presentation of food and they can even use the time of day as a cue for where food can be found (e.g., Biebach, Gordijn, and Krebs, 1989). But in these cases the animals' behavior do not pass the Bischof-Köhler test (see Tulving, 2005). That is, to pass the Bischof-Köhler test, future planning must occur in the absence of a current need or drive state, *in anticipation of* a future need. Consider the following scenario: One is packing a suitcase for a vacation on the beach. Although the current climate may be cold, one should prepare for the climate at the destination by packing shorts, swimming trunks, sandals, sun glasses, and sun screen. And one may actually identify items to be taken by imagining oneself on the beach (a simulation). Tulving (2005) refers to this kind of simulation as passing the *spoon test*. It is based on the story of a little girl who dreams that she goes to a party where they are serving chocolate pudding and all of the other children brought a spoon, but she did not bring one so she gets no pudding. The next night she goes to bed clutching a spoon in her hand. The requirement that a need must be anticipated serves to distinguish future planning from delayed reinforcement. For example, a hungry rat can

learn to press a lever for food and can learn to do so even if the food is delayed for a few seconds. Even if one could show that reinforcement could be delayed for several minutes, one might not want to call that future planning. According to Tulving, it is only when the motivation can be anticipated at a time when it is absent that the response is considered future planning - hence the example of packing for a beach vacation. However, as with episodic memory, the absence of future planning does not preclude the ability to take actions for the future; it only precludes the ability to imagine oneself experiencing the actions or the ability to project oneself into the future.

Are animals capable of this kind of future planning? Roberts (2002) concludes that they are not (but see Roberts and Feeney, 2009, for a change of heart). He cites several examples. First, he mentions that when monkeys are fed chow biscuits once a day, they eat some but typically have some left over. Often, however, they throw the remaining food out of their cage, in spite of the fact that they will be hungry later in the day. Apparently, the monkeys do not anticipate that they should save their food because they will be hungry later that day.

Another example comes from hoarding behavior (putting away food for future need). Although many animals engage in hoarding behavior, this behavior does not appear to be under cognitive control. For example, Lucas and Zielinski (1998) kept Carolina chickadees in an aviary where they could hoard seeds. In one condition hoarded seeds were pilfered by the experimenters, whereas in another condition the chickadees were allowed to retrieve the seeds. The investigators found that the birds in the pilfered condition actually continued to cache seeds at a higher rate than birds in the nonpilfered condition. If the birds were planning for the future, they should have been sensitive to the fact that their seeds were being pilfered and they should have cached fewer seeds. Of course, it could be argued that the birds were compensating for the pilfered seeds by caching more seeds. On the other hand, there is evidence that scrub jays are quite sensitive to the possibility of pilfering and will avoid locations that are pilfered (de Kort, Correia, Alexis, Dickinson, and Clayton, 2007). Furthermore, as noted earlier, when scrub jays are caching they are sensitive to the presence of other scrub jays and will later recache their food if they were observed, but only if they themselves have pilfered food from others' caches (Emery and Clayton, 2001).

Other research cited by Roberts (2002) indicates that when macaque monkeys are given a choice between two quantities of food, they generally opt for the larger amount, but when the two amounts are sufficiently large such that either amount is sufficient for their current degree of hunger, they no longer show a preference (Silberberg, Widholm, Bresler, Fujita, and Anderson, 1998). That is, they appear to show *temporal myopia*. Similarly, Hauser, Carey, and Hauser (2000) found that rhesus monkeys that observed slices of apple placed in each of two opaque containers preferred the container with two slices over the container with only one slice. However, when the choice was between four and eight slices, the monkeys were indifferent. Again, four slices were enough to satisfy the monkeys' hunger for apples, so choosing eight slices was not necessary.

There is also evidence that some animals do not show this temporal myopia. For example, Rumbaugh, Savage-Rumbaugh, and Hegel (1987) found that chimpanzees reliably chose the larger of two food quantities presented in a 4:3 ratio whether it was 4:3 or 8:6. McKenzie, Cherman, Bird, Naqshbandi, and Roberts (2004) found a similar result

with squirrel monkeys using a 2:1 ratio whether it was 2:1 or 4:8.

More direct evidence of future planning was reported by McKenzie et al. (2004, Exp. 7) in which monkeys chose between two and four peanuts. When four peanuts were chosen, the monkey kept and ate all four peanuts. If two peanuts were chosen, the experimenter returned 15 minutes later and gave the monkey eight more peanuts. Thus, a monkey that chose 4 peanuts obtained a total of 4 peanuts, but a monkey that chose 2 peanuts obtained a total of 10 peanuts. However, in order to make the strategic choice of two peanuts, a monkey would have to anticipate replenishment 15 minutes into the future. On baseline trials, without replenishment, both monkeys showed a significant preference for four over two peanuts but they showed a significant preference for two over four peanuts during the replenishment phase of the experiment. Of course, one could argue that the behavior of these monkeys does not pass the Bischof-Köhler test because the monkeys were motivated for the peanuts at the time they chose the smaller amount over the larger amount (so as to receive more total peanuts).

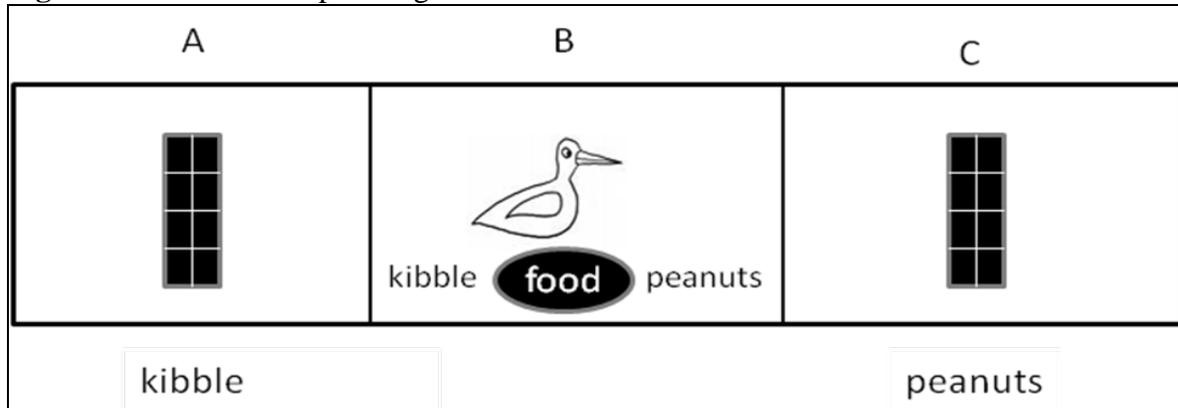
Raby and Clayton (2009) have argued that “the fact that action is taken to meet a current motivational state does not exclude the possibility that future thinking is involved” (p. 319). Although this position is certainly correct, it makes the same error that Tulving makes when he claims that one can have an episodic memory even if one expects to be asked about it. That is, as in the case of an expected question, one cannot rule out the possibility that a simpler mechanism may be responsible for what appears to be future planning. In the case of future planning, the simpler mechanism would be associative learning (or trace conditioning). On the other hand, it should be noted that when there is a long interval, perhaps of hours, between the behavior and the reinforcement, it would be difficult for associative learning to bridge such a long interval. Nonetheless, the best evidence for future planning would rule out associative learning by passing the Bischof-Köhler test.

A better test of the Bischof-Köhler hypothesis was provided by Naqshbandi and Roberts (2006). They gave monkeys a choice between one and four pieces of date. However, eating dates made them thirsty, and if they chose four pieces of date they were not given water for 3 hours, whereas if they chose only one piece of date they were given water after 30 minutes. Naqshbandi and Roberts reported that the monkeys learned to choose one piece of date and argued that their results passed the Bischof-Köhler test because the monkeys were not thirsty at the time they chose the one piece of date. However, the fact that the monkeys learned the consequences of their choice over 25 training trials makes it difficult to rule out associative learning. That is, the monkeys could have learned the aversive consequences of choosing four pieces of date. Furthermore, it should be noted that Paxton and Hampton (2009) were not able to replicate this finding.

Better evidence for future planning has been found in scrub-jays. In an ingenious study, Raby, Alexis, Dickinson, and Clayton (2007) gave scrub-jays peanuts and kibble in the evening in compartment B and allowed them to cache the food in sand-filled trays in two compartments, A and C, one of which they would have to spend the night in (see figure 3 for the design of this experiment). They had learned that the next morning, if they found themselves in compartment A, they would be given one of those two foods, say kibble, and if they found themselves in compartment C, the other food (peanuts). It was assumed that

the jays would prefer to have both foods present in the morning and, in fact, although they did not know where they would spend the night, they cached significantly more of the food in the compartment in which they would not receive that food in the morning. Thus, in keeping with the critical condition of Tulving's spoon test, the jays showed that in the absence of motivation to eat either kind of food, they could plan ahead and cache the food that they would not be given in the morning, depending on where they were forced to spend the night.

Figure 3. Test of future planning



Notes: Scrub jays were fed peanuts and kibble in the evening in compartment B and were allowed to cache both in compartments A and C. They were then forced to spend the night in either A (where they would receive kibble in the morning) or C (where they would receive peanuts in the morning) (after Raby, Alexis, Dickinson, and Clayton, 2007).

In more natural observational studies, chimpanzees have been observed to carry stones to nut-cracking sites and to prepare and carry sticks for termite-fishing to termite mounds (Boesch and Boesch, 1984; Lawick-Goodall, 1971), suggesting that they can anticipate future needs. Of course it would be important to demonstrate that those behaviors were not acquired by trial and error learning, having coincidentally carried a stone to the nut-cracking site one time and then later repeating that behavior because it was reinforced.

Chimpanzees have also shown similar ability to plan for the future under more experimental conditions. Mulcahy and Call (2006) first trained chimpanzees to use an appropriate tool to get a reward from an apparatus. The chimpanzees were then given access to several tools without access to the apparatus and then had to leave the test room for up to 14 hours. When they were returned to the test room all of the tools had been removed. Within as little as one trial the chimpanzees learned to take the appropriate tool with them when they had to leave the test room so that they would have the tool when they were allowed back in. The results of this experiment would appear to pass Tulving's spoon test. The chimpanzees took the tool with them at a time and to a place where it will not be useful so that they will have it at a later time when it will be useful. However, the results indicated that the probability that the appropriate tool was taken back was not very high.

More convincing evidence was reported by Osvath and Osvath (2008), who found in their experiment that apes consistently selected the correct tool to obtain a food reward that would be available in a different room and at a future time. Furthermore, when the apes

were shown the inaccessible food and were later given a choice of four tools that had not been seen before, one of which could be used to obtain the reward, a novel functional tool was selected significantly more often than the other objects.

Conclusion

It is a tribute to those who believe that humans are the only ones with the ability to mentally travel backward and forward in time (e.g., Suddendorf and Corballis, 1997, 2010; Tulving, 2005) that rather than base their claim on the inability of nonhuman animals to verbalize what they experience, they have proposed behavioral means of providing convincing evidence that they are wrong. It is also a tribute to animal researchers (in particular the Clayton, Roberts, and Crystal laboratories) who have come up with clever experiments to satisfy the criteria established by the still somewhat-doubting human researchers (e.g., Suddendorf and Corballis, 1997; Tulving, 2005). At present, there is sufficient evidence for the presence of both episodic memory and future planning in animals to suggest that there are animals that have some capacity for both, and this evidence warrants further study. Given the progress that has been made in this field in a little more than a decade, further research is likely to be very rewarding.

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References

- Atance, C. M., and Jackson, L. K. (2009). The development and coherence of future-oriented behaviors during the preschool years. *Journal of Experimental Child Psychology*, *102*, 379-391.
- Babb, S. J., and Crystal, J. D. (2005). Discrimination of what, when, and where: Implications for episodic-like memory in rats. *Learning and Motivation*, *36*, 177-189.
- Babb, S. J., and Crystal, J. D. (2006). Episodic-like memory in the rat. *Current Biology*, *16*, 1317-1321.
- Biebach, H., Gordijn, M., and Krebs, J. R. (1989). Time-and-place learning by garden warblers, (*Sylvia borin*). *Animal Behaviour*, *37*, 353-360.
- Bird, L. R., Roberts, W. A., Abroms, B. D., Kit, K. A., and Crupi, C. (2003). Spatial memory for food hidden by rats (*Rattus norvegicus*) on the radial maze: Studies of memory for where, what, and when. *Journal of Comparative Psychology*, *117*, 176-187.
- Boesch, C., and Boesch, H. (1984). Mental map in wild chimpanzees: An analysis of

- hammer transports for nut cracking. *Primates*, 25, 160-170.
- Clayton, N. S., and Dickenson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, 395, 272-274.
- Clayton, N. S., and Dickenson, A. (1999). Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *Journal of Experimental Psychology: Animal Behavior Processes*, 25, 82-91.
- Clayton, N. S., Yu, K. S., and Dickinson, A. (2003). Interacting cache memories: Evidence for flexible memory use by Western scrub-jays (*Aphelocoma californica*). *Journal of Experimental Psychology: Animal Behavior Processes*, 29, 14-22.
- Crystal, J. D. (2010). Episodic-like memory in animals. *Behavioural Brain Research*, 215, 235-243.
- Dally, J. M., Emery, N. J., and Clayton, N. S. (2006). Food-caching western scrubjays keep track of who was watching when. *Science*, 312, 1662-1665.
- de Kort, S. R., Correia, S. P. C., Alexis, D. M., Dickinson, A., and Clayton, N. S. (2007). The control of food-caching behavior by western scrub-jays (*Aphelocoma californica*). *Journal of Experimental Psychology: Animal Behavior Processes*, 33, 361-370.
- Emery, N. J., and Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 411, 443-446.
- Feeney, M. C., Roberts, W. A., and Sherry, D. F. (2009). Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Animal Cognition*, 12, 767-777.
- Friedman, W. J. (1991). The development of children's memory for the time of past events. *Child Development*, 62, 139-155.
- Gopnik, A., and Graf, P. (1988). Knowing how you know: Young children's ability to identify and remember the sources of their beliefs. *Child Development*, 59, 1366-1371.
- Hauser, M. D., Carey, S., and Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society of London*, 267, 829-833.
- Hayman, C. A. G., Macdonald, C. A., and Tulving, E. (1993). The role of repetition and associative interference in new semantic learning in amnesia. *Journal of Cognitive Neuroscience*, 5, 375-389.
- Iordanova, M. D., Good, M. A., and Honey, R. C. (2008). Configural learning without reinforcement: Integrated memories for correlates of what, where, and when. *Quarterly Journal of Experimental Psychology*, 61, 1785-1792.
- Jaynes, J. (1976). *The origin of consciousness in the breakdown of the bicameral mind*. Boston, MA: Houghton Mifflin.
- Laland, K. N., and Galef, B. G. (Eds.) (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.
- Lawick-Goodall, J. (1971). *In the shadow of man*. New York: Dell.
- Lucas, J. R., and Zielinski, D. L. (1998). Seasonal variation in the effect of cache pilferage on cache and body mass regulation in Carolina chickadees: What are the trade-offs? *Behavioral Ecology*, 9, 193-200.

- Maki, W. S. (1979). Discrimination learning without short-term memory: Dissociation of memory processes in pigeons. *Science*, *204*, 83-85.
- McCormack, T., and Atance, C. M. (2011). Planning in young children: A review and synthesis. *Developmental Review*, *31*, 1-31.
- McKenzie, T., Cherman, T., Bird, L. R., Naqshbandi, M., and Roberts, W. A. (2004). Can squirrel monkeys (*Saimiri sciureus*) plan for the future? Studies of temporal myopia in food choice. *Learning and Behavior*, *32*, 377-390.
- Mercado, E., III., Murray, S. O., Uyeyama, R. K., Pack, A. A., and Herman, L. M. (1998). Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): Repetition of arbitrary behaviors using an abstract rule. *Animal Learning and Behavior*, *26*, 210-218.
- Mulcahy, N. J., and Call, J. (2006). Apes save tools for future use. *Science*, *312*, 1038-1104.
- Naqshbandi, M., and Roberts, W. A. (2006). Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): Tests of the Bischof-Kohler hypothesis. *Journal of Comparative Psychology*, *120*, 345-357.
- Nelson, K., and Fivush, R. (2004). The emergence of autobiographical memory: A social cultural developmental theory. *Psychological Review*, *111*, 486-511.
- Osvath, M., and Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: Self-control and pre-experience in the face of future tool use. *Animal Cognition*, *11*, 661-674.
- Paxton, R., and Hampton, R. R. (2009) Tests of planning and the Bischof-Kohler hypothesis in rhesus monkeys (*Macaca mulatta*). *Behavioural Processes*, *80*, 238-246.
- Perner, J., and Ruffman, T. (1995). Episodic memory and autoegetic consciousness: Developmental evidence and a theory of childhood amnesia. *Journal of Experimental Child Psychology*, *59*, 516-548.
- Raby, C. R., Alexis, D. M., Dickinson, T., and Clayton, N. S. (2007). Planning for the future by western scrub jays. *Nature*, *445*, 919-921.
- Raby, C. R., and Clayton, N. S. (2009). Prospective cognition in animals. *Behavioural Processes*, *80*, 314-324.
- Richmond, J., and Nelson, C. A. (2007). Accounting for change in declarative memory: A cognitive neuroscience perspective. *Developmental Review*, *27*, 349-373.
- Roberts, W. A. (1998). *Principles of animal cognition*. Boston, MA: McGraw-Hill.
- Roberts, W. A. (2002). Are animals stuck in time? *Psychological Bulletin*, *128*, 473-489.
- Roberts, W. A., and Feeney, M. C. (2009). The comparative study of mental time travel. *Trends in Cognitive Science*, *13*, 271-277.
- Roberts, W. A., and Roberts, S. (2002). Two tests of the stuck in-time hypothesis. *Journal of General Psychology*, *129*, 415-429.
- Rumbaugh, D. M., Savage-Rumbaugh, E. S., and Hegel, M. (1987). Summation in the chimpanzee. *Journal of Experimental Psychology: Animal Behavior Processes*, *13*, 107-115.
- Silberberg, A., Widholm, J. J., Bresler, D., Fujita, K., and Anderson, J. R. (1998). Natural choice in nonhuman primates. *Journal of Experimental Psychology: Animal*

- Behavior Processes*, 24, 215-228.
- Singer, R. A., Abroms, B. D., and Zentall, T. R. (2007). Formation of a simple cognitive map by rats. *International Journal of Comparative Psychology*, 19, 417-425.
- Singer, R. A., and Zentall, T. R. (2007). Pigeons learn to answer the question “Where did you just peck?” and can report peck location when unexpectedly asked. *Learning and Behavior*, 35, 184-189.
- Staddon, J. E. R., Higa, J. J., and Chelaru, I. M. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior*, 71, 215-251.
- Suddendorf, T., Addis, D. R., and Corballis, M. C. (2009). Mental time travel and the shaping of the human mind. *Philosophical Transactions of the Royal Society B*, 364, 1317-1324.
- Suddendorf, T., and Busby, J. (2003). Mental time-travel in animals? *Trends in Cognitive Science*, 7, 391-396.
- Suddendorf, T., and Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs*, 123, 133-167.
- Suddendorf, T., and Corballis, M. C. (2010). Behavioural evidence for mental time travel in nonhuman animals. *Behavioural Brain Research*, 215, 292-298.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tulving, E. (1972). Episodic and semantic memory. In E. Tulving and W. Donaldson (Eds.), *Organization of memory* (pp. 381-403). San Diego, CA: Academic Press.
- Tulving, E. (1985). How many memory systems are there? *American Psychologist*, 40, 385-398.
- Tulving, E. (2005). Episodic memory and autoecesis: Uniquely human? In H. S. Terrace and J. Metcalf (Eds.), *The missing link in cognition* (pp. 3-56). New York: Oxford University Press.
- Zentall, T. R., Clement, T. S., Bhatt, R. S., and Allen, J. (2001). Episodic-like memory in pigeons. *Psychonomic Bulletin and Review*, 8, 685-690.
- Zentall, T. R., Singer, R. A., and Stagner, J. P. (2008). Episodic-like memory: Pigeons can report location pecked when unexpectedly asked. *Behavioural Processes*, 79, 93-98.
- Zhou, W., and Crystal, J. D. (2009). Evidence for remembering when events occurred in a rodent model of episodic memory. *Proceedings of the National Academy of Science USA*, 106, 9525-9529.
- Zhou, W., Hohmann, A. G., and Crystal, J. D. (2012). Rats answer an unexpected question after incidental encoding. *Current Biology*, 22, 1149-1153.
- Zinkivskay, A., Nazir, F., and Smulders, T. V. (2009). What–where–when memory in magpies (*Pica pica*). *Animal Cognition*, 12, 119-125.