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REVIEW ARTICLE

Episodic Memory in Primates

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Episodic memory refers to a system of memory with the capacity to recollect specific events from an individual's life. Some psychologists have suggested that episodic memory is a uniquely human phenomenon. We challenge that idea and present evidence that great apes and other primates may possess episodic-like memory. We review criteria developed to assess episodic-like memory in nonhumans, and how they apply to primates. In particular, we discuss the criteria of Clayton et al. [2001], who stated that episodic-like memory is based on the retrieval of multiple and integrated components of an event. We then review eight studies examining memory in great apes and apply the Clayton et al. criteria to each of them. We summarize the evidence that is compatible with the existence of episodic-like memory, although none of the data completely satisfy the Clayton et al. criteria. Morover, feelings of pastness and feelings of confidence, which mark episodic memory in humans, have not been empirically addressed in nonhuman primates. Future studies should be directed at these aspects of memory in primates. We speculate on the functional significance of episodic memory in nonhuman primates. Am. J. Primatol. 55:71–85, 2001. © 2001 Wiley-Liss, Inc.

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INTRODUCTION

> "Remembering past events is a universally familiar experience. It is also a uniquely human one. As far as we know, members of no other species possess quite the same ability to experience again now, in a different situation and perhaps in a different form, happenings from the past, and know that the experience refers to an event that occurred in another time and in another place. Other members of the animal kingdom can learn, benefit from experience, acquire the ability to adjust and adapt, to solve problems and make decisions, but they cannot travel back into the past in their own minds" [Tulving, 1983, p. 1].

Tulving, one of the leaders in the study of human memory, made this claim at the beginning of his landmark text, *Elements of Episodic Memory* [1983]. Since

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he introduced the term “episodic memory” [Tulving, 1972], the topic has been important in human memory research [see Schacter & Tulving, 1994], but it has been a term that has almost exclusively been used to refer to adult human memory. More recently, Tulving and Markowitsch [1998, p. 198] argued that “animals do not have the same kind of episodic memory system that humans do, that their declarative memory corresponds to semantic memory in humans [knowledge about the world], and that their episodic memory is best thought of as an ‘analog’ to human episodic memory.” Tulving is not the only memory researcher to consider episodic memory the sole domain of human beings. Conway et al. [1995, p. xvii] wrote, “Memory seems to be the psychological function most closely linked with one’s human uniqueness. Memories shape individual lives to an extent that is hard to imagine for other faculties such as seeing or speaking. Our memories are endogenous, private, internal, and controllable by our own minds; they capture events in the world as personal experiences.” Nelson and Fivush [2000, p. 284] wrote, “The practice of memory may be seen as akin to induction into language itself, a unique human process….” Suddendorf and Corballis [1997, p. 159] wrote, “We have argued that the ability to travel mentally in time constitutes a discontinuity between humans and other animals.” Suddendorf and Corballis argued that finding mental time travel in animals would be a significant discovery. Finally, Hart and Karmel [1996], primate researchers, commented that there is little evidence to support the notion of “personal memories” in apes, but that documenting such memory will be important in understanding self-knowledge and self-awareness in apes. Only Olton [1984] has argued for episodic memory throughout the animal kingdom, arguing that single-trial learning in delayed conditional discrimination is adequate to demonstrate mental time travel.

The goal of this paper is to assess whether the primate memory literature shows any evidence to support the contention that primates other than humans do possess episodic memory systems. At the time of the writing of this paper, only one published paper in the primate memory literature explicitly addresses episodic memory [Menzel, 1999]. Thus, our main goal is to argue for the importance of the initiation of study on this topic. In order to promote this, we delineate the criteria by which episodic-like memory may be assessed in nonhumans [Clayton et al., 2001], and then we consider evidence that already exists that bears on this question.

What Is Episodic Memory?

Tulving [1972, 1983, 1993] introduced the term “episodic memory” to refer to the human capacity to recollect individual events from their personal lives. Definitions of episodic memory have varied, but all center on one central idea, that episodic memory is a memory system that involves the retrieval of events from one’s personal past. Tulving and Markowitsch [1998, p. 202] define episodic memory as having to do “with the conscious recollection of previous *experiences* of events, happening, and situations.” They argue further that episodic memory is directed towards the past, whereas other memory systems are intended to inform the present. Wheeler [2000, p. 597] defined episodic memory as “the type of memory that allows people to reflect upon personal experience.” Cabeza [1999, p. 76] wrote that “episodic memory retrieval allows one to travel back in time and re-experience events that happened minutes ago or decades ago.” We consider three aspects of episodic memory to be important. First, the memory refers to a specific event from personal experience. Second, retrieval involves some form of “mental time travel” or reexperiencing of the past event [Tulving, 1983]. Third, there is a strong sense of confidence in the veracity of the memory [Koriat & Goldsmith, 1996].

We briefly consider two "typical experiments" in humans that investigate episodic memory: one drawn from a traditional verbal-learning paradigm using words as items to be remembered, and one drawn from studies on human memory that concentrate on real-world memory. In the first experiment, Gardiner and Java [1991] presented human participants with a list of words, which they were asked to study for a future memory test. Each word was only presented once. Later, they were given an "old/new" recognition test. In this test, they were presented with some words that had been presented on the earlier list and some words that were not presented on the earlier list. The participants were asked to decide "old" if the word had appeared on the list, and "new" if it had not. In addition, the participants were asked to distinguish whether they "remembered" the word from the list (that is, whether an experience of recollection accompanied the memory decision) or if they simply "knew" the word had been on the list. Gardiner and Java showed that human participants were accurate at deciding which words had been presented earlier and assigned many of them to the "remember" category. Subsequent studies have shown that items assigned to the "remember" category correlate with variables that affect human episodic memory [e.g., Wheeler, 2000].

Conway [1995] conducted a study on a phenomenon called "flashbulb memory." Flashbulb memories refer to salient and phenomenologically strong memories for the personal events surrounding the announcement of an important news event, such as the assassination of a political leader, an earthquake, or the start of a war. In Conway's case, he chose to study the memories of British citizens and non-British citizens concerning the unexpected resignation of Prime Minister Thatcher. Many months later, many British, but not Americans or Danes, could report where they were when they heard the news, from whom they heard the news, and their emotional state at the time that they heard the news.

Although the participants only heard the news for the first time once, they had subjectively very strong memories for the event. Paradoxically, a hallmark of most non-episodic memory is that repeated exposure to the to-be-learned stimulus is the key to forming strong, lasting memories [Bjork & Bjork, 1992]. However, for episodic memory, it is the salience and emotional significance that produces a strong memory trace [Tulving, 1983], as in the case of flashbulb memories [Conway, 1995].

Neuropsychological evidence also supports the idea of episodic memory as a distinct system, separate from other memory systems, such as semantic memory (memory for facts) or lexical memory (memory for words). Tulving [1989] and Nyberg et al. [1996], using PET imaging, showed that different areas of the brain are active during retrieval from semantic memory and retrieval from episodic memory. They found a left-hemisphere dominance in retrieval from semantic memory, but a right-hemisphere dominance in retrieval from episodic memory [Nyberg et al., 1996]. Many amnesic patients show deficits in episodic memory, while retaining semantic memory [Baddeley, 1990; Vargha-Khadem et al., 1997].

How do we transfer the concept of episodic memory from humans to nonhumans? This is a particularly thorny issue because of the way in which episodic memory is normally conceptualized. Episodic memory is thought of as a distinct neuro-cognitive system that stores events and provides for their retrieval, but its signature is the *mental experiences* that accompany that retrieval, namely feelings of pastness and feelings of confidence. Moreover, the usual way of assessing episodic memory in humans is with verbal tests. In the human literature, it is easy to ask a person, "What do you recall?" or "What happened to you?" We can thus gather a rich data base on what kinds of information people can recall, the context and source of those memories, and qualitative aspects of memory. Obviously, these kinds of verbal tests cannot be conducted except with a small number of language-trained apes. Thus, when transferring the concept of episodic memory from humans to nonhumans, there is an immediate methodological impediment. How do you test for episodic memory functions in nonlinguistic animals?

Clayton and Dickinson developed criteria, based on Tulving's [1972] original conception of episodic memory, to examine episodic memory in nonhumans [Clayton & Dickinson, 1998, 1999, 2000; Clayton & Griffiths, in press; Clayton et al., 2001; Griffiths & Clayton, in press; Griffiths et al., 1999]. According to their view, episodic memory stores information acquired through personal experiences about temporally-dated events and the spatial-temporal relation inherent in the event. Episodic memories are not of single bits of information; they involve multiple components of an event linked (or "bound") together. They sought to examine evidence of accurate memory of "what," "where," and "when" information, and the binding of this information, based on trial-unique learning events. Griffiths et al. [1999, p. 77] wrote, "In terms of purely behavioral criteria for episodic memory, the animal must be able to encode the information based on a single personal experience that occurred in the past, and then, accurately recall the information about what happened, where and when at a later date."

Clayton and Dickinson [1998] focused their research on food-storing birds—in particular, the scrub jay (*Aphelocoma coerulescens*). These birds in the wild cache extra food and return to the cache sites later when food is in short supply. In the laboratory, Clayton and Dickinson required jays to remember the location of cached food based on a single and unique trial of learning. In the studies, a jay must remember the type of food (what), the location of its storage (where), and select foods depending on their freshness (when (some foods decay more quickly than others)). In a typical experiment in Clayton's methodology, crickets are stored on one side of an ice-cube tray and peanuts are stored on another. Jays prefer to eat crickets, but they degrade more quickly. Thus, depending on how long ago the food was stored before testing, the birds' preference will switch from crickets to peanuts. Thus, by preferentially selecting crickets at short-retention intervals and peanuts at long retention intervals, Clayton et al. [2001] showed that the jays retain information about the what, the where, and the when.

Clayton et al. [2001] also argued that, based on their data, there is some evidence to suggest that the different kinds of information about the event are combined in a process known as binding, which means that different components of an event are bound together in memory. Thus, jays remember what, when, and where in an integrated manner, and retrieval of each component will not be independent of each other. This has functional utility: the memory serves no use unless the bird knows whether the stored food is fresh or not. Moreover, remembering what is stored is of no use to the bird unless it also knows where the food is stored. Therefore, it is not sufficient to form memories of each component of the event—it is necessary that these components be bound together into a cohesive unit. Clayton et al. [2001] argue that human episodic memory has a similar characteristic: we bind components of an event into a coherent whole [for examples of human binding, see Metcalfe et al., 1992].

Clayton et al. [2001] have provided a clear operational definition of episodic memory in nonhumans; that is, bound memories of what, where, and when components of an event, based on a single exposure to an event. The advantage of Clayton's model is that it allows for direct experimentation of memory based on operational criteria. However, a disadvantage of the technique is that one cannot know if the bird is experiencing a sense of the past when retrieving the information. Thus, their criteria bypass one of the fundamental features of Tulving's concept of episodic memory, that is, the "mental time travel," or reexperiencing of the past. Acknowledging this, Clayton and Dickinson [1998] refer to their findings as "episodic-like" memory. Of course, it is difficult to conceive of how one would get a jay to express that it is mentally reexperiencing past events. We think that it is potentially possible to address the issue of mental experience in primates, particularly the great apes. Nonetheless, we will use the Clayton-Dickinson model of episodic memory when assessing the data from primates.

Clayton et al. [2001] argued that the "when" component enables the bird to bind the event together, and is therefore the crucial aspect of episodic memory. The "when" component may be crucial in food-storing animals, such as the jays tested by Clayton and her colleagues. However, research with humans suggests that "when" information is the least well remembered and may not even be part of the episodic memory trace [Wagenaar, 1986; see Friedman, 1993, for a review]. In assessing primates, we are not convinced that any one of the criteria is more important than another, although all are important to test. Nor are we ready to commit to a position that nonhuman primate episodic-like memory will more closely resemble jays (with an emphasis on when) or humans (with an emphasis on the other components). This is a question not yet answerable. However, we do contend that a fourth component of episodic memory may be crucial to episodic memory to primates, and that is remembering "who" information [Griffiths & Clayton, in press; Menzel, 1999].

Menzel [1999] successfully used the Clayton-Dickinson model of episodic memory in a study of chimpanzees (*Pan trogolodytes*). Menzel added two features to the model. First, "who" information is also important in episodic memory. Thus, determining the important information about an event for a primate might also include information about the social players in the event as well as "what," "when," and "where" information. Indeed, Wagenaar [1986] found "who" information to be salient in a study of human autobiographical memory.

Second, Menzel argued for the importance of recall tests over recognition tests in assessing episodic memory. In humans, recall tests have been shown to maximize retrieval from episodic memory [e.g., Jacoby, 1991; Kelley & Jacoby, 2000]. In a recall test, the target event is not shown during testing, whereas in a recognition test, an aspect of the target memory is re-presented at the time of testing. For example, a recall test is equivalent to an essay exam or a "fill-in-the-blank" exam, whereas a recognition test is equivalent to a multiple-choice exam or a true/false exam. Recognition tests suffer from contamination from familiarity processes, which are not associated with episodic memory [Jacoby, 1991; Kelley & Jacoby, 2000]. Recall measures, however, may be impossible to obtain in many species (such as jays, monkeys, and any ape who has not been language-trained). Clayton and colleagues [Griffiths & Clayton, in press] argued that their memory tests demonstrated recall because the birds' response must be based on the integration of three different components of memory. Technically, however, the bird is still making an alternative choice of two tray locations directly in front of them. Thus, from the perspective of human memory, such decisions qualify as recognition tests. Similar problems in addressing recall exist with all primates other than a few language-trained apes.

Finally, episodic memory is a long-term memory system and not a short-term memory system. Therefore, in order to assess episodic memory, we must look at retention intervals that exceed the limits of short-term or working memory as generally conceived—usually no longer than 30 sec to 1 min [e.g., see Baddeley, 1998; Haberlandt, 1999]. To be conservative about not overlapping with short-term memory, the experiments that we review here are all those in which retention intervals of longer than 2 to 3 min are used between initial exposure and testing. This rules out a common methodology in animal learning experiments: the delayed matching-to-sample paradigm. Although delayed matching-to-sample is based on single-trial learning, retention intervals seldom exceed 40 sec [e.g., Dewsbury, 2000; Harper & Garry, 2000; but see Olton, 1984]. This type of single-trial learning is not relevant to the long-term memory involved in episodic memory. Other studies, which are based more directly on human models of memory, also are directed more toward parallels with short-term memory than with long-term memory [Buchanan et al., 1981; Sands & Wright, 1980; Washburn & Astur, 1998] because most of retrieval occurs within a minute of presentation.

Experimental Evidence in Great Apes

There is extensive literature on learning in apes [see Tomasello & Call, 1997]. One recent study has shown that chimpanzees can retain information for very long periods of time [Beran et al., 2000; for gorillas, see Patterson & Tzeng, 1979]. However, little of this research addressed the kind of learning that might contribute to episodic-like memory. We review eight empirical studies that provide data interpretable from the perspective of episodic memory: three studies on chimpanzees (*Pan troglodytes*), one study on bonobos (*Pan Paniscus*), three studies on gorillas (*Gorilla gorilla*), and one study on orangutans (*Pongo pygmaeus*) (see Table I). Each of these studies has retention intervals long enough to warrant the label "long-term memory," and each study involves learning based on single episodes, two necessary precursors for episodic memory. However, single-trial learning is not sufficient to demonstrate episodic memory. We only selected studies that show some evidence of memory retrieval of more than one component of the event. For each study, we apply the criteria of Clayton and Dickinson [1998] and Clayton et al. [2001)]; that is, we assess if "what, where, when, and who" information has been asked for, and if the components are bound or integrated. Considerable success has been achieved in "what" and "where" memory, but less on "who," and only inferences concerning "when." We also assess the information concerning if there is any evidence for mental time travel or feelings of confidence, although this aspect of the research is still in its infancy.

Chimpanzees. Tinklepaugh [1932] examined memory of spatial locations ("where") and type of food ("what") in several experiments in a study using single-trial learning with two juvenile chimpanzees. One of the chimpanzees was an 8-year old female (Dwina), and the second was a 6-year-old male (Bill). Both chimpanzees had participated in an earlier memory study by Yerkes and Yerkes [1928].

TABLE I. Studies Relevant to Episodic-Like Memory in Apes

Authors	Species	RI	Direct	Inferred
Tinklepaugh [1932]	Chimpanzees	72 hr	Where	What
Menzel [1973]	Chimpanzees	2 min	Where	What
Menzel [1999]	Chimpanzees	16 hr	What	Where
Savage-Rumbaugh [1999]	Bonobos	24 hr	What, where, who	
MacDonald [1994]	Gorillas	48 hrs	Where	How much
Gibeault and MacDonald [2000]	Gorillas	30 min	Where	How much
Schwartz et al. [2001]	Gorillas	24 hr	What, who	When
MacDonald and Agnes [1999]	Orangutans	10 min	Where	How much

In one experiment, one of two containers was baited with food. The chimpanzees watched which container was baited, but were prevented for various delayed intervals (up to 72 hr) before they could choose the container and receive the food reward. To accomplish this, Tinklepaugh [1932] removed the chimpanzees from the experimental context, and the chimpanzees were not returned until the retention interval (that is, the time lag between the end of the learning session and the beginning of the testing session) was over. Tinklepaugh varied the kind of food with which he rewarded the chimpanzees. In some cases it was a desirable food, such as bananas, whereas in other cases it was a less desirable food, such as carrots. During the retention interval, however, Tinklepaugh substituted a different food item from the one the chimpanzees had seen him place there. According to Tinklepaugh, both chimpanzees behaved differently, showing surprise, when they discovered the wrong food. Thus, Tinklepaugh argued that the chimpanzees remembered both the location ("where") and the content ("what") of the hidden food. However, given that the measure of surprise was a subjective one on the part of Tinklepaugh, it is with caution that we argue that this study supports memory of the "what" component.

Tinklepaugh [1932] noted differences in "confidence" from trial to trial. In some trials, the chimpanzees demonstrated behavior consistent with uncertainty or lack of confidence about their choices [Shields et al., 1997]. Both chimpanzees made wrong decisions and then would "appear surprised" when they were not rewarded with food. We view this subjective conclusion with caution.

In a landmark paper on spatial memory in chimpanzees, E. Menzel [1973] demonstrated single-trial learning of the "where" component of an event. In the study, Menzel hid 18 pieces of food in an open enclosure while one of four chimpanzees watched where the food was hidden. After a 2-min retention interval (just barely long enough to be included in this review), all of the chimpanzees were released into the yard. Not surprisingly, the chimpanzee who had witnessed where the food was hidden found the vast majority of the hidden food. In a second experiment, the chimpanzee who had witnessed which foods had been hidden moved toward the more desirable foods first, suggesting that the chimpanzee remembered what kind of food it was in addition to where it was hidden.

C. Menzel [1999] looked at "what"memory in chimpanzees with an explicit interest in studying episodic memory with the Clayton-Dickinson [1998] criteria. Menzel was able to achieve this by examining a chimpanzee (Panzee) who had received extensive language training and who can communicate the nature of many objects using a lexical keyboard [Beran et al., in press]. Use of this chimpanzee allowed for more specific information being communicated by the chimpanzee and the use of a recall format instead of recognition.

In the study, an experimenter hid foods and assorted objects just beyond the fence of Panzee's outdoor enclosure. Panzee could see the food being placed outside, but was moved back inside before she could get the food. The experimenter then left the area. Panzee's caretakers then noted what spontaneous communications Panzee used with them. The caretakers were blind as to what was hidden and when it was hidden. The caretakers were also blind as to the location of the foods or objects, ruling out any form of experimenter bias. The caretakers noted the lexigrams that Panzee chose to communicate, and the physical gestures that Panzee used to capture the caretaker's attention and to direct the caretakers to the hidden objects.

The results were striking. Even when the caretakers did not return to the lab until as many as 16 hr after the food had been hidden, Panzee indicated both memory for the food type (by selecting the appropriate lexigram) and possibly its location (by pointing in the general direction of where it was hidden). She was far more likely to use the lexigram for the hidden object while the object was hidden than she used the lexigram during a control period. She was also far more likely to elicit help from the caretakers when an object was hidden than when it was not.

C. Menzel [1999] interpreted these data as being evidence for episodic memory for three reasons. First, Panzee remembered both “what” and “where” components of the events. Second, Panzee’s retrieval of this information was spontaneous, that is, unprompted by any of her caretakers. Third, her working vocabulary is about 120 lexigrams, and therefore her use of the keyboard to indicate the hidden item approximates a recall measure. Buchanan et al. [1981] also used a recall measure with a language-trained chimpanzee in a list-learning paradigm. However, the retention interval between the beginning of the learning phase and the beginning of the retrieval phase was only, at maximum, around 30 sec. Therefore, we consider this to be more likely to be recall from short-term memory, whereas Menzel demonstrated retrieval from a long-term episodic-like memory system.

Bonobos. Savage-Rumbaugh (personal communication, 1999) conducted a pilot study with an adult female language-trained bonobo named Panbanisha. In the pilot study, eight memory trials were run following three separate events. Panbanisha spontaneously initiated two of the events, which were later tested, and one event was planned and initiated by the experimenter. In the first trial, Panbanisha asked Adam (a research assistant) to take “Coke to A-frame” and “juice to Treehouse.” “A-frame” and “Treehouse” refer to locations at the Language Research Center that the bonobos visit from time to time. A day later, Panbanisha was tested. She was asked who took the food outdoors for her yesterday to “Treehouse.” She selected Adam from a set of photos (a “who” memory). Then she was asked what food he took. Using the lexigram keyboard, she correctly selected “juice” and “Coke” (“what” memories). Memory for this event was scored as three correct out of three trials because she correctly retrieved three separate aspects of the event. In the second event, she asked Dan (another research assistant) to make a “gorilla balloon” video. A day later, she was asked what was on the video. She correctly selected “gorilla” from a set of possible agents (“who”), but incorrectly choose “sparklers” from a set of lexigrams. For this event, she was scored as being correct on one of two events. In the third trial (experimenter initiated), Mary (a research assistant) took blackberries to “Criss-Cross” (another Language Research Center landmark) and a “surprise” to “A-frame.” Later that day, Panbanisha correctly selected blackberries (“what”) and “Criss-Cross” (“where”) from a lexical keyboard. When asked who took the food, Panbanisha selected the wrong person, but later correctly answered what Mary had brought to the other location (“who”). For this event, she was scored as being correct on two of three trials.

In this pilot study, Panbanisha made eight memory decisions, six of which were correct. This pilot study suggests that bonobos are capable of retrieving at least three of the four components of specific past events and expressing them in recall format. However, given the small number of trials overall, and that one of the components was only tested in one trial, caution must be used when interpreting these data.

Gorillas. MacDonald [1994] was interested in the spatial memory capacity of lowland gorillas (*Gorilla gorilla gorilla*). In the course of the study of spatial memory, she conducted experiments that use single-trial learning and are therefore relevant to the topic of episodic memory. In the study, she examined spatial memory (the "where" component) in two Western lowland gorillas in the Toronto Zoo. One was a 20-year-old male, and the other was a 1-year-old male. Each was experimentally naive and had never received language training. In the first experiment, MacDonald set up eight containers in the daytime yard of the adult gorilla. All of the containers initially held food to familiarize the gorilla with the procedure. This conditioned the gorilla to inspect these containers for food. Once the experiment began, however, four sites were baited during two separate phases. During the *search phase* of a trial, four sites were baited. The gorilla was then allowed access to the yard and could search for the food. The gorilla visited each site and removed the food from the container that held food. The gorilla was then removed from the yard. While the gorilla could not see the yard, the same sites that were baited during the search phase were again baited. At some interval later, the *re-search* phase began. During this phase, the gorilla was again released into the yard. The gorilla could minimize the time spent re-searching for the food by only visiting those sites that he remembered as being baited earlier. After the gorilla had obtained the food, a new trial began. In the next trial, four of the eight containers were again randomly chosen to be baited for both the search and re-search phases.

The adult gorilla mastered this task [MacDonald, 1994]. He visited baited sites more than unbaited sites up to 48 hr following the search phase. Moreover, he consistently terminated his search after finding the four food containers, indicating that he remembered the last configuration of baited sites and how many sites were baited. Therefore, he recalled both the quantity and the location of the food sources based on a single exposure, up to 2 days later. Thus, the gorillas could retrieve information about the "where" component of an event that had only been experienced once.

MacDonald [1994] conducted a second experiment, which looked at spatial memory based on single-trial learning in a 1-year-old gorilla. The experiment was identical to the one with the adult, with the following exceptions. The 1-year-old was tested with hidden food in three of six containers. The delay interval between the search and re-search phases was started at 30 sec and gradually increased to 10 min. The infant, like the adult, showed above-chance memory concerning where the hidden food was located in the yard, although the retention intervals were much shorter with the infant gorilla.

In both of these studies, the only direct evidence is that the gorillas remembered where the food had been located because they were more likely to visit the baited sites than the unbaited sites. One criterion for episodic memory, however, is that more than one component be retrieved and that these components be bound elements. We argue, however, that because the gorillas did not continue to search the unbaited sites after the baited sites were depleted, they must have stored how much food was hidden as well as where it was hidden. Thus, although quantity does not fulfill a specific Clayton-Dickinson criterion, it does suggest that multiple aspects of the event had been represented by the gorillas.

Gibeault and MacDonald [2000] examined spatial memory in other gorillas at the Toronto Zoo. In this study, they were able to test a larger sample of gorillas. Eight of 16 sites were baited with food, similar to the search phase of the MacDonald [1994] study. There was a methodological improvement from the earlier study. In MacDonald's previous study [1994], when a baited site was visited during both search and re-search, the gorilla dislodged the containers during the visit, and it was obvious later that the site had been visited. Therefore, the gorillas did not have to remember that the site had been visited. However, Gibeault and MacDonald constructed the containers so that the gorillas could remove food from the container, but it would not be obvious; that is, the container looked the same before and after the food was removed. Therefore, the gorillas in the Gibeault and MacDonald study had to remember which containers they had visited.

Gibeault and MacDonald [2000] released two gorillas simultaneously into the yard in order to test if gorillas would compete for the food sites. The test of competition is not relevant here, but of interest is whether the gorillas avoided previously-visited sites—both ones that they had visited and ones that their partners had visited. The results supported single-trial learning of the "where" component. The gorillas first visited sites during the re-search phase that had been baited during the search phase. All of the gorillas tested were able to avoid visiting already-visited sites, suggesting that the gorillas remembered which sites had been visited. Like MacDonald [1994], Gibeault and MacDonald demonstrated directly only the "where" component of the event, but an inference of quantity may also be drawn.

A third study on gorilla memory was done by Schwartz et al. [2001], who specifically examined questions related to episodic memory. They explored memory for "what" and "who" information in a single-trial learning paradigm in an adult male Western lowland gorilla. The gorilla was expected to retrieve what particular food had been given to him, and by whom, on any given trial.

Before formal testing began, the gorilla was trained to associate specific cards with specific items of food. Thus, a card with a drawing of an apple on it was associated with both apples and the spoken word "apple." Five such foods were used in the training. The gorilla was also trained to associate three cards with three different experimenters. Thus, the gorilla could communicate both foods and people.

In one experiment, Schwartz et al. [2001] directly tested Clayton et al.'s [2001] theory that episodic-like memory should show integration between the various components of the original event. In this experiment, the gorilla was expected to make two responses, one about the "what" component (food) and one about the "who" component—that is, which experimenter gave the gorilla the food. The expectation is that for an integrated episodic memory, remembering one component should be associated with remembering the other components. This hypothesis was based on the idea that episodic memory binds components of an event together, and therefore retrieval of one component should be associated with retrieval of other components.

In the experiment, one of the experimenters gave the gorilla a specific food. Retention intervals were either short (5 min) or long (24 hr). At the time of test, in order to be reinforced, the gorilla had to respond with a card representing both the correct food ("what" component) and the correct person ("who" component).

The gorilla was accurate at both the short and long retention intervals at identifying both the food ("what") and the person ("who") [Schwartz et al., 2001]. Moreover, there was a positive correlation between the gorilla's likelihood of recalling the "what" information and the "who" information. This correlation means that remembering the food was more likely when the gorilla also remembered the person. This can be interpreted as meaning the two components were bound together in memory. The gorilla demonstrated both single-trial learning of "what" and "who" information, but, in keeping with the Clayton-Dickinson model, showed binding or integration between his memories of the two events.

Schwartz et al. [2001] argued that their data also supported the idea that the gorilla remembered when the food had been given as well, although they acknowledged that this was an inference. Given that the gorilla was given many foods during the 24-hr period between the event and testing, it is highly likely that some of the foods in the test set were given to him. Thus, at testing the gorilla must recall to which of several sessions of eating the experimenter expects him to respond. Because the gorilla was indeed accurate at 24 hr, he must have been discriminating between events that took place at different times.

Orangutans. MacDonald and Agnes [1999] used a spatial-memory methodology nearly identical to the one used for gorillas by MacDonald [1994], also demonstrating single-trial learning of "where" information. Three Sumatran orangutans (*Pongo pygmaeus abelii*) housed at the Toronto Zoo were tested. They tested one adult female (age 30) and two subadult males (ages 9 and 11). The apes were made familiar with the procedure by introducing them to the yard, in which all of the sites were initially baited. After becoming familiar with the task, the orangutans were introduced to the search and re-search task. Each orangutan visited all eight sites and found food in four of them during the search phase. The orangutans were removed from the yard and the sites were re-baited outside of the orangutans' view. Approximately 5–10 min later, the re-search phase began. The orangutans were again released into the yard, and could visit as many sites as they chose to.

MacDonald and Agnes [1999] were interested in a number of variables related to foraging, search behavior, and competition, in addition to memory. Our focus concerns the single-trial learning of "where" information. Both of the subadults, but not the adult female, were significantly better than chance at visiting the baited sites and ignoring the unbaited sites. Therefore, some orangutans were able to demonstrate single-trial learning and to retain information concerning spatial location ("where") for up to 10 min. One orangutan also showed a preference for a site when it had been baited with more food than the others, suggesting that the orangutan remembered "how much" in addition to where.

MacDonald and her colleagues have conducted single-trial learning experiments of "where" with two different species of monkeys, with positive outcomes [MacDonald et al., 1994; MacDonald & Wilkie, 1990; Tinklepaugh, 1932], but these studies do not demonstrate retrieval of multiple components, necessary to invoke episodic-like memory. Given the lack of evidence, either positive or negative, for episodic-like memory in monkeys, we have only considered those conducted on great apes.

DISCUSSION

Episodic memory involves binding components of an event into a unified memory, usually based on a single experience with that event. In humans, it is typically accompanied by feelings of pastness and confidence. In this review, we have shown that apes appear to be capable of episodic-like memory, in that they can retrieve different components of an event, based on single-trial learning. At least one study showed binding between different components [Schwartz et al., 2001], pointing to episodic-like memory.

However, based on the criteria set forth by Clayton and Dickinson [1998, 2000], it cannot be said with any certainty that apes have episodic-like memory, because there have been no definitive tests to determine if they can retrieve the "when" component of an event. Clayton and Dickinson [1998, 2000] established a set of criteria whereby episodic-like memory could be assessed in nonhuman animals. These criteria consisted of integrated memories of the "what," "when," "where" (and "who") components of an encoded event. We argue that the evidence suggests that some primates (the African apes) meet most of these criteria. For example, Schwartz et al. [2001] showed that the memory for the "who" component (that is, who gave the food) was correlated with the "what" component (that is, what food was given). An important future direction in examining episodic-like memory in apes (and other primates) is to demonstrate retrieval of the "when" component (indeed, we have such experiments planned). Moreover, like Clayton and Dickinson, we claim that these data only establish episodic-like memory, because we do not know the mental experiences of apes.

Tulving's [1983] criteria for episodic memory include that an episodic memory system allows one to mentally time travel, that is, mentally re-experience the earlier event. This involves two distinct subjective states. First, the rememberer knows that the event is not happening now, but is experiencing aspects of an event that took place earlier. Second, there is a feeling of veracity to the memory, that is, a subjective sense that the memory is accurate (even if it is, in fact, inaccurate [Roediger, 1996]). We call these aspects of human episodic memory feelings of pastness and feelings of confidence, respectively. There is no evidence to support the idea that either feeling exists in nonhuman primates or any nonhuman species. Moreover, at this time, we are not sure how this would be assessed. Perhaps this is a topic that can only be addressed with language-trained apes. Future investigation of this topic with these apes will reveal much about primate memory in general, and perhaps the origins of human episodic memory as well.

In humans, Wheeler [2000] argued that an important component of episodic memory is autonoetic consciousness, which refers to the ability of adult humans to know and self-reflect about the content, veracity, and nature of their experiences [also see Tulving & Markowitsch, 1998]. Autonoetic remembering can be shown in the distinction we make between "remembering" an event (we experience it in our mind's eye) and "knowing" an event took place (which does not require either mental time travel or personal presence). The ability to make this distinction does not develop in children until they are about 5 years old [Wheeler, 2000]. Like feelings of pastness and confidence, we are unable to conclude anything about the form of consciousness that accompanies episodic-like retrieval in nonhuman primates.

Finally, what functional significance would episodic memory have for nonhuman and nonverbal species? We propose two functions, one related to social interactions and the other related to foraging. Applied to foraging, episodic memory may allow primates to efficiently remember where food and other resources are located in space. Because primates generally live in tropical forest environments in which food sources are widely dispersed, up-to-date knowledge of food locations is important [Andrews, 1988; Garber, 1989; Gibeault & MacDonald, 2000]. Note that episodic memory is not necessary to remember where the trees are (spatial semantic memory); rather, it is used to remember specific visits to that tree. Episodic memories may save primates from visiting trees that have recently been depleted of food resources. This may be analogous to food-caching in jays [Clayton et al., 2001].

We suspect that episodic memory may function to help accurately track social relationships. Except for orangutans, great apes live in large social groups in which the social hierarchy is dependent on group interactions. Thus, remembering which individuals are friends or foes may offer important advantages in primate life. The role of friend and foe may be ephemeral or partially dependent on the location and situation [Cheney & Seyfarth, 1990]. Indeed, Cheney and Seyfarth argue that vervet monkeys remember past interactions and "keep track of who has cooperated with them in the past" [Cheney & Seyfarth, 1990, p. 60]. Therefore, a primate who can remember exactly how other group members have behaved in a variety of situations may be best able to anticipate their behavior in the future, an obvious advantage. Memory for specific past events is an efficient manner by which to accomplish this.

Although the relation of social relationships and episodic memory is speculative, we find it interesting that humans with impaired social functioning also show impaired episodic memory, suggesting a link between social relationships and the need for episodic memory. Autistic children, commonly thought to be lacking in social awareness and theory of mind [Baron-Cohen, 1995], show evidence of impaired episodic memory [Klein et al., 1999]. Similarly, Nelson and Fivush [2000] stressed the importance of memory conversations in developing strong mother–child bonds.

Episodic memory allows humans to develop a sense of self by comparing past actions to one's present state [Conway & Pleydell-Pearce, 2000]. Reflecting on the past allows us to live not just in the present but in the past and, by extension, the future. Therefore, it is possible that episodic memory may play a role, perhaps an essential one, in providing nonhuman as well as human primates with a sense of self-awareness because knowledge of self is necessary to interpret what these mental images of earlier times mean. Self-awareness has been a hotly debated topic in ape research [e.g., Gallup, 1982; Parker et al., 1994]. We assert that studies of episodic memory may be important in delineating the nature of self-awareness in apes.

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