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A Comparative Assessment of How Rhesus Monkeys and 3- to 4-year-old Children Remember Self-Agency with Spatial, Temporal, and Contextual Features in Working Memory

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A COMPARATIVE ASSESSMENT OF HOW RHESUS MONKEYS AND 3- TO 4-YEAR-OLD CHILDREN REMEMBER SELF-AGENCY WITH SPATIAL, TEMPORAL AND CONTEXTUAL FEATURES IN WORKING MEMORY

by

MEGAN L. HOFFMAN

Under the Direction of David A. Washburn

ABSTRACT

Comparative research on event memory has typically focused on the binding of spatial and temporal information in memory, but much less is known about how animals remember information about the source of their memories (i.e., whether the event is something they performed themselves or whether they observed it). The purpose of the present study was to examine how rhesus monkeys (*n* = 8) and 3- to 4- year-old children (*n* = 20) remember this information along with other relevant event features (object identity, spatial location, temporal properties and contextual features) in working memory. In Experiment 1, rhesus monkeys completed five different delayed matching-to-sample tasks to assess independent encoding of these five event components. In Experiment 2, the monkeys either performed or observed an event and then had to respond to a randomly selected pair of memory tests used in the previous experiment. In Experiment 3, children were presented with the same memory task, but were given a brief demonstration to learn how to perform the task. Both children and monkeys responded to these tests using photos and shapes (for the identity and spatial tests) and icons (for the temporal, agency and context tests). The monkeys demonstrated significantly above-chance performance on the identity, spatial, temporal and agency tasks. The children were above chance on the one component the monkeys had difficulty with (context), but conversely demonstrated difficulty on the temporal memory test. There was evidence of feature integration in both monkeys and children. Specifically, the children were significantly more likely to respond correctly to the second memory test if they had also been correct on the first memory test. Two of five rhesus monkeys also showed this effect, indicating that for these individuals, the features were integrated in working memory. Implications of this research are discussed in relation to self-awareness and episodic memory research in children and nonhuman species.

INDEX WORDS: Agency, Self-awareness, Rhesus monkey, What-where-when memory, Episodic-like memory, Episodic memory, Spatial, Temporal, Context

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1 INTRODUCTION

In a natural environment, many foraging and food-storing species must rely on memory for spatial and temporal information to locate and track the availability of food sources in the environment. However, the exact mechanism that supports this is less well understood and has been highly debated in recent years. Still, this is not to say that the study of animal memory in relation to foraging and other natural behaviors is a new area of study; the field began in the 1920's with research on learning and memory in wild and captive primate species (Hunter, 1913; Kohler & Winter, 1925; Tinklepaugh, 1932; Yerkes & Yerkes, 1928). Since that time, many other studies have shown that a number of different bird and mammal species are able to remember spatial information about the location of food sites in the environment (for reviews, see Tomasello & Call, 1997; Shettleworth, 1998). This has been established by designing laboratory studies in which olfactory cues can be controlled, either by having an animal hide an item which an experimenter later removes and/or hiding control items that the animal never sees to determine whether they can still locate these items through smell alone (Gibeault & MacDonald, 2000; Kohler & Winter, 1925; Lacreuse et al., 2005; MacDonald, 1994; MacDonald & Agnes, 1999; MacDonald, Pang, & Gibeault, 1994; E. W. Menzel, 1973; Tinklepaugh, 1932; Yerkes & Yerkes, 1928).

In addition to remembering where items are located in the environment, many species can also remember specific information about the types of foods at each location. The earliest discussion of this was by Tinklepaugh (1932) who studied spatial memory in monkeys and chimpanzees. Although the chimpanzees were able to remember multiple locations of hidden food items, when one of the items had been surreptitiously replaced with a less desirable food, they reacted with "disappointment" and "surprise," indicating that they had some knowledge of what had previously been at the locations or some expectation of what they expected to find at those locations. There are numerous studies demonstrating memory for this type of object information in different species, including pigeons, rhesus monkeys and rats (e,g., Roitblat, Penner, & Nachtigall, 1990; Tavares & Tomaz, 2002; Washburn, Hopkins, & Rumbaugh, 1989). Research has also shown that many species (e.g., honeybees, hummingbirds, rats, and nonhuman primates) are also able to retain temporal information about when they stored particular food items. This has been investigated by presenting animals with simulated foraging problems in which foods replenish or deplete at various rates; the animal conveys memory for temporal information by visiting the site only when enough time has passed for the food to remain fresh or be replenished (e,g., Burke & Fulham, 2003; Burke, Cieplucha, Cass, Russell, & Fry, 2002; Platt, Brannon, Briese, & French, 1996).

Even from this brief description it is clear that a number of different bird and mammal species can retain information about item type, spatial location, and temporal information and use this information in foraging or food-storing situations that they would face in the natural environment. In recent years, researchers have been building upon this research to determine whether these abilities are supported by an episodic memory system similar to what we experience as humans or whether these abilities can be explained through semantic memory. A related question pertains to how flexible this type of memory is in other species (e.g., can a particular species respond flexibly in different situations or can they only perform species-specific tasks they would encounter in a natural environment?). Before discussing the comparative work that has been done in this area, one first needs to address the construct of episodic memory – specifically, what is the nature of this memory system and how can it be studied in other species?

The present literature review begins with a brief history of the study of episodic memory in cognitive psychology. This is followed by a discussion of the theoretical and practical implications of applying this program of research to other species, which then leads into a comprehensive review of the studies that have been done with nonhuman animals. After reviewing the comparative studies in this area, the different paradigms are critically evaluated for strengths and weaknesses, and based on this analysis, a new comparative approach is proposed. This approach includes measures for assessing memory for self-agency and environmental context in other species. There have been numerous studies on agency and context memory in human participants, but this important characteristic has not been incorporated in event/episodic memory in other animal species. Finally, I describe a series of experiments which I designed to examine whether rhesus monkeys and human children remember agency information about recent events, along with spatial, temporal, and contextual features in working memory.

Brief History of Episodic Memory

There are distinctions in the types of long-term memories we encode, store, and retrieve. We are consciously aware of some memories, and these memories can be explicitly encoded and later retrieved, whereas others are implicit and appear to be encoded and retrieved with no conscious effort on our part. This distinction between implicit and explicit memory was first acknowledged by Korsakoff in his work with amnesic patients that retained implicit knowledge in the absence of any explicit memory for previously acquired knowledge (as cited in Schacter, 1987). The term declarative memory has also been used to describe the explicit memory system. Further subdivisions in long-term memory were proposed by Tulving (1972) who suggested two separate memory systems within the explicit/declarative memory system: 1) episodic memory, which includes memory for personally experienced past events and 2) semantic memory, which refers to our memories for generalized factual knowledge. The episodic/semantic memory distinction has been described as remembering (i.e., recalling the event when the information was acquired) versus simply knowing information without any explicit recall of the episode when the information was acquired (Roediger & McDermott, 2000). An individual recalling a past event from episodic memory understands that the event occurred in a particular spatial and temporal context. It is also said to be accompanied by a sense of self-awareness and knowledge that the memory is from one's personal past (Tulving, 2002). Furthermore, it is said to involve a subjective phenomenological experience in which the person recalling the past episodes reports feeling as if they are mentally revisiting the event or "mentally traveling back in time" to when and where the event took place.

This distinction between episodic memories and factual/semantic memories was first supported by case studies of individuals with neurological damage to medial temporal lobe structures including the hippocampal region. In these cases, patients were able to recall much factual information from semantic memory, but were unable to remember specific past events or form new episodic memories (Tulving, 2002). Although the ability to encode and retrieve semantic memories remained intact, these patients experienced selective deficits in episodic memory, suggesting that the two types of memory were supported by different neural mechanisms. The role of the hippocampus in encoding and retrieving episodic memories is further supported by brain imaging studies of nonclinical populations. However, a more complex picture has emerged from some of these studies, indicating that the two forms of memory interact in significant ways and may not be entirely separate. The hippocampus appears to play an integral role in initial encoding of information initially in memory, but over time, through the process of memory consolidation, connections are made with higher cortical regions and these areas also become activated when the memory is retrieved. Eventually these memories get reorganized and reallocated to these higher cortical regions and sometimes even become independent of the hippocampus. In contrast, episodic memories continue to remain dependent on the hippocampus (Rekkas & Constable, 2005). Therefore, it seems that both types of memories start out the same: as particular episodes in which we initially learned something about the world. In some cases, the source of this information is maintained, whereas in other cases we are only left with the factual knowledge that we obtained, but no memory of the episode itself. The hippocampus appears to serve a similar function in other species. Animals with damage to the hippocampal formation demonstrate deficits in remembering specific past episodes (Colombo & Broadbent, 2000; Eichenbaum & Fortin, 2003; Ergorul & Eichenbaum, 2004). The anatomical structure of the hippocampus is also similar across species (Morris, 2002). Therefore, it would seem reasonable to predict on the basis of these structural and functional similarities that humans and nonhuman species may share similar underlying mechanisms for integrating relevant features from past events in memory.

The way episodic memory has typically been studied in humans is through the use of verbal reports. In one of the most commonly used tests, participants are given a series of words to learn and are later asked which words they "remember" and which words they simply "know" are familiar (Gardiner & Richardson-Klavehn, 2000). These studies have indicated that "remember" responses are more likely to come from situations in which participants had engaged in deeper processing and are also associated with more activation of the hippocampus and medial temporal lobe. However, other species cannot provide such verbal reports, and as a result, it was once assumed that this form of memory could not be studied in these species. In recent years this assumption has been challenged. As with other cognitive processes, episodic memory can be studied in nonhuman animals by using behavioral tests that do not rely on verbal reports. If animals are able to succeed on these tests and their performance cannot be explained as the result of semantic memory processes, we can infer that they possess some other form of memory that allows for encoding of specific past episodes. Following this logic, some have proposed that the term *episodic-like memory* be used to describe the unique situation of nonhuman species that demonstrate behavioral evidence of this memory system, while still maintaining the traditional definition of episodic memory and its emphasis on a subjective conscious experience (e.g., Clayton & Dickinson, 1998).

Theoretical & Practical Implications

The field of comparative psychology has built an impressive literature detailing how different species are able to acquire information from past experiences, store this information in memory, and retrieve it when needed to solve novel problems or challenges. These comparative studies shed light on cognitive processes in other species, but also serve to improve our understanding of memory in general and can potentially lead to practical applications for improving human learning and memory. As discussed above, it has been well established that a number of different bird and mammal species are able to learn from past experiences and store general knowledge in memory based on these experiences (Shettleworth, 1998). However, much less is known about how animals encode individual past events in memory and whether they are able to retain memories for past episodes over extended periods of time in a way similar to humans. The ability to form episodic memories of past events has traditionally been investigated in humans using verbal report methods and initially it was believed that because animals lacked language they would be unable to encode such episodic memories. Furthermore, even if animals could encode such memories without language, it was believed that such a capacity would be difficult to assess without a verbal measure. However, in the past decade there has been a resurgence of interest in this question, with researchers developing behavioral tests to investigate episodic memory in different species (e.g., rats, pigeons, scrub jays, monkeys, and the great apes). Unfortunately, no researchers to date have attempted to make direct comparisons between animals and human participants in the study of episodic memory, so the results with animals are often compared to what we would *expect* humans to do in similar situations. It is understandably difficult to make direct comparisons between nonhuman animals and human participants; humans engage in a number of cognitive processes (e.g., verbal encoding, rehearsal, etc.) that may facilitate episodic memory, but that may not be crucial to the memory system itself. Therefore, any differences observed between animals and human participants may be due to the presence of such confounding variables. However, one way to make valid comparisons between animals and humans is to test children who are in the early stages of language development and are therefore less likely to use verbal labels and specific strategies when encoding past events in memory.

This comparison would not only be theoretically relevant, but would also provide practical applications for other areas of research. An animal model of episodic memory would prove useful in understanding the progression of episodic memory loss as a result of normal aging processes or specific neurodegenerative diseases that compromise this memory system. The model would also be useful in understanding memory deficits that result from developmental disorders. Recent studies have shown that individuals with autistic spectrum disorders (ASD) often experience deficits in episodic memory, but not in semantic memory. This deficit has been observed in both children (Millward, Powell, Messer & Jordan, 2000; Yamamoto, Saito & Kamio, 2004) and adults (Crane & Goddard, 2008) diagnosed with autism. These individuals do not exhibit memory deficits in other areas, but do appear to have more difficulty encoding personally experienced events. Some have argued that this may be due to difficulties in understanding the "self" (Hare, Mellor & Azmi, 2007), but it is also possible that these tests are not appropriate tests as they have relied too heavily on tasks involving verbal instructions which may be difficult for children who often experience delays in language acquisition. Tasks designed to be used with nonverbal animals are visually based and do not rely on verbal material or instructions. Consequently, such tasks could be easily adapted to provide more appropriate tests of episodic memory in children with ASD, as well as other unique populations that have verbal deficits or learning disabilities. However, before developing a comparative test of episodic memory that can be used in both animals and children, it is first necessary to provide some background describing what is known about episodic memory, as well as the different methods that have been used to study it in both humans and other species.

Tulving has argued that three qualities distinguish episodic memory from semantic memory: 1) a sense of self, 2) subjective time travel, and 3) autonoetic awareness (Tulving, 2002). To show evidence of episodic memory, an animal must be able to demonstrate that it has an awareness of itself as a unique agent in the past (and/or future). It has been difficult to find a way to assess these subjective qualities in nonhuman animals and many authors have acknowledged the challenges in developing such a test to determine whether animals have a sense of self that is not limited to the present (Dere, Kart-Teke, Huston & De Souza Silva, 2006).

> *A third clue is that mental time travel requires a traveler. No traveler, no traveling. The traveler in this case is what is referred to as "self." But an ordinary self will not do. By some criteria at least—the well known Gallup mirror test, for example—some nonhuman primates (chimpanzees and gorillas) also have minds in which their own selves exist as entities different from the rest of the world, but if one assumes that they are not quite capable of the human-type time travel, their selves exist only in the present, whereas ours exist in subjective time.* - Endel Tulving (2002)

However, it would also seem that this remains a difficult quality to assess in human participants. The existing methods we use with human participants rely heavily on language, and specifically on self-report, as a way of conveying information about participants' subjective, internal states. Although Tulving does not explicitly state that language is a necessary component of episodic memory, it is often an implicit assumption that language is either necessary for experiencing episodic memory and/or necessary for demonstrating it in the laboratory. Although language may be able to facilitate encoding and retrieval, it does not appear to be necessary for remembering past events. For example, human infants under two years of age, who have not yet learned language, are still able to encode and retrieve memories for recently experienced events (Bauer, 2002; Bauer

Hertsgaard & Dow, 1994). There are also examples of deaf adults, who were never taught sign language or were never able to develop their own gestural language with peers, yet are still capable of encoding memories for personal events (Schaller & Sacks, 1995). And of course there are a myriad of empirical demonstrations of memory in the absence of language from studies of nonhuman animals, as will be discussed below.

Comparative Studies of Episodic Memory

In a natural environment, many foraging and food storing species need to remember spatial information concerning the location of particular food sources. Many species consume different food sources, some of which (e.g., tree sap) are replenished quickly after being depleted and some of which (e.g., fruit, nuts) do not replenish until relatively long intervals once they are completely depleted. For such species, being able to keep track of the time since specific foraging episodes, would be extremely adaptive in determining when specific food sources will once again become available. Based on the natural behavior of many species, it would seem that an episodic memory system would facilitate survival, as animals could reduce energy expenditure and risk by avoiding revisits to locations that do not contain viable food sources. However, in some cases animals might be able to rely on semantic memory to recall information about food sources, spatial locations, and temporal ripening patterns. For example, a food-storing animal might always cache nuts in a particular set of locations and cache other foods in a different group of locations, eliminating the need to remember any particular past episode to recover the items. The animal might also adopt the strategy of only caching and recovering particular food types at different times of the year in response to a variety of environmental cues. Yet, there are reasons to suspect that nonhuman species would benefit from an episodic memory system, including situations in which animals have large territories, must migrate to a different area in search of food, or live in a rapidly changing environment.

As stated previously, episodic memory requires the encoding of an event in terms of its spatial and temporal context in memory. Before examining the integration of these components in nonhuman animals, it is first necessary to provide some background on each of these individual components. There have been an extensive number of laboratory studies showing that a variety of species are able to retain information about objects (*what*) that they have encountered. In these tasks, memory has most often been assessed using delayed matching-to-sample tasks (DMTS) in which an animal is presented with a particular stimulus and then, after a brief delay, the animal is presented with a discrimination task in which several alternatives are available and the animal must select the alternative that matches the sample (for a review, see Shettleworth, 1998). The study of spatial (where) memory in nonhuman species has also received considerable attention. These investigations have typically been conducted using delayed-response tasks that have been modeled after the foraging ecology of the species under investigation. In delayed-response tasks an animal learns that an item has been hidden in one of several locations (either by caching the item themselves, finding it in a foraging task, or by watching an experimenter hide the food item), and after some period of delay the individual is then allowed to recover the remaining food at the different locations. Using this approach, a variety of animals have been found to retain information about where food sources are located in a complex environment after both short-term and long delay intervals, and modify their routes to make recovery more efficient (for a review, see Shettleworth, 1998; Tomasello & Call, 1997). There has also been work examining whether animals are able to discriminate between various temporal intervals (when). In these tasks, animals are usually required to make a response, followed by a delay, and are then presented with a discrimination tasks in which they are required to make one response if the retention interval was of a particular length, and to make another response if the retention interval was a different length. Although these delays are usually relatively short (on the order of seconds) many species are able to discriminate between such temporal intervals (for a review, see Shettleworth, 1998; Zentall, Weaver, & Clement, 2004). Even before there was any discussion of an episodic-like memory system in animals, researchers were interested in whether animals were able to remember specific past episodes and integrate features from past events in memory Early work by Tinklepaugh (1932) and Menzel (1973) provided indirect evidence that chimpanzees retained information about food type along with its location. Kummer (1968) noted that baboons appeared to remember information about where water sources were located in the environment, even in the absence of any perceptual cues. Although not explicitly labeled as studies of *episodic memory,* this early research was the first attempt to examine how animals remember features of unique past experiences.

In recent years, a number of behavioral tests have been designed explicitly to assess episodic-like memory in animals. In some cases, tasks have been designed that incorporate the natural behavior of the species being studied, making it difficult to provide comparable tests for species that have a different suite of natural behaviors. In addition, different perspectives have emerged on precisely what the definition of episodic-like memory should include: some researchers have argued that the binding of spatial and temporal information in memory is integral to the definition, whereas others have maintained that spontaneous recall (which cannot be anticipated by the animal in advance) is the defining feature of the memory system in both humans and animals. As episodic memory typically involves spontaneous encoding of information (we recall things even though we may have never deliberately encoded them for later recall), some tasks have used unanticipated memory tests in which animals are given an unexpected probe trial in which they must report information about their previous behavior. Still, other experimenters have focused on the deliberate nature of episodic recall and have required animals to present explicit information about past events through the use of photographs or icons. These paradigms are discussed in detail throughout the following sections.

The Food-Caching Paradigm One of the most influential studies of episodic-like memory was done by Clayton & Dickinson (1999) with food-caching scrub jays. They presented the scrub jays with a situation that took advantage of their natural food storing behavior in the wild. They were allowed to cache different food types with varying rates of perishability in two separate locations in a sand filled tray. The scrub jays were first trained to learn that a highly preferred food (wax worms) was perishable and would be degraded shortly after caching, but a less preferred, but more stable food (peanuts) would remain fresh for a long time after caching. The jays were returned to the cache sites after either a short delay (4h) or a long delay (128h), If the jays were able to remember information about where particular food items were hidden, as well as the amount of time that had elapsed since they had stored them, they should preferentially search locations where they had stored the preferred wax worms when the delay had been short (4h), but switch to selecting the less preferred, but still fresh peanuts after long delays (128h). This is exactly what they found. However, this was not observed in a control group that had not learned this temporal contingency, suggesting that the results were not simply due to a natural predisposition in food caching behavior. It is important to note that in all of these tests, the food items had been removed from the locations and the sand substrate replaced to ensure that the birds were not responding on the basis of visual or olfactory cues. To control for familiarity (the jays may have simply adopted a strategy of searching for worms if the memory for the sand filled trays was recent or highly familiar), a subsequent experiment was done in which the birds were required to cache one food item (e.g., wax worms) and then after a delay of 120h cache another item (e.g., peanuts), ensuring that the sand filled trays would be equally familiar regardless of when the worms had actually been stored. The scrub jays were then allowed to search for the food items 4h after caching the second item. They showed memory for *what*, *where*, and *when* information by preferentially searching for worms if they had cached them only a short time ago (4h), but searching for peanuts if this preferred item had been cached in the distant past and was no longer fresh (128h). Again, this effect was not observed in a comparison group of scrub jays for which the wax worms were not perishable (Clayton & Dickinson, 1999). Similar studies have replicated these findings in other food-caching and foraging species, including magpies (Zinkivskay, Nazir & Smulders, 2009), black-capped chickadees (Feeney, Roberts & Sherry, 2009) and the great apes (Martin-Ordas, Haun, Colmenares & Call, 2010).

In subsequent work, Clayton, Yu, and Dickinson (2001) extended these findings by including three food items that differed in perishability in order to ensure that scrub jays were able to remember multiple features about more than one type of food type. They noted that in previous experiments the scrub jays could have simply learned to search for wax-worms if they had cached them recently, and may have only searched for peanuts as a default response. To test this, the scrub jays were allowed to cache peanuts along with one other perishable food items (mealworms or crickets). They were reintroduced to the caching tray after 4h delays, 28h delays and 100h delays. The perishability rates were as follows: the mealworms and crickets were both fresh after 4h delays; crickets remained fresh after 24h delays; and both foods had perished after 100h delays. This allowed the researchers to make different predictions about the scrub jays' behavior depending on whether crickets or mealworms had been cached. If the scrub jays had cached peanuts and mealworms, they should not search for the preferred item after the 24h delay, but if they had cached peanuts and crickets, the birds should search for the preferred crickets after the 24h delay. The scrub jays did just this, suggesting that they had not simply adopted the strategy of searching for the preferred food after a particular delay, but had remembered multiple features of both caching episodes. The scrub jays were also able to apply this knowledge to a new situation in which they were required to cache only mealworms and crickets.

Simulated Foraging Tasks The food caching paradigm has also been modified for use with rats and monkeys. In these tasks, there is period of training in which the animal learns that a preferred food degrades more quickly than a less preferred food. After learning this contingency, the individual is given the opportunity to explore a simulated foraging environment. The individual visits some or all of the experimental locations and is allowed to consume a portion of food found at the locations. Then, after either a short or long delay, the animal is returned to the environment and its behavior is recorded. If the individual can retain *what*, *where*, and *when* information about past foraging episodes, they would be expected to search for the perishable/preferred foods after short delays, but search the less preferred food items after long delays.

Babb and Crystal (2005) presented rats with an eight arm radial maze in which three locations were baited with a less preferred food (rat chow) and one location was baited with a more preferred food (chocolate). The rats visited these locations, consumed the foods at each location and then were removed from the maze. Then, the rats were returned to the maze after either a short delay (30m) or long delay (4h). The rats had to learn that, after a short delay, the food sites that previously contained food no longer contained food, whereas the four previously empty locations now did contain food. In contrast, if the rats were returned after a long delay, the foods that contained food before had been replenished. The rats were able to keep track of how much time had passed since their initial foraging experience. After short delays (30m) they did not return to previously visited locations, but after long delays (4h) they were more likely to search these old locations were which now replenished. In addition, on these trials they first visited the location that was replenished with the preferred food (chocolate) before visiting locations that had been replenished with the standard rat chow, indicating that they remember information about *what* specific food items were available at the baited locations and *when* each food site had previously been visited.

The foraging task has also been adapted for use in rhesus monkeys (Hampton, Hampstead, & Murray, 2005). In this task, monkeys were allowed to search three potential food sites, two of which contained foods and one which was empty. The food locations were randomly selected to contain a highly preferred food and a less preferred food. In training, the monkeys had learned that the preferred food (banana slices or grapes depending on individual preferences) degraded quickly, whereas less preferred foods (peanuts, primate treats, or primate food pellets) remained stable over long periods. The monkeys were allowed to recover food at each location and then were removed from the environment. They were returned after a 1h delay and a 25h delay; these delays ensured that recovery always occurred at the same time of day regardless of the delay length. The monkeys learned to avoid the empty location indicating that they remembered spatial information about the locations that contained food. However, the monkeys continued to visit locations where they had stored preferred/perishable foods even after 25h delays when the items were no longer fresh suggesting that they retained memory for which foods were located in particular locations, but not when they had been initially found. It should be noted, however, that this study is somewhat different in design than the other foraging task that has been described. The delays used in this study were longer than those used in studies with rats (Babb & Crystal, 2005), making it difficult to draw any comparisons between rats and monkeys. It is also important to note that in this study the monkeys were returned after both 1h and 25h delays on each trial, whereas in other experiments the animals are only returned after one delay. Being returned to the environment after the 1 h delay, may have interfered with monkeys' memory for the initial event.

Environmental Context Eacott and Norman (2004) took another approach, focusing on the environmental "context" of past episodes rather than the temporal context in which they occurred. In this experiment, an event could occur in one of two environmental contexts. Each context had different visual and tactile features, but both contexts shared the same spatial layout. The rats were exposed to one context and allowed to investigate two items at different locations (e.g., item A on the left, B on the right). The rats were then exposed to the other context, and this time the objects were reversed (e.g., item B on the left, A on the right). Then, after various delay intervals, the rats were given a memory test in which they were presented with one of the contexts, but this time only one object (A or B) was present; a copy of the object appeared at both locations. This resulted in four possible tests conditions. In each condition one of the objects appeared in a location that it had not been seen before in that particular context. As rats naturally prefer novelty, it was expected that if they had recalled the context of the object/location pairs, they would be more likely to investigate items that appeared in a novel context. The rats were more likely to approach these items, even when the items had been replaced with copies (to eliminate olfactory cues) and were not directly visible, requiring the rat to respond based on memory and not simply familiarity (Eacott, Easton, & Zinkivskay, 2005).

Unanticipated Memory Tests for Actions We often recall details of past episodes even though we had not intentionally encoded this information to recall at a later time. Yet, this aspect of episodic memory is not specifically addressed by the food caching and foraging paradigms. In these tasks, tests occur on every trial, so it is very possible that the animals come to anticipate being tested in the future, and may encode information differently because of this (e.g., by rehearsing information during the delay and using prospective instead of retrospective memory processes). In studies using unanticipated memory tests, an animal is presented with a cognitive task, and they are given a number of surprise “probe” tests to assess what they remember from their recently performed actions. Mercado, Uyeyama, Pack, and Herman (1999) studied memory for previously performed action events in a bottlenose dolphin that had been trained to understand a variety of gestural instructions. The dolphin had been trained to understand gestures that represented actions (e.g., hit), objects (e.g., ball), and body parts (e.g., tail flukes) as well as a “repeat” gesture that instructed her to repeat the behavior she had just performed. On each trial, the dolphin was instructed to perform a specific action with a particular object in her tank. Then, on some randomly selected trials, the dolphin was given the “repeat” gesture. This was a novel task, as these objects and actions had never been used together with the “repeat” instruction. The dolphin was highly accurate at performing the requested task, and she performed at levels significantly above chance when asked to repeat her previous behavior. As the dolphin was not expecting that she would have to repeat her action, such a task presumably required her to use retrospective memory of the prior event. However, there are some methodological issues that complicate this interpretation. For one, often the object remained in the same area of the tank after the dolphin performed the behavior, so it is possible that the dolphin could have solved the task by simply encoding spatial information and not object information. In addition, the dolphin could have used visual cues from these nearby items to help remember the previously performed action.

Zentall, Clement, Bhatt and Allen (2001) presented pigeons with a similar task that required them to perform a behavior (peck) or inhibit a behavior (refrain from pecking) in response to distinct cues. Then, on some randomly selected trials, pigeons were unexpectedly "asked" to report information about their previous behavior through the use of color keys that represented two behaviors (pecking and refraining from pecking). In the first phase of training, pigeons were presented with one of two samples (a vertical or horizontal line) indicating whether they should peck (vertical line) or refrain from pecking (horizontal line). After they successfully pecked the sample or refrained from pecking for a brief period (4s), they were presented with a choice between a red and green color key. This discrimination task allowed them essentially to "comment" on their previous behavior; they were reinforced for pecking one color (e.g., red) if they had pecked and reinforced for pecking the other color (e.g., green) if they had refrained from pecking. In the next phase of the experiment, pigeons were presented with yellow and blue keys. The presentations of the yellow key were followed by food reward, whereas the presentation of the blue key was not followed by a food reward. This task did not require the pigeons to peck at the key that produced food, but the pigeons typically did peck at this key and refrained from pecking the key that did not produce food. On randomly selected trials, this was followed by an unexpected question from the earlier phase of the experiment (the red and green comparison, which was analogous to asking the pigeons whether they had just pecked or did not peck). The pigeons selected the correct color key corresponding to their pecking behavior on 71% of the trials, which was significantly better than chance performance, indicating that they were able nonverbally to report information about their most recent action.

The pigeons also applied this to a new task that is somewhat closer to the way humans use episodic memory in everyday situations. Although we sometimes remember events we have been instructed to perform, our actions are often freely chosen and instructed by another individual. With this reasoning, pigeons were presented with a different task with novel stimuli. They were not reinforced with these novel forms, but some pigeons naturally pecked out of curiosity, while others abstained from pecking. The pigeons were still able to answer the "did you peck or not peck?" question even when presented after these novel stimuli and when no instruction had been given. Although these results are compelling, the retention interval in both of these studies was relatively short (on the order of seconds) and it is possible that the pigeons may have been responding on the basis of proprioceptive cues (including the position and sensation of the beak recently being used) rather than memory for past events.

Singer and Zentall (2007) acknowledged this possibility and presented a new task in which pigeons could not rely on proprioceptive cues. In this experiment, pigeons were unexpectedly asked "where did you peck?" instead of "did you peck?" They were first trained with a task in which a left or right sample box was illuminated. The pigeons pecked the sample and then were required to peck a center triangle key to continue with the trial. They were then presented with two color keys (red and green) and they learned that they should select one color if they pecked the left location and the other color if they pecked right location. In a second phase, pigeons were presented with blue and yellow samples and they had to learn the arbitrary association of selecting a corresponding line orientation (vertical or horizontal) for each color sample. However, this association was only done to mask the real purpose of the task. On these trials, the correct response was either on the left or the right, requiring the pigeon to peck to the left or right. On some probe trials, pigeons were required to select the center triangle key and then were unexpectedly presented with the red and green comparison (essentially asking "where did you just peck?"). The pigeons were as accurate on these trials as in the Zentall et al. (2001) study indicating that the pigeons were able to do this task without the use of proprioceptive cues. In a subsequent study, the center triangle key was replaced with a new stimulus to ensure that the triangle had not become a cue that a spatial memory test would be given and the pigeons remained significantly above chance on this new variation (Zentall, Singer, & Stagner, 2008).

Use of Lexigrams in a Chimpanzee In everyday situations, we are not always systematically questioned about our memories for past events. Rather, we often spontaneously retrieve information about past episodes in response both internal and external retrieval cues. Another approach to studying episodic memory in animals incorporates this characteristic and allows the animal to report information from past events without explicitly being prompted to do so. This approach was developed by Menzel (1999) to examine memory for spatial and object information in a symbol-trained chimpanzee. The chimpanzee, Panzee, had been trained to understand a large vocabulary of symbolic lexigrams that represented a variety of objects she encountered in her everyday life (humans, conspecifics, foods, objects, and locations). On each trial, Panzee watched from her enclosure as an experimenter hid a food or object in the wooded area surrounding her enclosure; the object was placed on the ground and covered with mulch and other ground cover so that it was not visible. She was not able directly to retrieve the object herself, so she had to go indoors to gain the attention of an experimentally blind caretaker. She did this by gesturing to the outdoors, covering her face in a gesture that meant "hide" and using her lexigram board to report the contents that had been hidden. The caretaker would respond to Panzee's requests to go outdoors and, through the use of pointing and gesture, she would reliably direct the individual to the location where the item had been hidden. She spontaneously reported the correct food or object that had been hidden on 84% of the trials, and directed the individual to the correct location on 100% of the trials. She remained highly accurate even after long delays (in many cases these delays extended overnight and on occasion over a period of days). Panzee's behavior was even more compelling considering that she did not have direct contact with the items and had to determine when to attempt to get help to retrieve them in the absence of any prompting by experimenters. In other tasks that have been used in episodic-like memory research, the animals engage in the actions themselves, and receive proproioceptive, tactile, and visual cues in touching and manipulating the objects. These cues likely facilitate memory for past events (Menzel, 2005), presumably by providing a more extensive number of retrieval cues. In the studies reviewed up to this point, the animals have only two or three alternatives to choose from in a memory test. However, Panzee had a much larger number of alternatives to choose from (256 lexigrams, and an almost limitless number of possible outdoor locations) making this test more analogous to human episodic recall.

Use of Photos to Assess Memory for Event Features In another study with a great ape, Schwartz et al. (2002) investigated whether a western lowland gorilla, King, was able to remember *what* and *who* information from past episodes. In this case, the samples and choices were presented in different modalities; an event was presented in real life, but the choices were presented as symbolic images mounted on wooden cards, making this a special case of DMTS. On each trial, King was given a particular food (apple, banana, pear, orange, or grapes) by one of three experimenters. Then, after either a short delay (7m) or long delay (24h) the gorilla was presented with five large cards with illustrations of each of the food items and was asked in English, by an experimentally blind tester, which food item he had received. He responded by handing one of the cards to the blind tester. The gorilla was significantly above chance at selecting the correct food item after both short delays (70%) and long delays (82%). In another experiment, King was asked to indicate what food he had eaten, as well as the person who had given him the food. The same five food cards were used, as well as a set of three symbolic person cards, each containing a unique symbol associated with the corresponding experimenter. The gorilla was significantly above chance at selecting both the correct food item and the person involved in the event after both short (9m) and long (24h) delays.

In a subsequent study, Schwartz and collaborators (2004) extended these findings by presenting King with a familiar person doing a novel activity, an unfamiliar person doing a novel activity, or a novel object. After an average retention interval of 7m the gorilla was given three alternative cards to choose from (one correct photo and two distractor photos selected from the same category). King demonstrated significantly above chance performance when identifying familiar people, unfamiliar people, and novel objects. The purpose of these experiments was to expand on the results of Schwartz et al. (2002) and show that this particular gorilla was capable of remembering events and identifying photos of people and objects from the events, a task for which he was not explicitly trained. An additional area of interest in episodic memory research is whether animal memory is affected by the same factors that affect memory accuracy in humans. Another experiment showed that King's memory for past events was impaired if he received misinformation after the event, a factor known to effect the accuracy of episodic recall in human participants. Schwartz, Hoffman, and Evans (2005) also examined whether King was able to remember spatial information from past events. The gorilla was shown a special object or event at one of three locations surrounding his enclosure (main enclosure, nighthouse, or tunnel gate). After a brief delay (5m) he was given three photo cards of the locations and asked, in English, by an experimentally blind tester, to return the card where he had witnessed the event. His overall performance, although above chance was not particularly compelling compared to his performance on previous tasks, and the authors speculate that this was likely due to changes in his diet during the experiment. Indeed, King performed at above chance levels during the first 20 trials of the experiment, but his performance significantly decreased during the last 20 trials of the experiment after abrupt changes in his diet resulted in changes in his reinforcement schedule.

Computerized What-Where-When Task In a delayed matching-to-sample task (DMTS), an individual is presented with a sample stimulus, which after a brief period disappears and is followed by a retention interval. Then, the animal is given a choice between two or more alternatives, one of which matches the sample. The animal is reinforced for selecting the choice that matches that sample. In some cases, the task requires a physical match to sample, whereas oftentimes the animal must symbolically match to sample on some abstract dimension (for example, the animal might have to select one symbol if the sample belonged to a particular category and another symbol if the object belonged to another category). These tasks have been used extensively to investigate memory in animals, but in the past these experiments only required animals to retain one component at a time from past events. New extensions of this approach have been used to determine whether animals are able to remember multiple features of an event, and whether the components are integrated in memory. Skov-Rackette, Miller, and Shettleworth (2006) first trained pigeons on three separate computerized DMTS tasks: 1) an *identity task,* 2) a *spatial task*, and 3) a *temporal task*. Each of these tasks began the same: the pigeons were shown a sample (a green triangle or red circle) that appeared in one of eight locations on the computer screen. After the sample disappeared, a short (2s) or long (6s) retention interval ensued. In the *identity task*, pigeons were reinforced for selecting the sample that had previously been presented from a set of two alternatives; in the *spatial task*, pigeons were reinforced for selecting the location where the sample had been presented from a set of eight possible locations indicated by grey boxes; and in the *temporal task*, pigeons were reinforced for selecting one icon (blue paw) if the delay was short and another icon (yellow sunburst) if the delay was long.

After pigeons reached a criterion of 80% correct on these DMTS acquisition tasks, they were presented with two question types on each trial, essentially requiring them to report two features of the event. This task was used to determine whether these components were integrated in memory (i.e., whether accurate memory for one memory component successfully predicts performance on a subsequent question). The pigeons performed at significantly above chance levels on the first question (87%) and the second question (80%). However, performance on the first question did not significantly predict performance on the subsequent question. If the components are encoded and retrieved independently, the probability of being correct on both trials is equivalent to the probability of being correct on the question 1 multiplied by the probability of being correct on question 2. However, the observed probability of being correct on both questions was not significantly different from this expected probability, indicating that the components were not integrated in memory.

In the previous experiment, it is possible that the memory components may have appeared to have been encoded and retrieved independently due to the extensive training pigeons received on individual tasks and the high level of accuracy they achieved on these tasks. If an animal performs correctly on the majority of the trials, there is less variability in the sample dataset and can make it difficult to detect a real effect that exists in the population. Therefore, a second experiment was done in which some tests were bound, meaning that a memory component not being tested was available as a cue at test. For example, a bound *what* test would present both choices (the green triangle and red circle) in the location where the sample had been presented. A bound version of the where test would place the sample that had been presented at the two choice locations. To make the task simpler and more analogous to tests in humans, the temporal component was not included in this experiment. An additional bound test (*what* + *where*) was also given and in this case, both choices (triangle and circle) appeared at the two choice locations. If the *what*, *where*, and *when* components are integrated, pigeons should do better on these bound tests than on unbound tests. The unbound tests were the same as those presented in the first experiment. The results indicated that the birds reached 90% correct on both *what* and *where* tasks, but there was no significant difference between bound and unbound trials. This suggests that components are encoded and/or retrieved from memory independently. If components had been bound together in memory there should have been greater accuracy for bound than unbound trials. However, it is important to note that because the pigeons were highly accurate on these tasks as a result of their training, there may not have been enough variability in the dataset to detect feature integration.

Hoffman, Beran, and Washburn (2009) used a similar task to assess memory for *what*, *where*, and *when* information in rhesus monkeys. The monkeys were presented with three DMTS tasks: 1) an *identity task*, 2) a *spatial task*, and 3) a *temporal task*. On each trial, the monkeys were shown an object selected from a large array of photographs, which appeared at one of two locations on the computer screen. The object then disappeared, followed by a short (1s) or long (10s) retention interval. In the *identity task*, monkeys were reinforced for selecting the sample that had previously been presented from a set of two alternatives; in the *spatial task*, monkeys were reinforced for selecting the location where the sample had been presented; and in the *temporal task*, monkeys were reinforced for selecting one icon (purple triangle) if the delay was short and another icon (black circle) if the delay was long. The monkeys were trained with each individual task and then were given tasks in which they had to: 1) report all three components sequentially, or 2) respond to one randomly selected question on each trial. The monkeys were significantly above chance at reporting object, spatial and temporal components when the question was randomly selected on each trial. When the questions were sequentially presented on each trial (so that monkeys had to respond to *what*, *where*, and *when* the event took place), all individuals remained above chance at remembering *what* and *where* information and two of four monkeys were also capable of reporting *when* the event took place. The reason why some monkeys were unable to perform well on the temporal task when it was presented sequentially is likely due to the fact that the time it took to respond to the previous *what* and *where* questions significantly lengthened the original retention interval. Although the monkeys may have only been presented with a 1s retention interval, the time it took to answer the first two questions lengthened the amount of time considerably, so that the resulting delay was much closer to 10s than the intended 1s delay. However, there was evidence that *what*, *where*, and *when* information were integrated in working memory; accuracy on the *what* and *where* questions predicted performance on the when question for two monkeys. Specifically, these individuals were more likely to be correct on the when question if they had also been correct on both *what* and *where* questions, suggesting that memory for when an event took place was integrated with memory for what and where the event occurred. Although there was no evidence of *what-where-when* integration in the other two monkeys, it is important to note that such integration may have obscured by the fact that these monkeys were highly accurate on all three questions. This high level of accuracy may have made it difficult to detect any binding of information even if it were present. It is also worthwhile to note that all of the monkeys succeeded when only one randomly selected question was presented on each trial. As the monkeys were unable to anticipate which question type would be presented, they presumably had to remember all three memory components in order to succeed on all three question types. It is important to acknowledge that, although the monkeys performed well on this type of memory task, this does not necessarily mean that they would show this proficiency on other spatial/temporal memory tasks. Some of the monkeys had participated in a similar memory task modeled after the children's memory game *Concentration,* but they were less proficient at this task and tended to perseverate on choosing incorrect stimuli that had been selected on previous trials (Washburn & Gulledge, 2002; Washburn, Gulledge & Martin, 2003).

A Comparison of the Strengths and Weaknesses of Comparative Tasks

These tasks that have used to examine episodic memory in animals vary on a number of features including: 1) the extent to which the task is standardized for use across species, 2) the type of information to be remembered, 3) the length of retention interval, and 4) the way memory for temporal information is defined and measured. The temporal issue has received attention in recent years, with many researchers acknowledging that the temporal component is poorly defined and may be a more specific instance of context encoding. It is reasonable to assume that one may encode the context of events in many different forms, including the temporal context, the spatial context, the emotional context, etc, with the important point being that the event occurred in a specific context in the past. In addition, there is debate, even among those who do agree that the temporal encoding is essential to episodic memory, about what exactly temporal encoding requires (is it encoding of time of day, time since an event took place, or relative memory for the sequence of events?) This ambiguity was recently addressed by Roberts et al. (2008) by presenting rats with two different tasks: one that could only be solved by remembering the exact time of day that an event took place and another that could only be solved by remembering how long ago an event took place. The rats appeared to encode temporal information in terms of the how long ago an event took place, not the precise time of day or date of the event, which is similar to the way humans appear to encode temporal information (Friedman, 1993).

However, in this process, it seems that other important aspects of the memory system have been overlooked. When we remember a past event, we not only recall where and when the event took place, but we also remember that we played a particular role in the past event. As acknowledged by Tulving in a quote presented earlier in this paper, self awareness is a critical component of the episodic memory system. This has been studied in the human memory literature, with a number of studies examining participants' source memory for events they performed and those they observed

(Hornstein & Mulligan, 2004; Manzi & Nigro, 2008). This type of source information has not been studied in the animal memory literature, but it is an important feature of episodic encoding by humans (Engelkamp, Jahn, & Seiler, 2003). This type of information makes it possible to distinguish between memories for things we directly observed ourselves from those we heard about through another source. This type of source information, along with environmental features at encoding, also makes it possible to distinguish between events that we actually performed from those we simply imagined or dreamed. There has only been one study that has assessed how animals encode other environmental features from past events (Eacott & Norman, 2004) and no researchers have attempted to assess whether animals remember information about their own role in past events. These are important features of episodic memory and would increase the validity of existing tests of episodic memory in animals. Before discussing how these features could be integrated into tests with animals, it is necessary to review studies of source memory with human participants.

Self-Agency and Context

The ability to remember the origin of one's memory is referred to as source memory or source monitoring, and has been a prominent area of research in the area of cognitive psychology, especially within the field of eyewitness memory. The ability to remember the source of one's knowledge or memories is important in everyday life, but is most obvious in situations in which one's memories are highly influential, such as in eyewitness testimony. An individual's memory for a particular past event can be compromised by presenting misleading information immediately following the event. In this case, the person may recall the information, but not remember the source or context in which this information was obtained and incorrectly attribute it to the event itself. In a related situation, which has been described as unconscious transference, an innocent bystander or another person encountered sometime after the event can be incorrectly identified as the perpetrator because a witness incorrectly attributes the familiarity of the person as a result of them being the perpetrator of the crime. (Mitchell & Johnson, 2000). Such source memory errors have been shown to occur even in relatively stress free laboratory settings. For example, if participants are asked to label a series of names as either those belonging to famous people or non-famous people, they will later incorrectly identify many of the non-famous names as "famous" because they are highly familiar from the previous experimental session (Jacoby, Woloshyn & Kelley, 1989). This is not surprising, as the probability of making of source monitoring errors has been found to increase when the contextual source information from events overlaps perceptually or semantically (Mitchell & Johnson, 2000).

In this case, source memory is defined as one's memory for the specific environmental context in which a particular event occurs. However, the term *source memory* has also been used to describe memory for one's own role in a past event (Englekamp, 1998). This feature is a relevant characteristic of episodic encoding, and may also affect how other features are encoded in memory. For example, greater personal involvement in a past event may actually improve memory for the event itself. This prediction would make sense in light of the self-reference effect which has shown that we are better at retaining information if we are able to relate it to ourselves. In order to determine the extent to which personal agency or involvement facilitates memory, some researchers have investigated whether people recall more accurate information from actions that they perform themselves compared to actions they simply observe performed by another person, most typically an experimenter (Englekamp, 1998). A number of studies have shown a general memory advantage for self-performed tasks in human adult participants (Engelkamp, 1983; 1998, as cited in Nilsson, 2000; Engelkamp & Dehn, 2000; Manzi & Nigro, 2008). This effect also has been observed in studies of typically developing children (Baker-Ward, Hess, & Flannagan, 1990), but appears absent in those diagnosed with autism spectrum disorders (ASD). In fact, some studies have shown that children with ASD are significantly more accurate at recalling actions performed by other individuals than those they performed themselves (Millward, Powell, Messer & Jordan, 2000; Yamamoto, Saito & Kamio, 2004). This is not surprising considering the fact that individuals with ASD have also shown impairments in other tasks that are related to the self, including self monitoring, processing of self-referential information, and in developing self concepts.

In addition to being able to recall the events better, some studies have shown that people also make more accurate source memory judgments for self-performed events (Senkfor et al., 2002, as cited in Hornstein & Mulligan, 2004) than for events performed by others. However, some studies have failed to replicate the finding that performing an event facilitates memory (Cohen, 1981; 1983, as cited in Nilsson, 2000) or more specifically, that performing an event leads to better source memory concerning one's involvement (Cohen & Faulkner, 1981, as cited in Nilsson, 2000; Koriat, 1991, as cited in Hornstein & Mulligan, 2004; Manzi & Nigro, 2008). It is not clear from these studies whether actually performing an event leads to any enhanced encoding in memory, but it is clear that human participants do appear to label their memories as those involving the "self" and those involving "others" and can do so reliably even when they do not anticipate being tested on this information.

These results fit with what we know about social learning in humans. The ability to understand the actions of another individual and represent them in memory has been said to be an important process in social learning and imitation. In recent years, studies have found that performed and observed actions are represented similarly in the brain. Neurophysiological studies have identified mirror neurons in the premotor and parietal lobes of the macaque brain that fire when a monkey performs an action and when it observes the action being performed by another individual (Iacoboni & Dapretto, 2006). It has been speculated that this provides the neural mechanism underlying the ability to imitate actions performed by another individual; the actions of a demonstrator must be encoded by the observer in order to successfully reproduce the behavior at a later time. Another technique has been used with human participants to study the mirror neurons system. Researchers have used transcranial magnetic stimulation (TMS) to stimulate the motor cortex while simultaneously recording the resulting motor-evoked potentials (MEP) from extremity muscles. Then, participants are either instructed to grasp an object themselves or observe as another person grasps an object. The amplitude of the MEPs increases when the participant grasps an object and when they observe another individual grasping an object (Rizzolatti & Craighero, 2004). This suggests that neurons in the prefrontal cortex are activated in response to both observed and performed actions. However, because human participants are able reliably to discriminate between events they perform and events they observe, the source of these events must be represented in other areas of the brain. Research has pointed to the hippocampal region of the medial temporal lobe, as well as regions of the prefrontal cortex as areas that are necessary for encoding source information. This has been determined by brain-imaging studies (Mitchell & Johnson, 2009) and studies of patients with hippocampal damage who demonstrate source memory deficits (Gold, et al., 2006). This ability to attend to and encode our own actions and actions produced by other individuals would be beneficial for other highly social species. It is would also be adaptive for such species to be able to discriminate between these two types of memories. For example, the ability to distinguish between events we performed ourselves and those we observed makes it possible to determine whether we will be capable of performing the same action in the future. It would also appear to be an important prerequisite for other forms of social knowledge, such as understanding what other individuals know and may therefore be relevant to studies of theory of mind.

The Present Study

As it should be clear from this literature review, our understanding of how different species encode information in memory is still relatively limited; there are numerous questions remaining, and for the data from nonhuman animals that do exist, it is difficult to draw conclusions when there are no comparable experiments done with human participants. Also, the comparative studies have varied broadly in their paradigms and methodologies, making it equally difficult to draw species comparisons. Therefore, in the present study I directly compared rhesus monkeys and 3- to 4-year-old human children on a common memory test. This is a particularly good comparison group, as children at this age have fully developed hippocampal structures and are able to encode and retrieve episodic memories from long-term memory. Children at this age are also in the early stages of language learning, so they are less likely than adults to use deliberate verbal rehearsal strategies, and this too makes them an ideal comparison group for rhesus monkeys. The goal of the present study is also to build on the knowledge produced from previous tasks by incorporating essential features of episodic memory that have been overlooked. To my knowledge, no studies have directly investigated how nonhuman species remember information about their own involvement in past events. Although we may never know whether animals experience and retrieve memories for past events in the same way as humans, we can certainly provide animals with the opportunity to convey source information about their own involvement in a past event. Including this source-memory (or agency) component may elucidate the phylogenic similarities in this memory system which would prove useful in developing animal models of episodic memory. This would also have implications for other areas in comparative cognition. For many years researchers have tried to examine self-awareness in animals using the mirror-mark test (Gallup, 1970; Gallup, 1979). In this procedure, a mark is surreptitiously placed on an individual's forehead while it is anesthetized. The individual is supplied with a mirror and after regaining consciousness is examined to determine whether they perform any behaviors directed at examining the spot on their forehead. There are problems with this approach because for many species, the act of staring at another individual is a threatening or aggressive behavior. Another problem with this approach is that it equates physical recognition with self-awareness.

The present set of experiments was designed to examine whether rhesus monkeys and children between the ages of 3.5 and 4.5 years of age were able to remember information about their own role in past episodes along with other event features (i.e., identity, spatial, temporal, and contextual knowledge). These experiments build on previous research, in which the author and colleagues examined whether rhesus monkeys could be trained to associate abstract icons with performing and observing past events. The methods and results from those experiments were used in designing the experiments in the present study. The next section provides a description of the methods and results from that initial work.

2 PREVIOUS STUDY OF AGENCY IN RHESUS MONKEYS

The monkeys completed a series of training tasks to see whether they were able to use symbolic icons to convey information about their recent behavior. Two initial sessions were intended to familiarize the monkeys with the task of moving the picture on the computer screen, while also teaching them that sometimes they would have to watch the picture and not use the joystick. The first session only required monkeys to move a picture to a selected location on the computer screen. The location was selected randomly on each trial and the monkey had to determine which location had been selected by trying to move the joystick to that location (the picture only moved when the monkey moved the joystick in the corresponding direction of the chosen location). The picture remained in the location and flashed once every second for a total of 3 seconds before disappearing. After a brief delay (1s) two choice icons appeared on the screen (a star within a circle and a purple box with vertical lines). The monkeys had to learn one icon (star shape) if they had moved the picture and the other icon (purple box) if they had watched the picture move. The icons always appeared in the same position on the screen, so the task was fairly simple. In the next session, the monkey had to learn to refrain from touching the picture while it was moving on the screen and to select the corresponding icon after a brief delay. The monkeys completed 3,000 trials in each of these sessions.

Agency Training

The monkeys then completed the following training tasks in which various controls were introduced: 1) a basic discrimination task in which performed and observed trials were mixed together and monkeys had to select the appropriate icon, 2) the discrimination task with choice positions randomized on each trial, 3) an added control so that the joystick/picture moved at the same speed on performed and observed trials, 4) an added control so that the joystick/picture moved along the same path on performed and observed trials, 5) another control added in which the monkeys had to remove their hand from the joystick after each trial, and 6) a longer delay interval (10s) added to the task. The number of trials completed and the percent correct on the last 100 trials of each task are shown in Table 2.1. All of the monkeys were significantly above chance on the last 100 trials of each training task, as determined by a binomial test, $p < .001$.

Table 2.1: Accuracy on the last 100 trials of each agency training task

Agency Training Tasks		Murph		Gale		Willie		Chewie	
		Trials	Last	Trials	Last	Trials	Last	Trials	Last
1	Discrimination	6,228	98%	10,656	92%	8,924	96%	9,807	95%
2	Choice Positions	8,720	91%	15,276	96%	15,854	87%	13,636	98%
3	Joystick Speed	3,000	99%	4,000	85%	3,715	82%	2,000	90%
4	Joystick Path	13,970	92%	14,820	94%	15,578	77%	15,553	88%
5	Remove Hand	15,577	96%	15,609	79%	15,292	73%	15,715	96%
6	10s Delay	6,907	76%	23,088	88%	15,581	56%	19,715	91%

Results from the final task (10s delay) indicated that monkeys were able to retain information about their behavior after a brief delay interval. The monkeys did respond fairly quickly on most of these trials (three of the monkeys responded within 5 seconds on 95% of the trials; one monkey responded within 10 seconds on 95% of the trials). However, there were trials in which the monkeys took substantially longer to respond. This provided a unique opportunity to examine memory for agency after extended retention-intervals (1 minute – 3 minutes). Two of the four individuals were reliably accurate even after these extended delays. Murph was correct on 79% of these trials (*n*=14) and had a median response latency of 1m 48s. Chewie was correct on 66% of these trials (*n*=183) and had a median response latency of 1m 15s.

DMTS Tasks

These monkeys had previously participated in a *what-where-when* memory experiment (Hoffman, Beran & Washburn, 2009). In this study, they learned to respond to three separate delayed matching-to-sample tasks: 1) an *identity task*, 2) a *spatial task*, and 3) a *temporal task*. A similar version of these tasks was presented to the monkeys to determine whether they still understood the objective of the tasks. In the identity task, a picture appeared at one of two locations in the top left and right portions of the computer screen. It remained in this location and flashed once every three seconds and then disappeared from view. There was a brief (1s) delay in which the screen was blank before the monkeys were presented with a choice between two photos. The spatial task was identical except that in the test phase the monkeys had to now make a choice between the two spatial locations. The temporal task was slightly different; the same picture on each trial was presented in the center of the computer screen. The photo disappeared and was followed by a short or long delay. These icons were the same as those used in the previous what-where-when memory study. Then, the monkeys had a choice between the two temporal icons.

Table 2.2: Review of DMTS tasks

Delayed Matching-to-Sample Tasks												
	Identity			Spatial			Temporal			Agency		
	Trials	Correct	*p*	Trials	Correct	*P*	Trials	Correct		Trials	Correct	*p*
Murph	1,344	97%	***	1.201	81%	***	3,062	94%	***	3,439	75%	***
Gale	1,577	92%	***	1.926	81%	***	2,505	91%	***	3,374	80%	***
Willie	1,706	86%	***	3.164	84%	***	3,016	93%	***	7,234	58%	***
Chewie	1,412	81%	***	2.562	92%	***	1,000	83%	***	4,794	95%	***

Paired Memory Tests

The monkeys were also given trials with two randomly selected questions on each trial. This provided an opportunity to measure accuracy when the test type could not be anticipated beforehand and to examine whether accuracy on the first test predicted accuracy on the subsequent test. Figure 1.1 shows each monkey's accuracy on the different question types when they were presented first in the test pairing. A binomial test was done to determine whether each monkey's accuracy differed from chance performance (50%). Each monkey was above chance on the identity and temporal tests, $p < .001$. In addition, three of four individuals were above chance on the spatial memory test and two of the four monkeys also scored at above chance levels on the agency test, $p < .001$. There was also evidence that some of the features were integrated in memory. This was determined using a binary logistic regression to examine the relationship between outcome of the first memory test and outcome of the second memory test. If the monkeys correctly responded to the spatial memory test when it was presented first, they were significantly more likely to be correct on the second memory test, $\chi^2(1, N = 7{,}908) = 12.63$, *Exp(B)* = 1.19, $p < .001$. If the monkeys were correct on the agency test when it was presented first, they were also more likely to be correct on the second memory test, $\chi^2(1, N = 7{,}674) = 4.32$, *Exp(B)* = 1.11, $p < .05$.

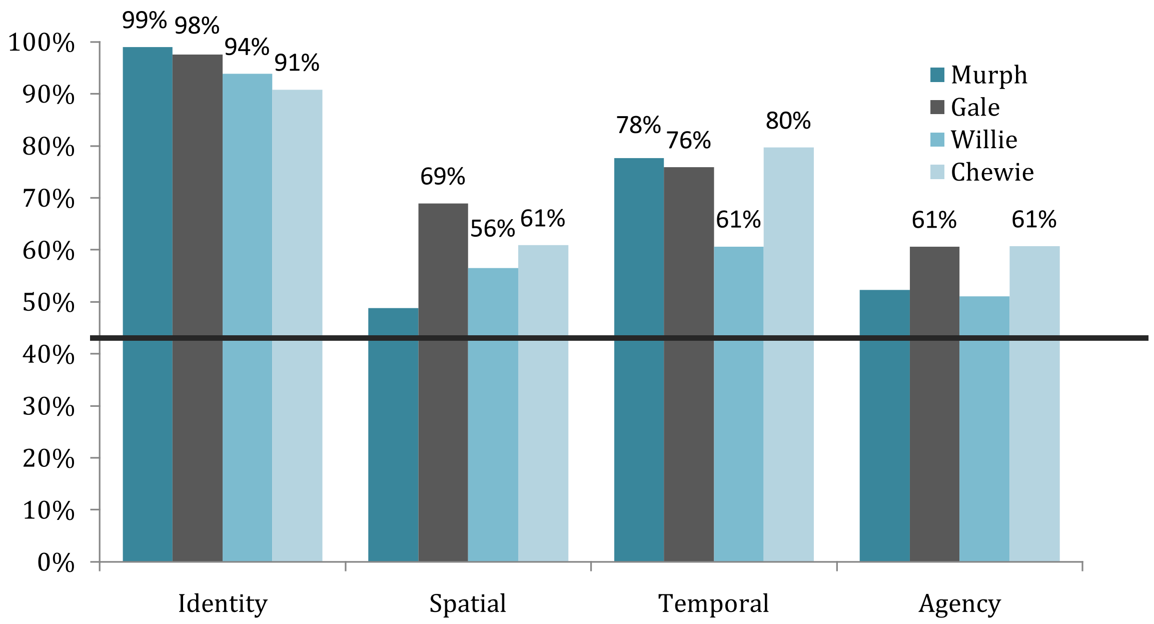


Figure 2.1: Results from a preliminary study examining agency in rhesus monkeys.

3 EXPERIMENT 1

The purpose for this experiment was to examine how rhesus monkeys remember separate event features in working memory. There were five conditions in this study; each one was designed to assess memory for a different feature from past events. 1) In the *identity condition*, monkeys had to remember the identity of a particular object they had seen. 2) In the *spatial condition*, monkeys had to remember where the object had appeared. 3) In the *temporal condition*, the monkeys had to remember how long ago the event occurred. 4) In the *agency condition*, the monkeys had to remember whether they performed the event or observed the event. 5) In the *context condition*, the monkeys had to remember information about the environmental context from the event. The same basic memory task was used in all conditions; a monkey observed an event on a computer display in his home cage and after a brief retention interval (5s) was presented with a two-choice discrimination in which he had to make a behavioral response to convey information about the event. The event portion of the memory task was consistent across conditions; the only thing that varied was the type of information the monkey had to remember. This made it possible to assess differences in retrieval rates for these different conditions, but also served as a necessary scaffolding stage needed for subsequent experiments which would test how these features were integrated in working memory. In many comparative studies with animals, the task goals may not be immediately apparent to the animals and so some initial training is often required. The tasks in the present study are relatively novel (in order to control for prior learning) and not specific to any one species (so that the testing paradigm can be used across species). Although some tasks were relatively straightforward, other tasks required animals to learn abstract icons in order to convey information about past events. As such, monkeys required some training to learn "the rules of the game" for each condition/task and to ensure that they understood the objective of each task.

Participants

Eight joystick-trained, adult male rhesus monkeys (*Macaca mulatta*) participated in this study. The monkeys all had prior experience with computerized testing and had participated in previous cognitive studies (see Washburn, Beran, Evans, Hoffman & Flemming, in press). The individuals that participated in this experiment included animals (Murph, Gale, Willie and Chewie) that had some prior experience on *what-where-when* memory tasks (Hoffman, Beran & Washburn, 2009) as well as monkeys that were naïve to these tests (Lou, Hank, Han, Luke and Obi). All were familiar with the task of matching stimuli based on physical resemblance and association. Each monkey had a computerized test system (or "Rumbaughx"; Washburn et al., in press) set up in its home cage and had the opportunity to work on the task at their own pace during testing sessions. Each monkey participated on a voluntary basis, receiving supplemental food rewards (flavored chow pellets) in exchange for participation. No monkey was reduced in body weight or otherwise deprived of food or fluids for purposes of testing.

General Procedure

In each condition, monkeys were presented with a delayed matching-to-sample (DMTS) task, in which they experienced an event presented on the computer screen, followed by a memory test in which they had to choose between two alternatives, one of which corresponded to the recent event. The event phase in each of these conditions was the same – a photo moved along a diagonal path to one of two locations in the upper left and right corners of the computer screen. The critical difference between the tasks/conditions was that each one tested monkeys on a different feature from the event. The format of the memory tests for each task/condition was consistent, with monkeys receiving a choice between two alternatives and being reinforced with food/auditory feedback if they were correct. The nature of the choice stimuli varied depending on the task/condition; for the identity and spatial conditions, the alternatives were physical representations from the events (i.e., the monkeys had a choice between two photos, or two spatial locations/boxes), whereas for the temporal, agency, and context conditions, the monkeys were trained to associate icons/shapes with different contingencies (e.g., the monkeys learned that if they had experienced a short delay, they should select the purple triangle, but if the delay had been long, they should choose the black circle). In all conditions, monkeys received the same type of feedback for correct and incorrect responses. If they made a correct choice, the monkeys received a fruit-flavored primate chow pellet and heard an ascending tone that they had learned to associate with positive outcomes. If they made an incorrect choice, they simply heard a brief and low buzz tone to inform them that their choice was incorrect. To reduce proactive interference, all trials were followed by a 3s interval before the next trial was available to the monkey. To begin a trial, the monkey moved the cursor to a start box in the center of the computer display.

In many cases, DMTS tasks are relatively straightforward and require matching on the basis of physical similarity. However, three of the DMTS tasks in this experiment were designed to assess relatively abstract features of past events (e.g., one's level of involvement or the amount of time that has elapsed since an event) using icons that correspond to event features. Consequently these tasks required some prior training for the monkeys to learn the associations between the various contingencies (e.g., performing an action) and its associated icon. The nature of the training procedures varied for each condition/task. The specific methods for each *training task* and *experimental task* are described in later sections. The monkeys completed each *training task* when they reached a performance criterion of 75% correct (and a minimum of 2,000 trials) or when they completed the maximum number of trials (10,000 or one month of testing on the same task). The monkeys completed each *experimental task* when they reached a performance criterion of 85% correct on three consecutive sessions and a minimum of 2,000 trials or when they reached the maximum number of trials (10,000 trials or one month of testing on the same task).

The monkeys were each given 3-4 testing sessions each week. Each session was 4-h in length and the monkeys were given the opportunity to complete up to 3,000 trials during each session. Because the monkeys worked at their own pace on this task, the specific number of trials completed during each session varied depending on the type of task and motivation of the animals. The monkeys could take as long as they needed to respond to each memory test. Therefore, on some trials the delay length was substantially longer than the initial delay selected by the computer program. One way to deal with this would be simply to begin a new trial if a monkey took too long to respond, but this approach is problematic because monkeys might simply have waited longer to respond on trials in which they were uncertain (thereby strategically or unintentionally avoiding these trials but artificially inflating their accuracy level). Indeed, many studies have indicated that monkeys are sensitive to their uncertainty during cognitive tasks and will take the opportunity to opt out for a smaller reward rather than risk failing a memory test for which they are not prepared (Smith & Washburn, 2005). In light of this, monkeys were presented with memory tests on each trial regardless of their response latency. In addition, trials with variations in response latencies (on the order of 10-20 seconds) could actually be useful in understanding how monkeys represented temporal intervals and whether the icons were used flexibly or based on discrete intervals.

Identity DMTS The identity task was used to assess how rhesus monkeys remembered information about item identity in working memory. The monkeys did not receive any additional training on this task because the objective of matching based on physical similarity was familiar to all of the monkeys due to prior experience on similar tasks. The stimuli in this task consisted of 80 visually distinct photographs. On each trial, one photo (the "sample") was chosen at random from the set and presented in the bottom-center portion of the computer screen. From this position, the photo moved along a diagonal path to one of two locations in the top-right and top-left portion of the computer screen, each of which was defined by a dark grey box (7.5cm x 7.5cm). The object remained in this location for 3s and then disappeared from view so that all that remained was a blank, white computer screen. After a 5s retention interval, the monkeys were given a choice between two photos (one that matched the photo presented earlier and a distractor photo that did not match the sample). These choices appeared in the left and right hand portions of the computer monitor, and the position of the correct photo was randomized across trials to ensure that the correct photo appeared approximately equally often in the left and right positions (see Figure 3.1).

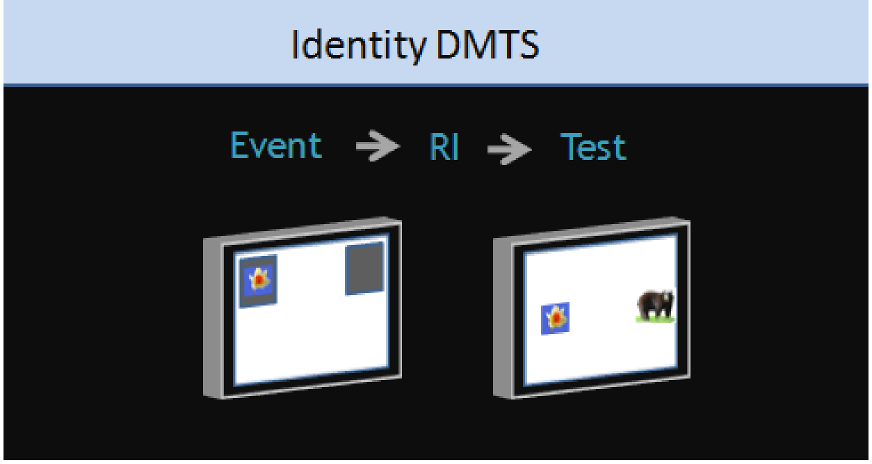


Figure 3.1: An illustration of the identity DMTS task used with rhesus monkeys

Spatial DMTS The spatial task was used to assess how rhesus monkeys remembered basic spatial features from computer-generated events. For some of the monkeys, this type of spatial problem was a unique challenge they had not encountered before in an experimental setting and therefore we provided these individuals with a series of training tasks with increasing delay intervals (no delay → 500ms delay → 2s delay) before presenting them with the experimental task. In each of these training tasks, a photo moved to a particular location on the screen. This was followed by either an immediate choice (the photo remained in the location and the monkeys simply needed to use the joystick to select the location of the photo) or a delayed choice (the locations/photos disappeared and were followed by a brief delay before the choice icons appeared).

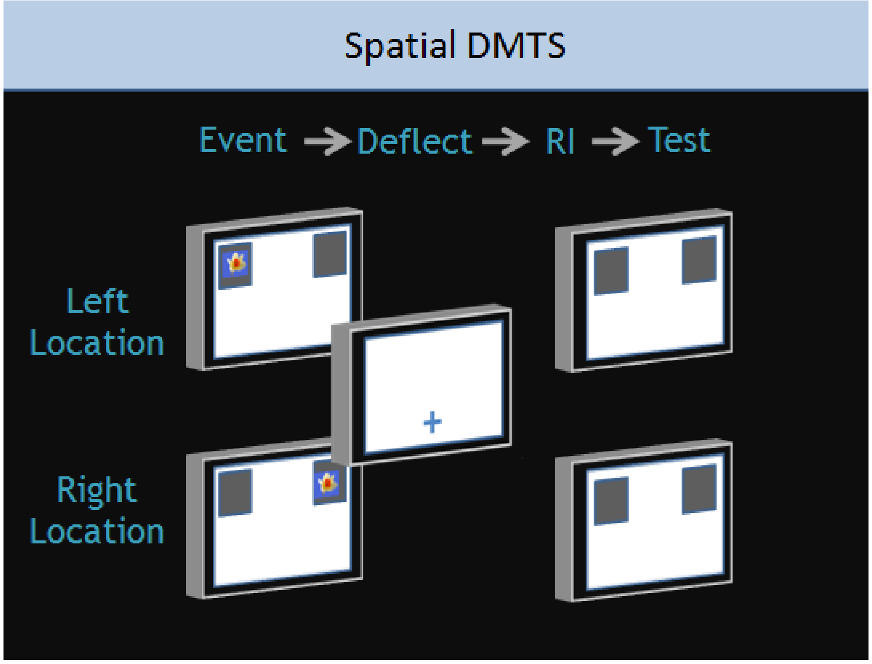


Figure 3.2: An illustration of the spatial task used with rhesus monkeys

After demonstrating that they were able to perform the task after these delays (with at least 75% accuracy on the last session), the monkeys moved on to the experimental version of the task. The experimental version of the spatial task was the same as the procedure described earlier for the identity task, but with one difference. After the photo moved to one of the locations and then disappeared, the monkey had to deflect the joystick cursor down to contact a large blue "+" shape in the bottom-center portion of the screen, at which point the delay began (see Figure 3.3). This control was needed to ensure that monkeys could not keep their hand on the joystick and use their hand position as a proprioceptive cue when given the memory test. After the 5s retention interval, the monkeys had a choice between the two spatial locations and had to select the location where the photo had been moved. As both locations were identical in all respects and both were present during the event, the only way this task could be solved was by encoding spatial information about the event itself.

Temporal DMTS The temporal task was used to assess how rhesus monkeys remembered temporal information from the computer-generated events. The temporal distinction was on a relatively short time scale (5s and 15s) and required animals to match symbolically based on this distinction. This type of task typically requires more trials for monkeys to learn. Therefore, all of the monkeys completed a training task to teach them this temporal distinction. In this task, the monkeys simply observed a picture (a clipart image of a clock with wings) on the computer screen which remained on the screen for a 3 s interval. This was followed by a short or long delay, and then a choice between two shapes (a purple triangle and black circle). The locations of the choice icons were randomly determined on each trial, so that monkeys had to attend to the icon itself rather than learning to move the cursor right or left depending on the delay length. In order to be successful on this task, the monkeys had to learn the arbitrary association between each delay length and icon. After monkeys were performing reliably on this training task (75% correct on the last session), they proceeded to the experimental task. The only difference between the training and experimental tasks was that a randomly selected photo (instead of the same image) was used on each trial and the photo moved to a location rather than simply being displayed in the center of the screen. The monkeys then had a choice between the two temporal icons, and they were reinforced for selecting the appropriate icon (see Figure 3.3).

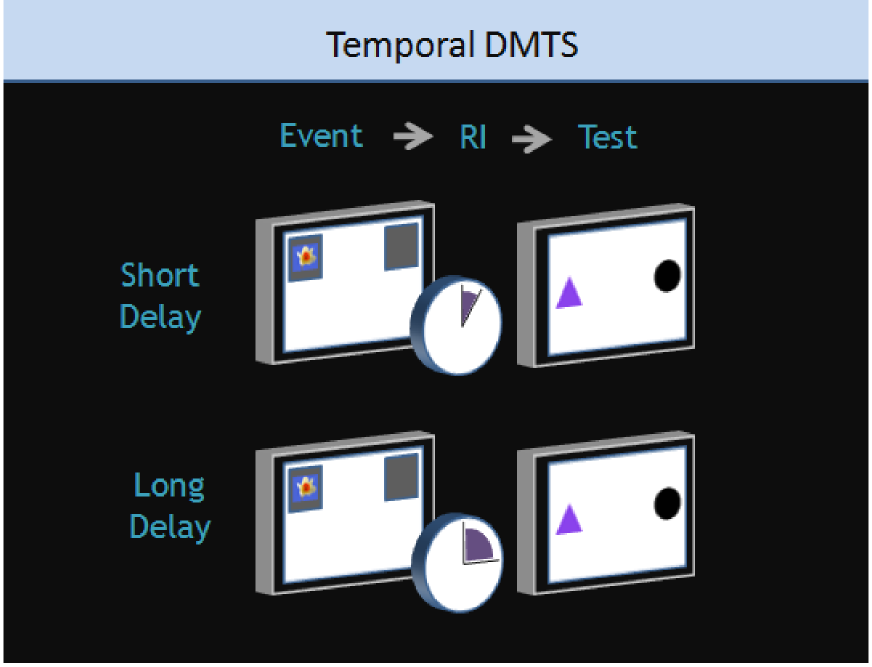


Figure 3.3: An illustration of the temporal DMTS task used with rhesus monkeys.

Agency DMTS The agency task was used to assess how monkeys remembered information about their own involvement in a computer-generated event, specifically, whether they watched the event or played an active role in it. This task possibly posed a greater challenge to the monkeys, as it required them to associate their own past actions with arbitrary icons (a circle with a star in the center and a purple box with vertical lines). In the past, the monkeys had never been required to encode their own action events in memory or use icons to convey information about these behaviors. To help monkeys learn that the icons could be used to convey information about their own role in a past event, they were presented with three training phases. In the first phase, the monkeys were given sessions which consisted entirely of performed trials. This was to familiarize the monkey with the task of moving the picture on the screen. Although the monkeys all had extensive experience with using a computer joystick, this particular task required them to hold the joystick in a particular position, as the cursor would only move in a straight diagonal path to the selected location. After a 1s delay, monkeys made a choice between two icons (a circle with a star in the center and a purple box with vertical lines). The position of the choice icons (left or right) was randomly determined on each trial. The monkey was reinforced for selecting the appropriate icon (purple box with vertical lines) with food and auditory feedback. In the second phase of training, the monkeys had to watch as the picture moved independent of their own involvement. To ensure that monkeys did not try to participate, code was included in the program to re-start the trial if the joystick was touched while the picture was moving. The purpose of this was to familiarize monkeys with the idea that on some trials they did not get to move the picture. After the picture was moved and disappeared, a brief 1s delay followed before the monkeys were shown the choice icons. The monkey was reinforced for selecting the appropriate icon (star inside circle). In the final phase of training, the trial type (performed or observed) was randomly determined on each trial. After a 1s delay, the monkeys were given a choice between the two agency icons. The monkeys were able to move on to the experimental version of the task when they either: a) met 75% correct criterion on the last session, or b) completed 10,000 trials. The event phase of the experimental task was the same as for the other tasks, but as with the spatial task, the monkey had to deflect the joystick cursor down to make contact with a large "+" icon at the bottom of the screen. This was to ensure that the monkeys would not be able to use proprioceptive cues or motor memory about their recent hand position on the subsequent memory test. This control ensured that the monkeys were responding on the basis of their memory for self-agency and not simple motor memory (e.g., "it must be a performed trial because my hand was just touching the joystick). After deflecting the joystick, the monkeys experienced a brief retention interval (5s) followed by a choice between the two agency icons (a grey star inside a blue circle and a purple box filled with wavy black lines). An illustration of this task is provided in Table 3.4.

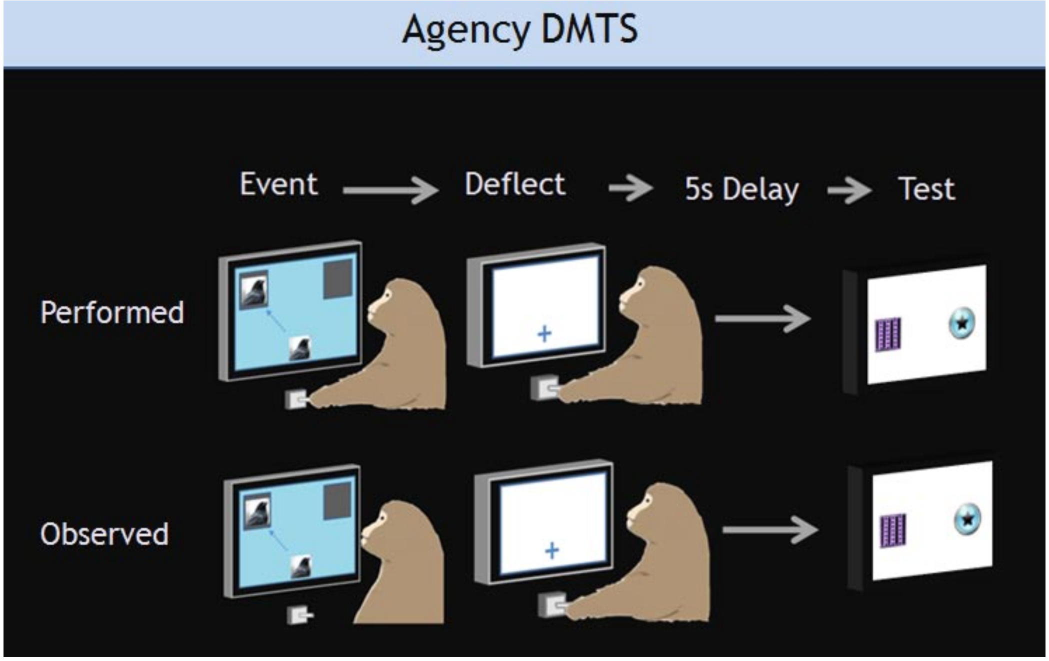


Figure 3.4: An illustration of the agency task.

In both the training phases and experimental task, the performed and observed trials were equated on all relevant measures to ensure that monkeys were responding on the basis of their own actions and not some other cue that differentiated the two conditions. There are many ways an animal could differentiate performed and observed trials other than relying on memory for their past actions. For example, if an animal moved the object at a slower rate than the computer, the animal might learn to make the discrimination between these two conditions on the basis of the joystick speed and not their own involvement. Therefore, in this task, the speed at which the monkey could move the object was identical to the speed at which the object was moved by the computer. The specific path along which the object moved was also held constant across the two trial types; the object always moved in a smooth diagonal direction from the bottom center of the screen to one of the locations in the upper part of the screen. To ensure that both observed and performed trials were equivalent, monkeys were not able to choose the location where they would move the object; the joystick cursor would only move in the randomly selected direction. There was also another important reason for not allowing monkeys to choose where they moved the picture. If monkeys were able to select the location, they could adopt the strategy of always selecting the same location on all trials. Although this would not pose a problem for this individual task, it would have posed a problem for Experiment 2, where monkeys completed randomly selected pairs of memory tests. If monkeys were to adopt the strategy of selecting one location more often than the other, they could remember this general rule and succeed on spatial memory tests without relying on memory. Consequently, the computer program randomly selected the location on all trials.

Context DMTS The context task was used to assess how rhesus monkeys remembered contextual information about the background or environment during computer-generated events. As with the temporal and agency tasks, this task was relatively abstract and required animals to learn the association between background lighting and arbitrary icons. Each monkey received two training phases before this task. In the first phase (no delay training), the background display was randomly chosen on each trial. This background was presented simultaneously with the choice icons (a sun and night skyline) which were positioned randomly on each trial. The monkeys had to select the sun icon if the background was bright or the night icon if the background was dim. In the second phase (1s delay training), the background was displayed for 3s, but then disappeared and was replaced with a blank, white computer screen. After a 1s delay, the monkeys were shown the two choice icons. In this situation, the monkeys now had to remember the background display and respond accordingly. In the third phase of training, the delay was extended to 5s to determine whether monkeys could retain this information about background display (see Figure 3.5). It was necessary to reach 75% correct performance on this final training task to progress to the experimental task. However, none of the monkeys were able to reach this performance criterion and therefore could not continue to the experimental task, which would have included the typical event phase used in the other conditions.

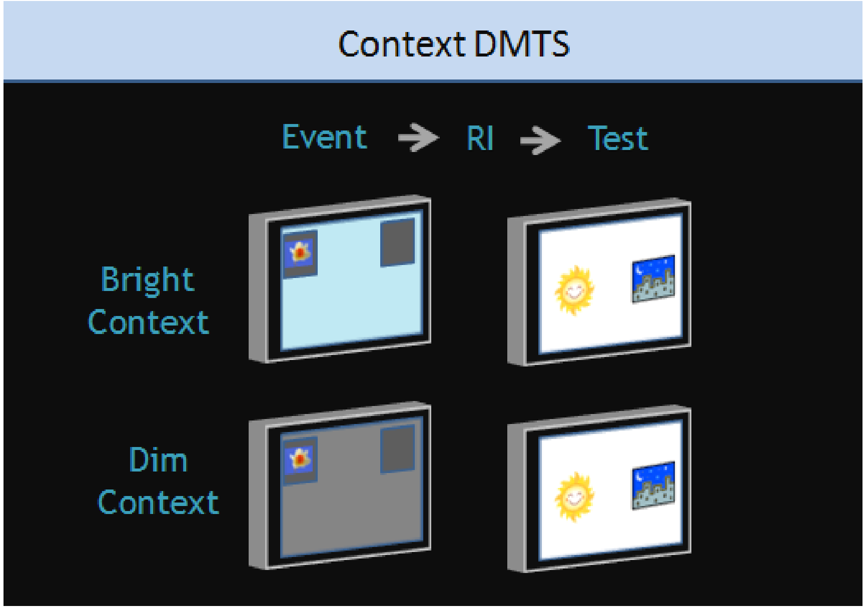


Figure 3.5: An illustration of the context task.

Results

The data for each individual monkey and task were analyzed using binomial tests to determine whether performance was significantly different from chance (50%). This made it possible to determine whether each individual monkey was able to retrieve a specific feature from memory and whether there were individual differences in retrieval accuracy. Because there was not a time limit for completing each trial, there was variation in response latencies for each individual and task. In this situation, the best method for measuring central tendency was to calculate the median scores and the 95th percentile scores to determine where the majority of the trials fell along the response timescale. A binary logistic regression was also used to determine whether response latency was a significant predictor of performance on the subsequent memory test.

Identity DMTS The monkeys did not receive any training before completing the identity task. The task was relatively straightforward because it required the monkeys to match based on physical similarity and all of the monkeys had prior experience on such matching tasks. The results from each monkey are displayed in Table 3.1. The monkeys that did not participate in prior research examining what-where-when memory (Obi, Luke, Lou, Han, and Hank) are labeled in the table with an asterisk (*) to indicate that they were naïve to the task prior to this study. Each monkey reached the performance criterion (85% correct on three consecutive test sessions) and their overall accuracy was significantly above chance (50%) using a binomial test, $p < .001$. The majority of the monkeys reached the criterion within a relatively small number of sessions (3-5). However, one monkey (Hank) took a larger number of sessions and trials to reach this criterion. The median response latencies and 95th percentile score for latencies were calculated to determine where the majority of the responses fell along the timescale. The monkeys responded within 7 seconds on 95% of the trials. However, there were individual differences in response latencies, with some monkeys taking longer to respond on the memory test. The median and 95th percentile scores were also calculated for each individual monkey and are given in Table 3.1.

Table 3.1: Results from the identity DMTS task

Identity DMTS							
	Trials	Response Latencies		All Trials		Last Session	
Chewie	n = 1,801	Md = 2.83	P_{95} = 18.32	85.90%	***	85.16%	***
Gale	n =7,34	Md = 2.25	P_{95} = 3.27	95.92%	***	91.43%	***
*Han	n = 2,063	Md = 2.34	P_{95} = 7.36	94.43%	***	95.50%	***
*Hank	n = 5,970	Md = 2.94	P_{95} = 5.74	76.33%	***	85.71%	***
*Lou	n = 2,474	Md = 2.42	P_{95} = 6.16	98.26%	***	97.86%	***
*Luke	n = 731	Md = 2.28	P_{95} = 4.48	90.56%	***	95.94%	***
Murph	n = 512	Md = 2.25	P_{95} = 3.81	97.07%	***	95.20%	***
*Obi	n = 710	Md = 2.67	P_{95} = 5.93	92.68%	***	95.80%	***

Spatial DMTS The results from the training phases and experimental version of the task are shown in Table 3.2. Four of the eight monkeys had experience with spatial memory tests like this one and did not require any training. The other individuals completed a series of training tasks to familiarize them with the task of matching based on physical location. The training task was identical to the experimental task except shorter delays were used. The number of trials and percent correct for each training task are shown in Table 3.2. The monkeys that did not participate in prior research examining what-where-when memory (Obi, Luke, Lou, Han, and Hank) are labeled in the table with an asterisk (*) to indicate that they were naïve to the task prior to this study. The monkeys first completed training sessions with a 500 ms delay, but they remained at chance levels (50%) even after a substantial number of trials. Consequently, they were moved to an easier version of the training task (no delay) in which the photo remained in the location and the monkeys simply needed to use the joystick to select the location of the photo. The monkeys did learn how to respond on this version of the task, and all but one individual (Hank) reached criterion on the subsequent training tasks (500ms delay and 2s delay). After a month of training and a large number of trials (>15,000), Hank failed to reach criterion on this task and consequently did not move on to the experimental version of the spatial task. The seven monkeys that completed the experimental version of the spatial DMTS task all reached criterion (85% correct on three consecutive testing sessions). The overall percent correct for each monkey also was significantly above chance (50%), $p < .001$. There were individual differences in response latencies, with some monkeys taking longer to respond on the memory test. The median response latencies and 95th percentile score for latencies were calculated to determine where the majority of the responses fell along the timescale. The monkeys responded within 11 seconds on 95% of the trials. Additional values for each monkey are given in the Table 3.2. The latencies for this task were slightly longer than those in the identity DMTS task because the monkeys had to deflect the joystick cursor to the bottom of the screen after each event.

Table 3.2: Results from the spatial DMTS task

Spatial Training								
	500 ms		No Delay		500 ms		2s	
*Obi	*n*=2,153	49.51%	*n*=5,000	90.54%	*n*=6,208	89.42%	*n*=6,621	95.05%
*Luke	*n*=672	52.23%	*n*=3,000	88.27%	*n*=3,244	79.41%	*n*=3,441	95.50%
*Han	*n*=6,076	57.55%	*n*=2,183	98.44%	*n*=3,210	77.73%	*n*=1,931	80.84%
*Hank	n=9,566	50.61%	n=5,617	96.83%	n=26,059	75.40%	n=15,514	60.40%

Spatial DMTS							
	Trials	Response Latencies		All Trials		Last Session	
Chewie	*n* = 4,312	Md = 6.27	P_{95} = 27.25	73.54%	***	85.71%	***
Gale	*n* = 6,873	Md = 5.23	P_{95} = 6.74	80.68%	***	85.83%	***
*Han	*n* = 11,619	Md = 5.19	P_{95} = 12.86	77.73%	***	85.60%	***
*Lou	*n* = 8,841	Md = 5.41	P_{95} = 11.88	88.19%	***	90.20%	***
*Luke	*n* = 1,543	Md = 5.31	P_{95} = 7.75	87.23%	***	96.60%	***
Murph	*n* = 2,935	Md = 5.17	P_{95} = 7.67	87.80%	***	91.67%	***
*Obi	*n* = 1,528	Md = 5.09	P_{95} = 7.52	88.42%	***	89.61%	***

Temporal DMTS The results from the training phases and experimental version of the task are shown in Table 3.3. The monkey that failed to meet criterion on the identity and spatial tasks (Hank) was excluded from this and future tasks. Because he had difficulty on physical matching tasks, it was expected that he would encounter more difficulty when the task required matching with icons. The remaining monkeys completed a temporal training task to familiarize them with the delays and temporal icons that they would use to respond to this task. On each trial, a large clipart image of a clock appeared on the screen for 3s, followed by either a short (5s) and long (15s) delay interval. The delay was randomly selected on each trial and the temporal choice icons appeared in randomly chosen positions so the monkey had to learn by trial-and-error that short delays were associated with one icon (the purple triangle) whereas long delays were associated with a different icon (the black circle). All seven monkeys reached criterion on this task and moved on to the experimental version. All seven monkeys that completed the experimental version of the temporal DMTS task reached criterion. The overall percent correct for each monkey was also significantly above chance (50%), $p < .001$. The median response latencies and 95th percentile score for latencies were calculated to determine where the majority of the responses fell along the timescale. The monkeys responded within 5 seconds on 95% of the trials. Additional values for each monkey are given in the Table 3.3. The monkeys that did not participate in prior research examining what-where-when memory (Obi, Luke, Lou, and Han) are labeled in the table with an asterisk (*) to indicate that they were naïve to the task prior to this study.

Table 3.3: Results from the temporal DMTS task

Temporal Training				
	All Trials		Last Session	
Chewie	n = 5,159	80.77%	n = 1,000	85.40%
Gale	n = 3,898	68.70%	n = 348	81.61%
*Han	n = 7,704	75.80%	n = 1,000	83.70%
*Lou	n = 7,950	73.52%	n = 1,000	88.80%
*Luke	n = 6,032	79.01%	n = 1,000	89.40%
Murph	n = 3,868	76.01%	n = 842	84.20%
*Obi	n = 5,525	71.62%	n = 572	81.47%

Temporal DMTS							
	Trials	Response Latencies		Percent Correct		Last Session	
Chewie	n = 2,167	Md = 2.59	P_{95} = 9.01	88.83%	***	85.95%	***
Gale	n = 2,044	Md = 2.61	P_{95} = 3.95	79.65%	***	87.54%	***
*Han	n = 2,853	Md = 2.36	P_{95} = 5.10	84.33%	***	84.49%	***
*Lou	n = 4,008	Md = 2.48	P_{95} = 4.26	86.85%	***	86.22%	***
*Luke	n = 4,797	Md = 2.34	P_{95} = 5.03	87.39%	***	94.19%	***
Murph	n = 2,503	Md = 2.28	P_{95} = 3.30	88.77%	***	91.00%	***
*Obi	n = 9,968	Md = 2.72	P_{95} = 5.35	87.15%	***	88.68%	***

Agency DMTS The results from the training phases and experimental version of the task are shown in Table 1.4. The monkeys that did not participate in prior research examining what-where-when memory and prior agency research (Obi, Luke, Lou, and Han) are labeled in the table with an asterisk (*) to indicate that they were naïve to the task prior to this study. The monkeys each completed two orientation sessions; in the first session, they had to use the joystick to move a photo to a predetermined location on the computer screen and in the second session they had to refrain from touching the joystick while the photo moved. In both of these sessions, they were presented with a choice between the two agency icons and had to learn to select one icon in response to the first type of event and the other icon in the second type of event. The purpose of these orienting sessions was to teach monkeys how to perform each event type and to teach them that the different events were associated with different responses. In the training task, they were presented with a random selection of performed and observed trials and they had to distinguish between performed and observed events after 1s delay intervals. Four monkeys reached criterion on this task. The remaining individuals completed the maximum number of trials without reaching this criterion. However, because these monkeys were extremely close to the set criterion, they were allowed to move on to the experimental version of the agency task.

The total number of trials and percent correct for each monkey on the experimental agency task are displayed in Table 3.4. The overall percent correct for each monkey was also significantly above chance (50%), $p < .001$. The monkeys completed the task when they reached the criterion (85% correct on three consecutive sessions) or completed 10,000 trials on this task. Four of the seven individuals met criterion on this task. However, because these individuals were very close to the criterion (~70%) and were significantly above chance, they were permitted to continue to the final DMTS task in this experiment. The median response latencies and 95th percentile score for latencies were calculated to determine where the majority of the responses fell along the timescale (see Table 1.4). The monkeys responded within 11 seconds on 95% of the trials. Additional values for each monkey are given in the Table 3.4.

Table 3.4: Response Latencies and Percent Correct for the Agency DMTS

Agency Training				
	All Trials		Last Session	
Chewie	*n* = 5,381	81.88%	*n* = 177	90.96%
Gale	*n* = 8,718	71.68%	*n* = 325	88.31%
*Han	*n* = 25,579	61.77%	*n* = 1,295	68.11%
*Lou	*n* = 38,631	62.88%	*n* = 236	69.92%
*Luke	*n* = 15,877	71.89%	*n* = 1,619	95.99%
Murph	*n* = 14,363	66.73%	*n* = 1,388	80.84%
*Obi	*n* = 12,360	59.03%	*n* = 508	66.93%

Agency DMTS							
	Trials	Response Latencies		All Trials		Last Session	
Chewie	*n* = 8,407	Md = 6.55	P_{95} = 10.81	79.16%	***	79.40%	***
Gale	*n* = 7,583	Md = 4.31	P_{95} = 5.52	82.91%	***	90.60%	***
*Han	*n* = 16,129	Md = 7.30	P_{95} = 10.65	62.54%	***	62.54%	***
*Lou	*n* = 8,835	Md = 8.02	P_{95} = 14.39	57.36%	***	62.50%	***
*Luke	*n* = 3,132	Md = 7.88	P_{95} = 10.22	68.10%	***	66.73%	***
Murph	*n* = 12,490	Md = 7.44	P_{95} = 9.63	72.48%	***	74.47%	***
*Obi	*n* = 13,569	Md = 7.77	P_{95} = 10.31	61.89%	***	59.36%	***

Context DMTS The monkeys completed a series of training tasks to teach them the association between the background display and the context icons. In the first training task, the monkeys were shown the background at the same time as the context icon. The monkeys quickly met criterion on this no delay version of the task. In the next training task, the background appeared for 3s and disappeared for 1s before the monkeys were given the choice between the context icons. Only three of the seven monkeys reached the training criterion on this task (see Figure 3.5). These individuals moved on to complete the 5s delay task. There were four individuals that did not meet the criterion: two of the monkeys were included in the 5s delay task to determine whether a longer delay interval (and consequently longer waiting times between trials) would improve accuracy, but the other two monkeys (Gale and Murph) did not complete the 5s delay task This is because these monkeys had completed the context training prior to the other individuals, and it was only after their training that I considered including the 5s delay as a control. In the 1s delay task, there was very little cost to responding incorrectly on a trial. The monkeys may not have been sufficiently motivated to learn how to perform this task because they could simply respond randomly on each trial and get a large number of pellets. In contrast, there was a longer wait time if a monkey responded incorrectly after a 5s delays and if the monkeys were responding randomly they would receive 20% of the pellets they normally would in a session. However, presenting the monkeys with a longer delay time did not improve accuracy for these individuals. In fact, none of the individuals reached criterion, even after they completed a large number of trials (10,000 trials or persisting on the task for one month without improvement).

Figure 3.5: Results from the context DMTS task.

Context Training						
	500 ms Delay		1s Delay		5s Delay	
Chewie	*n* = 4,159	84.23%	*n* = 14,600	53.30%	*n* = 3,262	51.69%
Gale	*n* = 4,177	84.70%	*n* = 8,086	66.87%	----------	---------
Han	*n* = 3,000	88.80%	*n* = 8,016	65.70%	*n* = 4,489	50.79%
Lou	*n* = 1,940	92.73%	*n* = 16,531	65.82%	*n* = 11,005	56.68%
Luke	*n* = 7,209	94.65%	*n* = 10,581	72.89%	*n* = 2,764	52.42%
Murph	*n* = 3,609	96.70%	*n* = 7,160	68.52%	----------	---------
Obi	*n* = 2,602	92.43%	*n* = 2,352	65.65%	*n* = 12,729	52.39%

4 EXPERIMENT 2

The purpose of this experiment was to examine how rhesus monkeys remembered information about self-agency, along with spatial, temporal and contextual features when they were not able to anticipate which feature they would be tested on. The previous experiment provided baseline measurements of how monkeys remembered the individual components in memory as well as a way to measure differences in retrieval accuracy for the different features, but the present study was designed to determine whether retrieval of any given feature was a reliable predictor of retrieval of the other features. If so, this would indicate that the components are integrated to form a cohesive memory for the past episode. In the past, research with rhesus monkeys has shown some evidence for *what-where-when* memory integration (Hoffman, Beran & Washburn, 2009). For example, for some individuals, the ability to retrieve temporal information concerning a past event was a reliable predictor of whether they were successful at retrieving the other event components. Of particular interest in the present study was whether successfully retrieving information about the environmental context in which an event occurred and/or one's involvement in a past event was a successful predictor of whether monkeys will retrieve the additional memory components as well. If a monkey's performance on the agency and context tests reliably predicted their ability to retrieve other event features, this would indicate that these may indeed be relevant features that are integrated in memory for past events.

Participants

The same eight rhesus monkeys from the previous experiment participated in this experiment. Note that even those monkeys that failed to learn some portion of the Experiment 1 tasks were tested in the present study.

Event Presentation

At the beginning of each trial a start box appeared in the center of the screen. In order to begin the trial, the monkey used the joystick to move the cursor to the start box. A photo was randomly selected from the same set of images used in the previous experiment. The photo appeared at the bottom-center of the computer screen. It appeared against one of the two context backgrounds (dim or bright) used in the previous experiment. On each trial, the computer program also determined whether the trial would be a performed or observed trial. On monkey-observed trials, the object moved across the screen in a diagonal path to a randomly selected location (top-left or top-right), as in Experiment 1. In contrast, on monkey-performed trials, the object remained stationary until the monkey touched the joystick. The monkey could only move the joystick in the general direction of the selected location (i.e., the program only responded to input in that direction). However, to ensure that monkeys were aware that they were in control on these trials, the photo stopped moving if the monkey released the joystick and would resume again once the monkey moved the joystick in the appropriate direction. Although it was necessary to ensure that monkeys understood that they played a role in monkey-performed trials, it was also essential to control for any visual cues that might serve as a basis to discriminate the two trial types. In order to control for these cues, the movement of the object was constrained to the same path and speed on performed and observed trials. Although the monkey was responsible for moving the object on performed trials, the computer program constrained the photo's movement so that it moved along a straight diagonal path and at the same speed as monkey-observed trials.

After the photo reached the location (defined by a dark grey square) it remained there for 3s before disappearing. The program randomly selected a retention-interval for each trial (5s or 15s), but before the retention-interval could begin, the monkeys had to deflect the joystick cursor to make contact with a large blue "+" in the bottom-center portion of the screen. This control was also used in the previous experiment and was necessary to ensure that the monkeys could not use information about their hand position to solve the memory tests.

Paired Memory Test

The retention-interval was followed by two randomly selected memory tests. Because there were five different question types (identity, spatial, temporal, context and agency), this randomization process resulted in 20 different trial-types. These trial types can be broken down according to which memory test was presented first: 1) An *identity test* followed by another test type (i.e., identity-spatial, identity-temporal, identity-context, identity-source), 2) A *spatial test* followed by another test type (i.e., spatial-identity, spatial-temporal, spatial-context, spatial-agency), 3) A *temporal test* followed by another test type (i.e., temporal-identity, temporal-spatial, temporal-context, temporal, source), 4) An *agency test* followed by another test type (i.e., agency-identity, agency-spatial, agency-temporal, agency-context), and 5) A *context test* followed by another test type (i.e., context-identity, context-spatial, context-temporal, context-agency), The memory tests were identical to those used in the previous experiment; however, in this experiment the monkeys did not know which tests they would be given and had to complete two tests after each event. As in the prior experiment, the monkeys continued to receive auditory feedback after each test, and if correct, they received a flavored primate pellet. There was a 5s interval between each trial to reduce the chance of proactive interference and the monkeys always had to make contact with the start box to initiate a new trial. An illustration of the paired memory test is provided in Table 4.1.

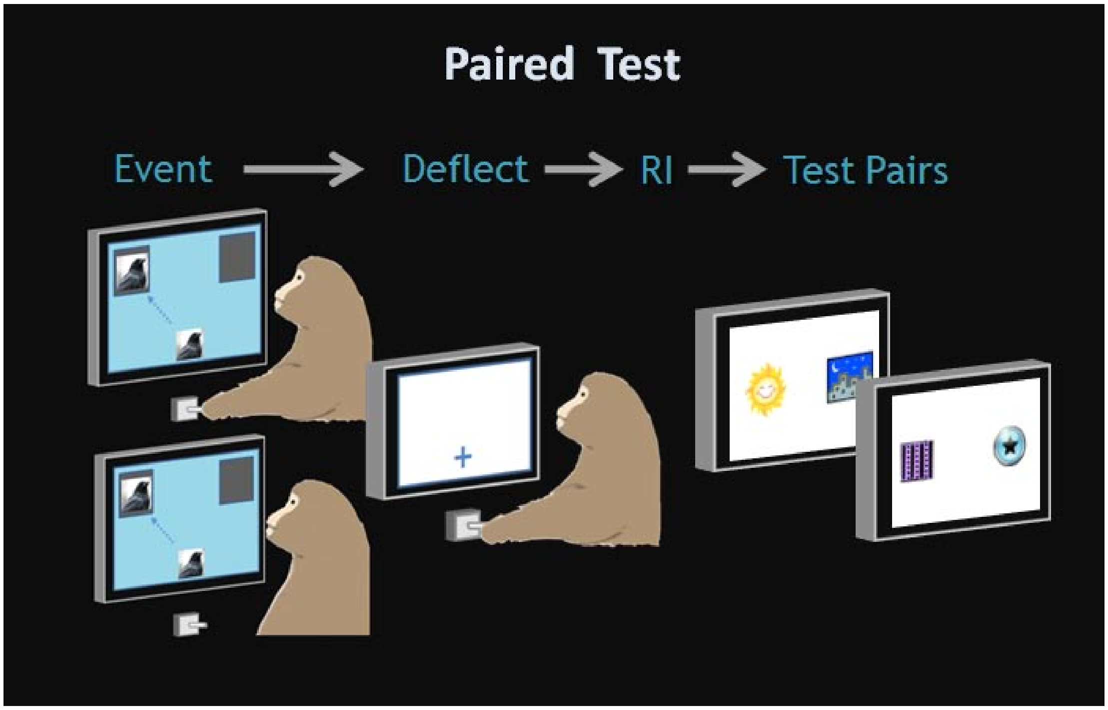


Figure 4.1: An illustration of the paired memory test used with rhesus monkeys.

Results

The monkeys completed at least 5,000 trials on this task (1,000 trials of each test type) and were allowed to work on the task for 5 to 6 test sessions per week for a six week period. The monkeys completed an average of 13,252 trials in this experiment (with an average of 23 sessions and 582 trials per session). There were 20 possible test pairs so this large number of trials was necessary to have a sufficiently large sample for each test pair/condition.

A binomial test was conducted to determine whether performance on the different test types was significantly different than chance (50%) and the results are displayed in Table 4.1. The monkeys were significantly above chance on the identity, spatial, temporal and agency tests when they were presented as the first test in the pair. However, only two of the eight monkeys were significantly above chance (p < .001) on the context test. There was one monkey who also exhibited chance performance on the spatial task. The monkeys were less accurate at recalling many of the components if they had to do so after first responding to a different memory test. Even in this situation, the monkeys all remained above chance on the identity and temporal components, but two individuals were no longer above chance on the spatial test and agency tests (the same individuals in both cases).

The monkeys who had retained context information continued to do so when it was presented as the second memory test, and one individual actually performed better on the context test when it was presented second and was significantly above chance when the test was given in this position. Although these differences were statistically significant, they were not the high levels observed in the previous experiment, but did indicate that monkeys retained some features from past events in memory. This analysis included all of the trials completed, so the percentage correct does not reflect how learning may have improved monkeys performance over time. In the next analysis, the first 500 and last 500 trials were examined to determine how accuracy changed over time.

Table 4.1: Accuracy when presented as first test

Accuracy When Presented As First Test

	Trials	Identity		Spatial		Temporal		Agency		Context	
Chewie	2,380	78%	***	58%	***	90%	***	55%	***	52%	
Gale	2,895	95%	***	63%	***	76%	***	55%	***	49%	
Lou	3,398	83%	***	57%	***	81%	***	54%	***	57%	***
Murph	3,068	93%	***	64%	***	90%	***	61%	***	53%	***
Obi	1,510	91%	***	52%		87%	***	56%	***	52%	

Accuracy When Presented As Second Test

	Trials	Identity		Spatial		Temporal		Agency		Context	
Chewie	2,380	76%	***	51%		71%	***	52%		52%	
Gale	2,895	88%	***	53%	**	65%	***	52%	*	51%	
Lou	3,398	75%	***	51%		65%	***	52%		54%	***
Murph	3,067	89%	***	54%	***	73%	***	54%	***	53%	***
Obi	1,510	84%	***	49%		66%	***	53%	*	53%	*

Accuracy and Experience The first block of 500 trials was analyzed to determine whether monkeys were significantly above chance on the first trials they experienced. The only memory tests included in this analysis were the first test from each pair. The results from the first block of 500 trials revealed that all of the monkeys were significantly above chance on the identity and temporal tests. One of the five monkeys was also significantly above-chance on the agency test during these initial trials. However, none of the monkeys showed above chance performance on the spatial or context tests. The last block of 500 trials was also analyzed to determine whether accuracy improved across sessions. The previous experiment consisted of a long series of tasks and the monkeys may have needed to have some period to relearn the different tasks and icon associations. In the last block of trials, all of the monkeys were significantly above chance on the spatial test and two additional individuals showed above chance performance on the agency test. The data and results from these analyses are displayed in Table 4.2.

Table 4.2: First and last trial blocks

First and Last Trial Blocks							
		First Block of 500 Trials			Last Block of 500 Trials		
Identity	Chewie	*n* = 96	68.75%	***	*n* = 102	82.35%	***
	Gale	*n* = 91	86.81%	***	*n* = 101	100.00%	***
	Lou	*n* = 108	67.59%	***	*n* = 100	91.00%	***
	Murph	*n* = 98	76.53%	***	*n* = 100	99.00%	***
	Obi	*n* = 93	76.34%	***	*n* = 96	97.92%	***
Spatial	Chewie	*n* = 101	51.49%		*n* = 100	63.00%	*
	Gale	*n* = 96	55.21%		*n* = 102	64.71%	**
	Lou	*n* = 96	50.00%		*n* = 81	61.73%	*
	Murph	*n* = 113	51.33%		*n* = 101	63.37%	**
	Obi	*n* = 109	51.38%		*n* = 103	43.69%	
Temporal	Chewie	*n* = 96	84.38%	***	*n* = 103	91.26%	***
	Gale	*n* = 97	65.98%	**	*n* = 104	79.81%	***
	Lou	*n* = 93	68.82%	***	*n* = 113	86.73%	***
	Murph	*n* = 89	73.03%	***	*n* = 90	92.22%	***
	Obi	*n* = 98	82.65%	***	*n* = 111	89.19%	***
Agency	Chewie	*n* = 103	52.43%		*n* = 107	47.66%	
	Gale	*n* = 108	60.19%	*	*n* = 98	53.06%	
	Lou	*n* = 99	58.59%		*n* = 98	57.14%	
	Murph	*n* = 110	54.55%		*n* = 110	64.55%	**
	Obi	*n* = 94	51.06%		*n* = 103	59.22%	$p < .10$
Context	Chewie	*n* = 104	53.85%		*n* = 88	43.18%	
	Gale	*n* = 108	45.37%		*n* = 95	40.00%	
	Lou	*n* = 104	55.77%		*n* = 108	54.63%	
	Murph	*n* = 90	50.00%		*n* = 99	56.57%	
	Obi	*n* = 106	51.89%		*n* = 87	47.13%	

Response Latencies The monkeys responded relatively quickly on the majority of trials (on 95% of the trials monkeys responded to both questions within 4 seconds). The response latencies for each monkey are given in Table 4.3. However, one concern is that monkeys may have taken longer to respond on some types of trials and may have used this as a cue in the memory test. For example, the monkeys could have potentially taken longer to respond when there was a long delay than when there was a short delay. They could have moved away from the test station during these longer delays and then upon returning could use their recent behavior as a cue to guide their responses (e.g., I had to walk back over to the test station before responding, so I should select the long icon). In addition, the added time could have made the distinction between short and long delays more pronounced and may have made the task easier. However, the response latencies for short and long delay trials indicated that monkeys responded just as quickly on both trial types. The median response latency was 2.22 seconds for short delay trials and 2.31 seconds for long delay trials. For both trial types, 95% of the trials completed fell below the 4 second mark, indicating that the monkeys responded quickly on both types of trials. The response latencies also did not vary as a function of whether the monkey performed or observed the event. The median response latency was 2.27 seconds for both performed and observed trials, and the majority of the responses (95%) were made within 4 seconds.

Table 4.3: Response latencies for the first and second memory tests

Response Latencies							
		Latency for Test 1			Latency for Test 2		
	N	Median	P_{95}	SD	Median	P_{95}	SD
Chewie	11,899	2.20	4.59	69.59	1.89	2.95	527.62
Gale	14,472	2.11	3.11	708.12	2.03	3.13	806.61
Lou	16,988	2.38	3.88	776.00	2.31	3.69	374.49
Murph	15,330	2.22	3.38	363.47	2.18	3.41	961.24
Obi	7,552	2.45	4.55	42.63	2.22	3.80	48.61

Comparing Accuracy for Performed and Observed Trials Another question was whether monkeys were more likely to retrieve correctly the event features if they had performed the event than if they had simply watched the event. If there was an enhancement effect for performing the trial, this effect would likely be most apparent when the task was still relatively novel. Each monkey's performance on the first 500 trial block were examined to see whether performing the event led to enhanced memory for this agency information, as well as the other event features. A binomial logistic regression was used to determine whether monkeys were more accurate at recalling individual features on performed or observed trials. Although they were significantly above chance at reporting the identity component for both observed and performed trials, an enhancement effect was found for the identity test: the monkeys performed significantly better on this test when they had performed the event themselves. However, the monkeys performed significantly better on the agency test when they had observed the event than when they had performed it. The percent correct for both trial types and the results of the analyses are provided in Table 4.4.

Table 4.4: Comparing accuracy on observed and performed trials

Comparison of Observed and Performed Trials												
	Observed			Performed			Binary Logistic Regression					
	Trials	Correct		Trials	Correct		B	S.E.	Wald	df	*Exp(B)*	*P*
Identity	249	71%	***	237	79%	***	-0.47	0.21	4.79	1	1.59	0.029
Spatial	247	54%		268	50%		0.19	0.18	1.10	1	0.83	0.294
Temporal	222	73%	***	251	77%	***	-0.25	0.21	1.43	1	1.29	0.232
Agency	264	69%	***	250	41%	**	1.19	0.19	41.01	1	0.31	0.001
Context	275	49%		237	54%		-0.17	0.18	0.87	1	1.18	0.351

However, the monkeys were more likely to select the observed icon (64%) than the performed icon (36%) on these trials (i.e., they were just more likely to select the observed icon regardless of the type of trial) and this is why they appeared to be more accurate on observed trials.

Integration of Features The probability of getting the second test correct increased for two of the monkeys if they had also been correct on the first memory test. This was determined using a binary logistic regression to determine whether performance on the first test was a reliable predictor of performance on the subsequent memory test (see Table 4.5). The odds ratio, which is denoted by *Exp(B)*, can be interpreted as the relative increase in the dependent variable given a one unit increase in the independent variable. For Murph, the probability of correctly responding to the second test in the pair increased by a factor of 1.11 if he had responded correctly to the other memory test, $p < .001$. For Gale, the probability of correctly responding to the second test in the pair increased by a factor of 1.13 if he had responded correctly to the other memory test, $p < .001$.

Table 4.5: Binary logistic regression to examine feature integration

Feature Integration							
	N	B	S.E.	Wald	df	*Exp(B)*	*P*
Chewie	11,900	0.06	0.04	1.94	1	1.06	0.164
Gale	14,477	0.12	0.04	10.85	1	1.13	0.001
Lou	16,992	0.05	0.03	2.02	1	1.05	0.155
Murph	15,339	0.10	0.04	7.52	1	1.11	0.006
Obi	7,552	0.06	0.05	1.28	1	1.06	0.257

Separate analyses were also done for each of the 20 test pairs to determine which specific event features showed evidence of integration. The results from this binary logistic regression are given in Table 4.6. For two individuals, performance on the spatial memory test was a significant predictor of performance on the agency test. However, the odds ratio indicated that there was an inverse relationship between the two outcomes. Specifically, if these monkeys had been correct on the spatial test, they were actually less likely to be correct on the agency test. Some monkeys also showed this pattern on the agency-temporal and context-temporal test pairs. The one feature that did show evidence of integration with other features was the temporal component. For one monkey, the chance of being correct on the spatial memory test increased if he had been correct on the temporal test that came before it. This same monkey, along with another individual, was also more likely to be correct on the identity test if he had correctly responded to the temporal test that preceded it.

Table 4.6: Binary logistic regression for separate test pairs

Feature Integration for Separate Test Pairs

		Chewie		Gale		Lou		Murph		Obi	
		Exp(B)	*p*	*Exp(B)*	*p*	*Exp(B)*	*p*	*Exp(B)*	*p*	*Exp(B)*	*P*
Identity	Spatial	1.15	0.49	1.30	0.41	1.14	0.448	1.48	0.14	0.98	0.96
Identity	Temporal	1.25	0.30	0.98	0.97	1.38	0.088	1.03	0.93	0.85	0.70
Identity	Agency	1.07	0.74	0.86	0.72	1.20	0.308	0.84	0.52	1.04	0.91
Identity	Context	1.16	0.44	1.16	0.63	1.10	0.626	1.07	0.81	1.38	0.40
Spatial	Temporal	1.23	0.26	1.06	0.71	1.15	0.323	0.81	0.24	1.44	0.08
Spatial	Agency	0.96	0.79	0.78	0.11	1.11	0.451	0.74	0.04	0.61	0.02
Spatial	Context	0.74	0.07	1.00	1.00	0.90	0.448	0.84	0.26	0.90	0.62
Spatial	Identity	1.01	0.97	1.60	0.12	1.20	0.255	1.59	0.05	1.32	0.36
Temporal	Spatial	1.31	0.31	1.47	0.03	1.10	0.573	1.44	0.15	0.81	0.49
Temporal	Agency	0.82	0.49	1.14	0.47	1.01	0.935	1.16	0.56	0.85	0.61
Temporal	Context	1.11	0.71	0.98	0.92	1.36	0.080	0.82	0.37	0.81	0.45
Temporal	Identity	0.94	0.84	1.65	0.03	0.76	0.229	1.21	0.60	2.55	0.01
Agency	Spatial	0.90	0.51	1.09	0.57	1.04	0.761	0.94	0.65	0.96	0.85
Agency	Temporal	1.42	0.06	0.62	0.00	0.96	0.792	0.74	0.09	1.09	0.69
Agency	Context	1.00	1.00	0.93	0.61	0.95	0.697	0.91	0.52	1.47	0.06
Agency	Identity	0.79	0.24	1.20	0.39	1.22	0.205	1.01	0.97	1.16	0.59
Context	Spatial	1.00	0.98	0.94	0.66	0.80	0.100	1.05	0.75	0.93	0.74
Context	Temporal	0.90	0.57	0.74	0.06	0.74	0.041	1.06	0.74	1.36	0.17
Context	Agency	1.29	0.12	0.99	0.96	0.92	0.570	1.07	0.63	0.73	0.12
Context	Identity	1.13	0.53	1.43	0.09	0.86	0.323	1.40	0.15	0.77	0.34

5 EXPERIMENT 3

The aim for this experiment was to assess how children between the ages of 3.5 and 4.5 years of age performed on the paired memory task used with rhesus monkeys. To date, there are no comparative studies assessing episodic-like memory or even working memory for *what-where-*

when information in children and a nonhuman species on a comparable memory test. A question of particular interest for the present research is whether children are able to remember information about their own role in past events along with spatial, temporal and contextual features. This study is also particularly relevant because it provides a useful new methodology which may be able to be used with various different populations of children, including those with developmental disabilities and/or episodic memory impairments. The task itself can be used to assess whether particular populations of children and adults (e.g., those on the autistic spectrum) have episodic memory impairments or whether their failures on episodic memory tasks result from the verbal nature of the tasks traditionally used in this area of research. If such episodic impairments are less prevalent when spatial/visual tasks are used in lieu of verbal tasks, an experimental paradigm like the one proposed here could be used to teach children and adults more effective encoding strategies to improve their memory.

Participants

The participants in this study were 20 children between the ages of 42 m (3.5 years) and 55 m (4.5 years). The majority of the children were in the middle part of this range; 15 of the 20 participants in this study were within one month of their 4th birthday (47-49 m). The remaining five children were the following ages: 42 m, 52 m, 53 m, 54m, and 55m. The children were recruited and tested at the Learning and Development Lab and the Child Development Center at Georgia State University.

Procedure

The procedure was very similar to the one used with rhesus monkeys in Experiment 2, but with minor changes to ensure that children were able to understand the objective of the more abstract memory tests (i.e., the temporal, context, and agency). In contrast to monkeys which learned the rules of each DMTS task through trial-and-error, children had a very limited amount of time to complete this experiment. Consequently, they were given a brief demonstration at the beginning of the experiment in which they learned about the different types of events and delays used in the task. The demonstration began with the experimenter asking the child if he or she wanted to play a fun game on the computer. Then, the experimenter said they would show the child how to play the game. There were eight basic parts to the demonstration – each one accompanied by experimenter narration and a visual animation that mirrored the memory task itself. The experimenter script is described here (with a description of the visual display in brackets). Screen captures of the animations used for each stage of the demonstration are also provided in Figure 5.1.

Demonstration The instructions began with a novel photo of a cat (one that would not be used in experiment) and two spatial locations defined by dark grey boxes measuring 7.5cm x 7.5cm. The experimenter said to the child "I'm going to show you a picture" and pointed to the photo of the cat.

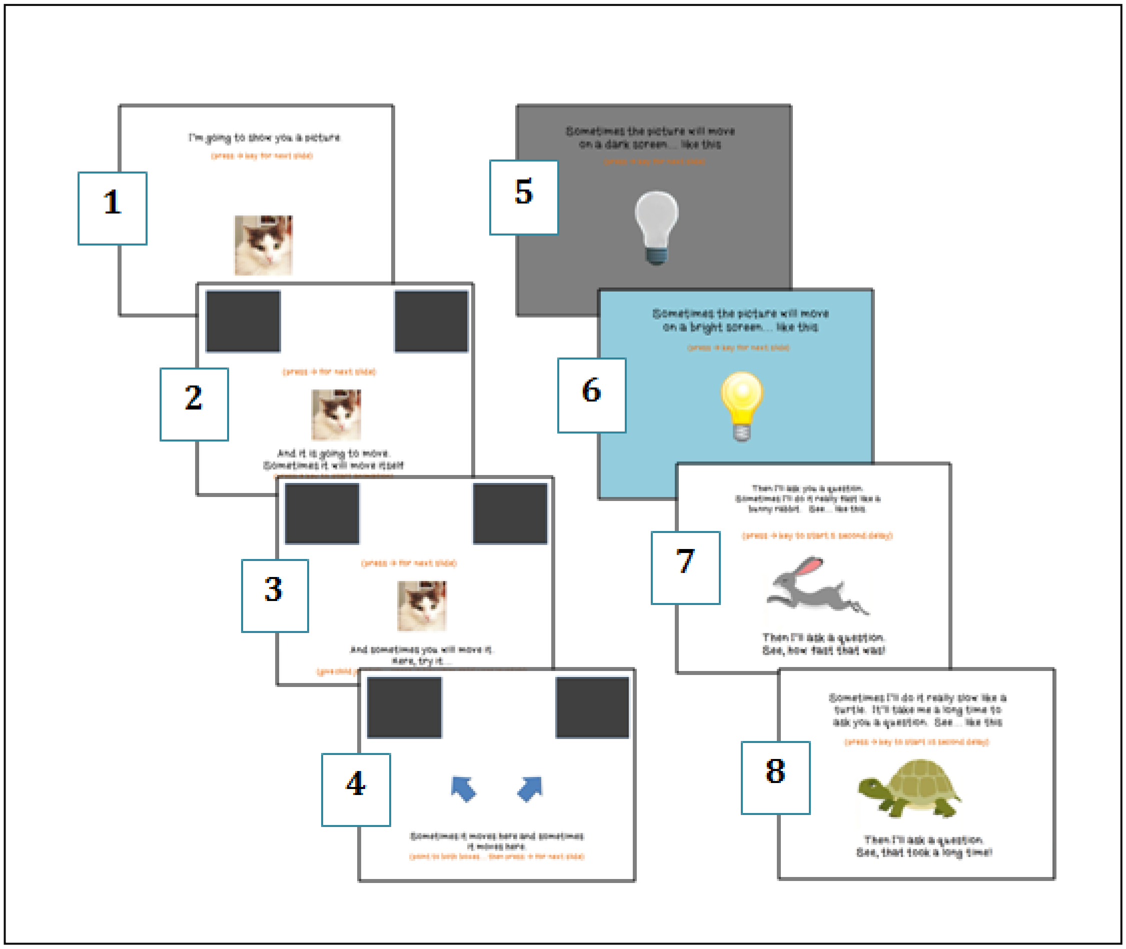
1) The experimenter added, "…and it is going to move. Sometimes it will move itself." The experimenter then clicked a button to begin the animation and the photo moved to the upper-left corner.
2) Then, the experimenter said "…and sometimes you will move it. Here, try it." The experimenter gave the child the joystick (which had been positioned behind the computer screen). The child only needed to move the joystick in any direction for picture to begin (and continue moving) until it reached upper-left location.
3) The experimenter pointed out that the picture could move to either of the two locations on the screen, saying "Sometimes it will move here and sometimes it will move here" while pointing to each location.
4) Next, the experimenter familiarized the children with the context backgrounds. A dark background appeared on the screen, with the corresponding icon (a dark shaded light bulb)

in the center of the screen. The experimenter told the child, “Sometimes the picture will move on a dark screen… like this” and pointed to the dim background and icon on the screen.

5) The context background changed to the bright screen and the corresponding icon (the brightly lit light bulb) appeared on the screen. The experimenter said, “Sometimes the picture will move on a bright screen… like this” while pointing to the background and icon.
6) Finally, the experimenter familiarized the children with the delay intervals that would be used in the study. The icon for the short delay (a rabbit) appeared on the screen and the experimenter said, “Then I’ll ask you a question. Sometimes I’ll do it really fast like a bunny rabbit. See… like this.” The screen went blank and a 5s delay interval followed. The bunny rabbit icon reappeared on the screen and the experimenter said, “Then, I will ask you a question…see how fast that was?”
7) Next, the icon for the long delay (a turtle) appeared on the screen and the experimenter added, “Sometimes I’ll do it really slow like a turtle… like this”. The screen went blank and a 15s delay interval followed. The turtle icon reappeared on the screen and the experimenter said, “Then, I will ask you a question…see, that took a long time!”

The demonstration concluded with the experimenter asking “OK, are you ready to play?”

Testing Session This demonstration phase was followed by a 10 m testing session, in which the children completed 10 trials (one for each type of paired memory test). The children were randomly assigned to one of two conditions (condition A or condition B). The same question pairs were presented to both groups, but in a different order to control for potential order and interference effects. For example, although both groups would receive a paired memory test in which they had to report both agency and temporal



1 I'm going to show you a picture
(press → key for next slide)

2 (press → for next slide)
And it is going to move.
Sometimes it will move itself

3 (press → for next slide)
And sometimes you will move it.
Here, try it…

4 Sometimes it moves here and sometimes it moves here.
(point to both boxes… then press → for next slide)

5 Sometimes the picture will move on a dark screen… like this
(press → key for next slide)

6 Sometimes the picture will move on a bright screen… like this
(press → key for next slide)

7 Then I'll ask you a question. Sometimes I'll do it really fast like a bunny rabbit. See… like this
(press → key to start 5 second delay)
Then I'll ask a question.
See, how fast that was!

8 Sometimes I'll do it really slow like a turtle. It'll take me a long time to ask you a question. See… like this
(press → key to start 15 second delay)
Then I'll ask a question.
See, that took a long time!

Figure 5.1: Screen captures showing each stage of the demonstration.

memory, group A would be given the tests in a different order (temporal → agency) than group b (agency → temporal). The photos used as stimuli in this study were 10 photos selected from the rhesus monkey experiment. The photo, location, delay length, background context, and whether the event was to be performed or observed was semi-randomly determined. There were parameters in the computer code to ensure that each photo was only selected once in the session and there were an equal number of each trial type (e.g., short/long delays for the temporal component).

There were some minor differences in the apparatus used in this task compared to those in Experiment 2. The monkeys used a vertically mounted gamepad joystick to move the photos on the screen and to select choice stimuli. However, children in this age group did not have much experience with these types of devices and in pilot testing they often did not have the manual dexterity needed to move the joystick in a specific direction and hold the joystick in this position for several seconds while the photo moved on the screen. Consequently, the program was modified to respond to user-input in any direction (i.e., the child simply needed to move the joystick in any direction and the photo would begin moving) and the joystick did not need to be held down while the object moved; however, the children were not told this and they continued to maintain contact with the joystick and appeared to be under the impression that they were in absolute control of its movement.

The experimenter in this study gave the participant basic task instructions during the test session (e.g., "move the picture") and also provided instructions for the memory tests after each event (e.g., "which picture did you see?"). The experimenter was not entirely blind to the correct answer (for many of the tests, such as the temporal and agency tests, this would not be possible). However, the experimenter followed a carefully designed script to avoid any unintentional cuing during the memory tests and did not make eye contact or otherwise engage children when the memory tests appeared on the screen. There were other sources of information in the environment that could also serve as cues in this experiment. In some cases, the parent remained in the room because the participant was anxious in the experimental setting and did not want to separate from his or her parent. In these cases, the parents sat behind their child and were carefully instructed not to help their child by providing any "answers" during the task. However, none of the children sought help from their parents or from the experimenter during this experiment. Another concern was that children might be tempted to touch the joystick on all trials. To ensure that they only had access to the joystick on performed trials, it was positioned behind the computer screen. The experimenter gave the child the joystick on performed trials, but always put it back behind the computer screen after the event was completed. This was done to ensure that the child could not use the joystick as a visual cue during the memory test (i.e., "If the joystick is in front of me, I must have moved the picture.")

Event and Memory Tests The experimenter controlled the task using a wireless mouse. Each trial began with a start box in the center of the screen, which the experimenter clicked to begin a trial. The program displayed on-screen instructions and a script for the experimenter. If the child needed to perform the event on a given trial, the experimenter's instructions were to say, "OK, you get to move the picture" and give the joystick to the child. After the event was completed, the joystick was placed back behind the computer screen (see Figure 5.2).

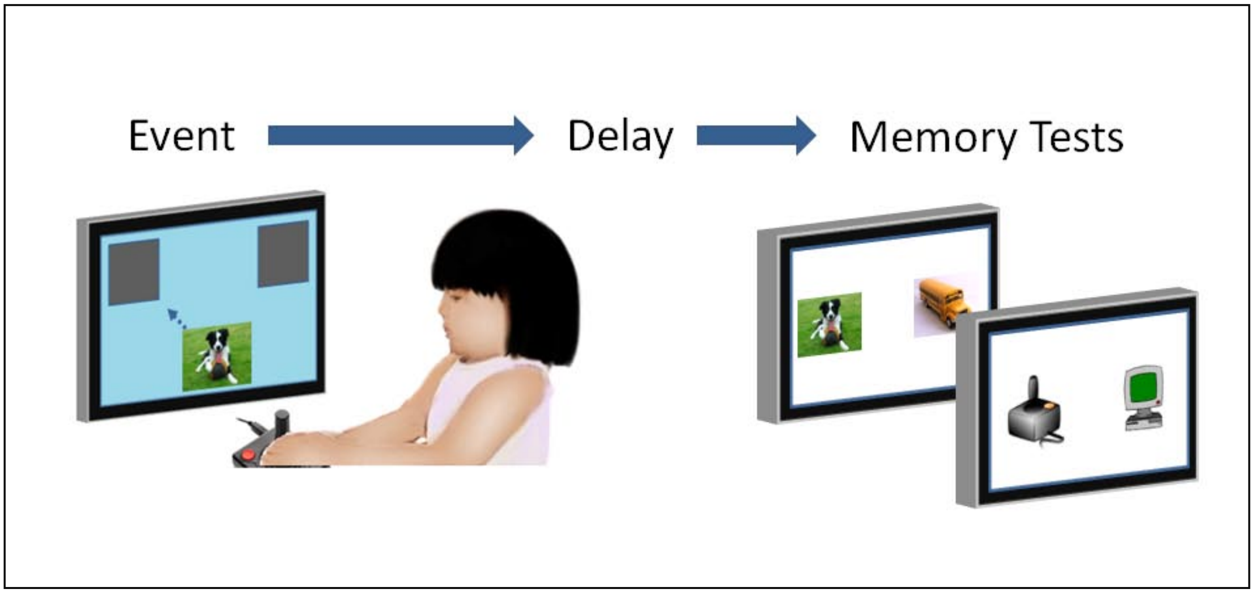


Figure 5.2: An illustration of the task used with children.

The children each received the paired questions in a randomly determined order. The choice icons appeared on the screen and the experimenter followed a verbal script when asking the children about the event (see Figure 5.3). The experimenter asked the child the question as it was written in the script and pointed to both choice icons that corresponded to each possible response (in the order of left → right). The children were encouraged to point to one of the choice icons, but they could also respond verbally if they had trouble using the choice icons. To ensure that children did not become frustrated by incorrect responses, they always received positive feedback after each memory test. After they made a selection, the experimenter would say "good job" and move on to the next memory test or trial. At the end of the experimental session, the children were allowed to select a toy as a gift for participating.

Identity	"What picture did you see? Was it this one [L] or this one [R]?"
Spatial	"Where did the picture go? Did it go here [L] or here [R]?"
Temporal	"Did you have to wait a short time or a long time? Did I ask you fast like a bunny rabbit [L] or slow like a turtle [R]?"
Context	"Did the picture move on a dark screen [L] or a bright screen [R]?"
Agency	"Did you watch the picture move [L] or did you move it [R]?"

Figure 5.3: The script and icon choices used with children.

Results

The children did not appear to engage in any type of overt verbal rehearsal strategy during the delay intervals. In a small number of cases, a child would initially comment that the delay was long, but they did not appear to maintain this information in working memory by continuing to rehearse this information. Instead, they tended to focus on something else in the environment to look at or comment on before the memory test became available. Some children spontaneously labeled the photos or asked the experimenter "what is that?" if they were confused about the photo. The experimenter responded by saying "I don't know. We will have to find out later." This was done to keep the task consistent across trials.

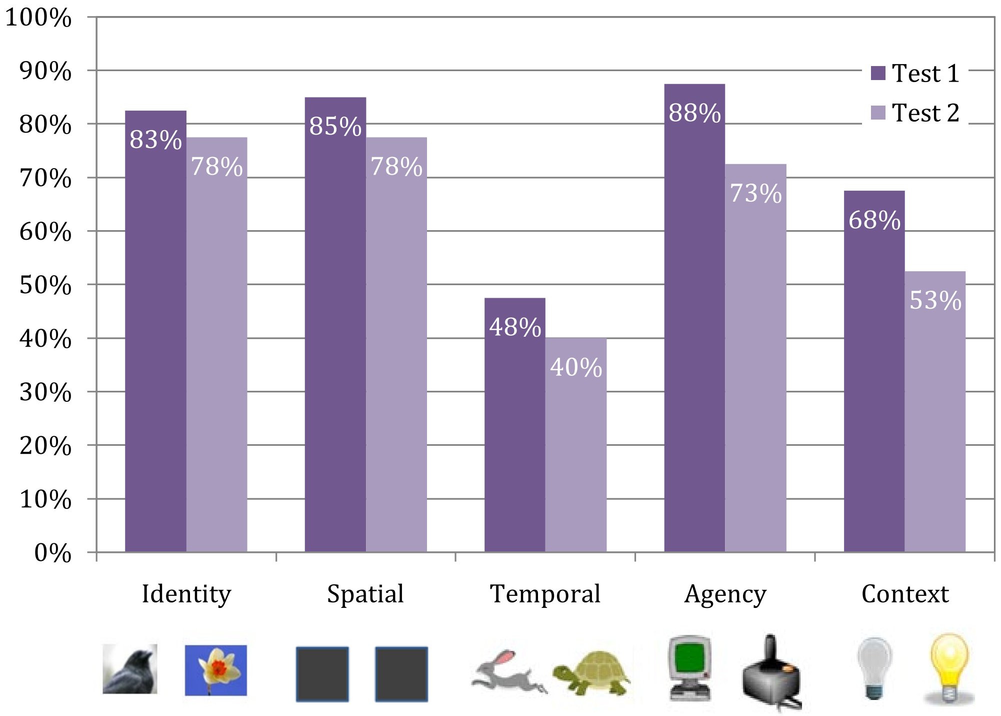


Figure 5.4: The childrens' accuracy for each event feature.

The children performed at levels significantly greater than chance on the identity (83%), spatial (85%), agency (88%), and context (68%) tasks when they were presented first in the test sequence. However, they were not significantly above chance at the temporal task (48%). The children remained above chance on the identity, spatial, and agency tasks even when they were presented as the second memory test. In contrast, the children were no longer above chance on the context memory test when it was presented as the second test in the sequence (see Figure 5.4).

Memory for the Temporal Feature One of the possibilities could be that the children were overestimating or underestimating the delay length on all trials (i.e., always selecting the short or long temporal icon on all trials). They did show a general bias in selecting the short temporal icon more often (67.5%) than the long temporal icon (32.5%), and this difference was statistically significant, $\chi^2(1, N = 40) = 5.74$, $p < .05$. They showed this bias across both short and long delay trials (see Figure 5.5).

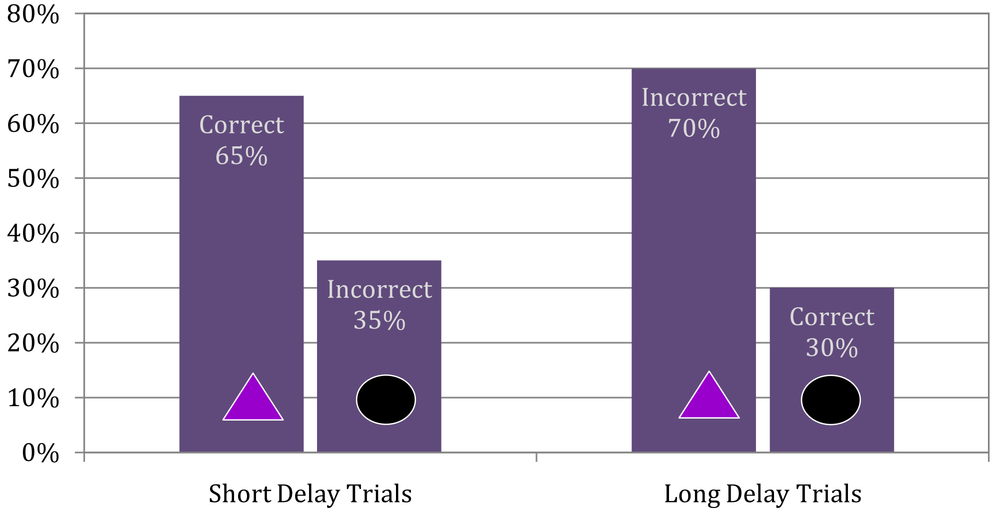


Figure 5.5: Frequency of choosing the short and long delay icons on the first test.

It is likely that most children at this age are just beginning to learn about temporal intervals and the difference in delays used in this task may have been too subtle for the children to distinguish. The data also were analyzed separately for each child to see whether this was the general trend for all of the children in the study or whether a few individuals that scored extremely low on the temporal tests were driving this effect. The scores were approximately evenly distributed: 10% of the children were incorrect on all four temporal tests, 35% correctly responded to one of the four tests, 25% were correct on two of the four tests, and 30% were correct on three of the temporal tests.

Comparing Accuracy for Performed and Observed Trials The children were only above chance at remembering the identity, spatial, and agency features from observed events. However, when they performed the events themselves, they were significantly above chance at reporting all of the features, including the temporal component, which the children were not above chance on initially when all trial types were lumped together (see Figure 5.6) The difference in accuracy for the temporal feature on performed and observed trials was statistically significant, as determined by a chi-square difference test, $\chi^2(1, N = 40) = 8.02, p < .01$. This analysis only included data from the first memory test. The data from the second memory test were not included because the added amount of time taken to respond on these memory tests resulted in poorer performance and including them here might have obscured any real effect agency had on memory.

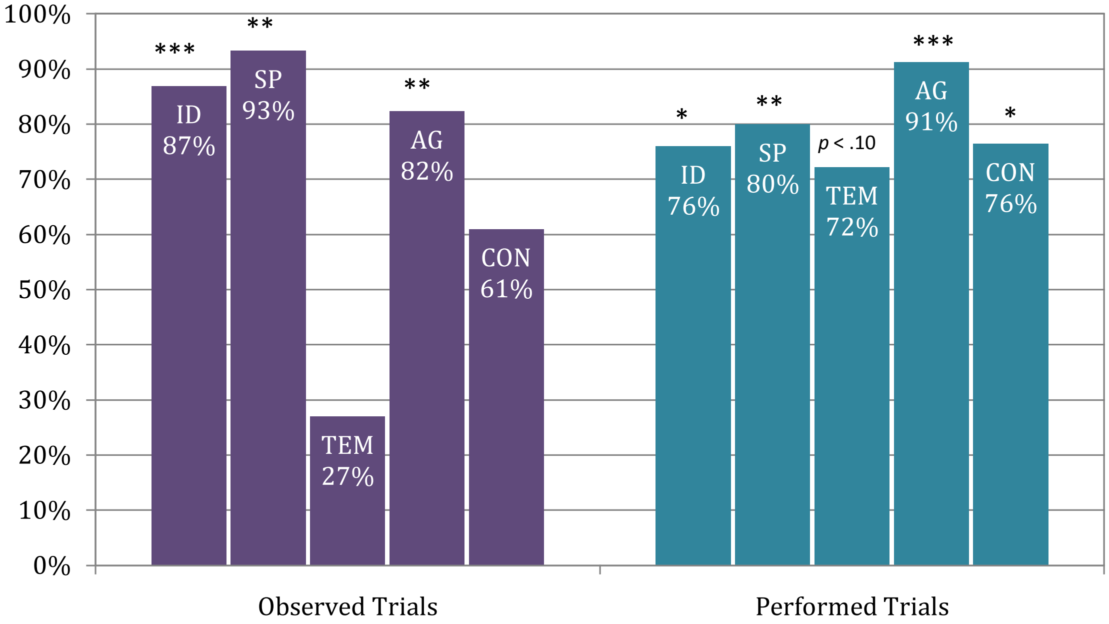


Figure 5.6: Accuracy when analyzed as a function of trial type (observed/performed)

Feature Integration One of the important questions in this experiment was whether children were more likely to respond correctly to the second question if they had correctly retrieved the previous event feature from memory. A binary logistic regression was used to determine whether successful performance on the first memory test predicted subsequent performance on the second memory test. The results indicated that children were significantly more likely to respond correctly to the second memory test if they had been successful on the first memory test $\chi^2(1, N = 100) = 12.63$, $Exp(B) = 2.22$, $p < .01$. However, due to the large number of possible test pairings and relatively small number of trials, it was not possible to use binary logistic regression to examine this relationship in more detail (i.e., at the level of specific test pairings). However, a chi-square difference test was used to examine the relationship between correct retrieval of specific event features. This was done by comparing the number of trials in which children correctly retrieved both features from memory to what we would expect based on accuracy rates for each of the components alone (this expected value was calculated by multiplying the observed probabilities for the two features). There were differences between the expected and observed probabilities for some test pairs (identity-spatial, identity-temporal, and spatial context), but these differences were not significant using a chi-square difference test (see Table 5.1).

This is likely due to the small number of trials within each test pairing (n=20) because the binary logistic regression on all trials did reveal a significant relationship between the test outcomes. For binary logistic regression with one predictor variable, a minimum sample size of 100 is needed to ensure sufficient power to detect a statistical effect (Long, 1997; Peduzzi, Concato, Kemper, Holford & Feinstein, 1996). This criterion for minimum sample size was met when all trials types were included in the analysis ($N = 200$), but not when separate analyses were performed on each possible testing pairing ($N = 20$).

Table 5.1: Results of chi-square tests used to test for feature integration in children

Examining Integration in Paired Tests with Children							
	N	Test 1	Test 2	Expected Probability	Observed Probability	χ^2	*P*
Identity – Spatial	20	80%	81%	65%	75%	0.48	0.490
Identity - Temporal	20	80%	44%	35%	50%	0.92	0.337
Agency – Identity	20	80%	80%	64%	70%	0.11	0.736
Context – Identity	20	60%	80%	48%	50%	0.00	1.000
Spatial – Temporal	20	81%	44%	36%	25%	0.48	0.490
Agency – Spatial	20	80%	81%	65%	70%	0.11	0.736
Spatial – Context	20	81%	60%	49%	70%	1.67	0.197
Temporal – Agency	20	44%	80%	35%	40%	0.11	0.744
Temporal – Context	20	44%	60%	26%	25%	0.00	1.000
Context – Agency	20	60%	80%	48%	35%	0.92	0.337

6 DISCUSSION

The previous research leading up to this set of experiments showed that monkeys are able to retain basic information about their recent behavior on a computerized task and use this information along with other event features to respond to pairs of memory tests. Two of the four monkeys retain information about their own behavior even after relatively long delay intervals (1m – 3m). However, the monkeys could have solved this challenge by using proprioceptive information about their recent hand position to respond to the memory tests. The present set of studies used a more stringent control (the monkeys were required to deflect the joystick down after each event whether or not they had performed the event). The monkeys showed that they still performed the agency discrimination even when they had to deflect the joystick cursor to the bottom of the screen after each event. It did appear to cause some interference though, as the monkeys had been more accurate in the previous agency tests which only required them to remove their hand from the joystick.

The rhesus monkeys performed the identity, spatial, temporal, and agency tasks at above chance levels, but none of the monkeys reached this level of performance on the context task and responded at chance levels even after extensive training. The monkeys have used background color as a discriminative stimulus on other tasks (Flemming, Beran & Washburn, 2007) and in the present study the monkeys discriminated between the two backgrounds when no delay interval was included. Therefore, it seems that the monkeys learned the basic discrimination, but that they either had trouble applying it to longer delay intervals or had trouble remembering the information after delays. It is possible that the background did not attract the monkeys' attention or that the brightness dimension was not relevant to the monkeys. Even though monkeys were not above chance on the context test, it was included in the paired memory test because it could be that retrieval of context was dependent upon retrieval of other features.

The rhesus monkeys also were successful on the identity, spatial, temporal tests when they could not anticipate which test type they would receive. Two of the five individuals also were successful on the agency task in this format. Although there is not much evidence that monkeys engage in any form of visuospatial rehearsal to maintain information in working memory (Washburn & Astur, 1998), it is certainly possible that receiving the same type of memory tests across a large number of sessions made the task easier. In contrast, the use of randomly selected memory tests is more similar to the type of tasks that we routinely engage in everyday and therefore provides a more accurate, albeit more difficult, measure of working memory for these event features. The monkeys did improve on the memory tests over trials; although most of the monkeys were not initially above chance on the spatial, agency, and context tests, many monkeys improved and demonstrated above chance performance on the last 500 trials.

There was also evidence that the identity, spatial, temporal and agency features were integrated in memory. For two monkeys, the probability of correctly retrieving the feature from the second memory test was significantly higher if the monkey had responded correctly to the first memory test. This indicates that, at least in this experimental situation, some monkeys reliably integrated features from past episodes. These monkeys also tended to perform better than the other individuals on the different memory tasks. It is possible that being able to integrate features from past events facilitated encoding and subsequent retrieval. However, it does not appear that integration is necessary for successful performance on these tasks, as three individuals failed to show any evidence of integration, but still performed at significantly above-chance levels on the individual memory tests. It is often difficult to interpret null results from statistical tests to examine binding/integration, as real effects can be obscured by high levels of accuracy across different tests. In previous work with pigeons, Skov-Rackette et al. (2006) acknowledged this issue and noted that although pigeons did not show evidence that components were integrated in memory, it is possible that their high level of performance would have made integration difficult to detect. However, in the present study this was not an issue because all of the monkeys performed at similar levels, yet only some showed evidence that the features were integrated in memory. There do appear to be marked individual differences, both in monkeys' accuracy at recalling independent features and their ability to integrate features in memory.

In the human literature, there is research examining the role that active participation plays in enhancing memory for event features. In many situations, performing an event, as opposed to being a passive observer has been found to improve memory for object information. This effect also was observed in the rhesus monkeys, with the identity component being recalled at a higher rate for events they performed than events they observed. It did not appear that this was the result of the monkeys paying more attention to the events they performed than those they observed because the monkeys were significantly above chance at recalling features from both test conditions. A different effect was observed for recalling agency information; monkeys were more likely to recall their role in the past event correctly if they had observed the event rather than performed the event. It is possible that having to inhibit using the joystick on these trials made the trials more salient to the monkeys. The majority of the time the monkeys themselves are in control of the joystick and cursor during experimental tasks and this may have made these observed events distinctive, and thus more memorable than other trials.

The children performed differently than the monkeys on some of the types of memory tests. In contrast to the monkeys, the children were better at remembering the context feature of past events, but had more difficulty with the temporal dimension. The children performed at chance levels even when they were given the temporal test first. It is not clear why children performed poorly on the temporal tests. It is possible that the children could not yet perceptually distinguish between the two intervals used in the task. It is also possible that the delays were so aversive to children that they all appeared to be long delays. However, the children were not more likely to choose the long delay; in fact, they were significantly more likely to label long delays as "short". Another possibility is that children may have understood the delays perfectly, but were confused by the icons. However, the children often verbalized their responses and there were no situations in which their verbal labels conflicted with their icon choices (i.e., they did not select the turtle and say "short" when asked how long they had to wait). Therefore, it is unlikely that this could account for their performance. It is more likely that children perceived most of the delays as short because they were relatively short, and had the long delay been substantially longer (on the order of minutes) the children may have been able to perform the task.

In recent studies, children from this same age group have demonstrated the ability to remember temporal order information from a series of past events. In one experiment, children were led by an experimenter to different locations where they hid a series of objects (Hayne & Imuta, 2011). The 4-year-old children remembered the temporal order of the past events, while 3-year-old children had difficulty reporting this information. Therefore, this appears to be a sensitive period during which children are beginning to understand the concepts of time and order. However, the majority of the children in the present study were the same age as those that passed the temporal order test in the Hayne and Imuta (2001) study. It would seem, therefore, that children at this age do appear to remember temporal information, but that the scale of the temporal discrimination or the intervals themselves may have been too similar for children to distinguish in the present study.

The children, like the rhesus monkeys, showed an enhancement effect for performing events. The children were better at retrieving the temporal, agency, and context features from memory when they had performed the event than when they had only observed the event. This difference was not statistically significant for the agency and context tests, but the difference was significant for the temporal test. The children were above chance at retrieving the temporal feature from events they performed themselves, whereas they were not above chance at retrieving this feature on observed trials. Studies with human participants (e.g., Engelkamp, 1983; 1998, as cited in Nilsson, 2000; Engelkamp & Dehn, 2000; Manzi & Nigro, 2008) also have shown a memory advantage for performed events, but these studies have been limited to examining memory for item information (words or actions) and order (position in a list). These studies have found that participants were better at retrieving item information about words in a list when they performed the tasks themselves, but were conversely better at retrieving information about the position of the item if they had observed someone else reading/performing the list of words/actions. However, in these tasks the visual feedback varied dramatically for performed and observed trials. This difference in perceptual perspective could have served as a retrieval cue and may account for these results. The present study was able to control for such perceptual or visual cues by eliminating the "experimenter" and eliminating additional cues that could be used to solve the task (i.e., hand position, joystick path, etc). The multiple test types also made it possible to examine retrieval of specific types of information that had not been addressed in previous work (i.e., spatial, temporal and contextual features). Using these controls, the present study demonstrated a similar advantage for performed trials in a nonhuman primate species and human children.

Implications for Comparative Research

The results from this study have implications for the design of future comparative memory studies. The rhesus monkeys in these experiments demonstrated that they were able to encode information about their own role in past events and successfully retrieve this information even when they were unable to use proprioceptive cues about their recent hand position to solve the task. In some previous work by Singer and Zentall (2007), pigeons were able to convey information about their recent behavior (pecking or inhibiting their behavior) on unexpected memory tests even when they had to peck a key on probe tests before responding to a memory test (to eliminate proprioceptive information about beak movement). However, this task is qualitatively different from the one used in the present study. The pigeons either pecked (event) or did not peck (absence of event) on each trial, whereas in the present study the monkeys always observed an event (a picture moving to a location), but had to determine whether they were directly involved in the event. The pigeons simply had to determine if something had happened, but the monkeys had to determine the source of their memory for the event. In a study by Mercado et al. (1999), a bottlenose dolphins was able to repeat a recently performed behavioral action with multiple components (action type, body part used and object involved). The dolphin was able to do this even when she did not know she would be tested, but again, this task is qualitatively different from the one used with monkeys. The dolphin could succeed on this task by simply remembering her most recent behavior and not by necessarily referencing a specific episode. However, the results from the present study indicate that at least one species is able to retain information about their recent role in an event and to access this information about the source of their memories after brief delay intervals.

These findings also have implications for task design in comparative memory research. In the event memory and episodic memory literature, there has been no discussion concerning how the extent of an animal's involvement affects performance. Some studies have used tasks in which an animal directly engages in the behavior and other studies have used tasks in which the animal watches an experimenter perform the event. However, no one has acknowledged that these studies may be qualitatively different and making comparisons across such different studies may be inappropriate. The present research indicates that the animal's involvement in a task should be taken into consideration when designing tasks and when comparing performance across different studies/species.

The fact that the monkeys were able to retain information about their own role in a past event also has implications for research on self-awareness. The ability to recognize oneself as a unique agent in the world has often been examined using the mirror mark test which relies on an individual's ability physically to recognize itself in a mirror (Gallup, 1970; Gallup, 1979). A number of monkey species have failed to show evidence of recognition using the mirror mark test and instead attempt to threaten the individual in the mirror (see Anderson, 1984). However, the problem with the mirror mark test is that it equates physical recognition with self-awareness, which is not necessarily correct. There are adult humans with neurological deficits (e.g., prosopagnosia and Capgras syndrome) that have difficulty recognizing individuals from visual features, but they do not appear to lack self-awareness or knowledge that other individuals exist as distinct entities. Although they have significant difficulty with physical recognition based on visual features, they are able to recognize other individuals from their voice and other cues (Beyn & Knyazeva, 1962; Hirstein & Ramachandran, 1997). Therefore, physical recognition is not necessary for self awareness or awareness/recognition of other individuals. Consequently, having a task that does not rely on physical recognition may prove useful in getting at this issue in nonhuman species.

The main purpose for these experiments, however, was to measure self-awareness as it relates to past action events. The experiments meet Tulving's (2002) requirement for self-awareness, at least in a limited behavioral sense, and provide a new method for assessing how animals remember personal information about their role in past events. Tulving argued that the self-awareness required for episodic memory must extend to an awareness of the self in the past and the future (Tulving, 2002). Although the results do not indicate that monkeys are experiencing mental time travel and the phenomenological experience of remembering that we associate with episodic memory retrieval, they do suggest that monkeys have knowledge of a self that is not limited to the present. Future research is needed to examine whether this knowledge extends further into the distant past and whether monkeys are also capable of anticipating future actions.

The results suggest that, at least for some individuals, agency information is integrated along with other event features in working memory. In the previous what-where-when memory study with rhesus monkeys, there were similar individual differences, with only some monkeys displaying evidence of integration (Hoffman et al., 2009). These results suggest that agency information is a relevant dimension and can be retrieved from working memory along with other event features. Knowing how these features are initially encoded in working memory is essential to understanding how they are later retrieved, even in respect to long-term episodic memory. If animals fail on long-term episodic memory tasks, it is difficult to determine whether this is a result of encoding or retrieval failure. Consequently, being able to assess initial encoding is an important step in building an understanding of how animals represent past experiences in memory.

Implications for Developmental Research

There is research which suggests that the 3 to 5 year-old period of development is a particularly important stage in which children learn about the sources of their knowledge as well as the knowledge and beliefs of other individuals (Gopnik & Graf, 1988; O'Neill & Gopnik, 1991). In one study, Gopnik and Graf (1988) presented 3- and 5-year-old children with a task in which they learned about the contents of a drawer through three separate sources of information: 1) they directly experienced the information themselves by seeing the item, 2) they heard about the contents from an experimenter, or 3) they inferred the contents from a clue. The 5-year-old children made source judgments about how they obtained information about the drawer contents, but three years olds were not able to do this task. Further experiments indicated that 4-year-old children also were capable of making these source memory judgments, but that at three years of age this ability had not yet developed sufficiently (O’Neill & Gopnik, 1991).

The present study replicated and extended these findings. The 4-year-old children in the present study made judgments about whether they had performed or observed a recent event. Researchers have also examined whether participants are better at remembering events they perform themselves compared to those they simply observe (Engelkamp & Dehn, 2000). Adult participants are more likely to accurately recall features from events they perform themselves than those they observed performed by an experimenter. There are some exceptions to this general finding and in some situations observing an event can actually facilitate encoding of event features, but this appears to be due to the increased visual feedback and cues available in observed tests. There is research with children between the ages of 6 and 9 years of age which indicates that this effect is apparent even in young children (Baker-Ward, Hess & Flannagan, 1990). This was also observed in the present study with a younger age group; children between the ages of 3.5 and 4.5 years were significantly better at recalling some event features (temporal information) if they had performed the event themselves.

This research and other studies examining memory for performed and observed events can have important implications for work with atypically developing children and adults. Research on episodic memory processing in adults with autistic spectrum disorders (ASD) appears to suggest that adults with ASD are more likely than intellectually matched controls to experience difficulty recalling personally experienced events (Crane & Goddard, 2008). Other studies have indicated that a similar effect appears in children diagnosed with ASD, as they have more difficulty remembering features from events they performed than those performed by another individual (Millward, Powell, Messer & Jordan, 2000; Yamamoto Y, Saito T, Kamio Y. (2004). However, some studies have failed to show any difference for remembering components from performed and observed tasks (Hill & Russell, 2002; Russell & Jarrold, 2010). It is difficult to sort out exactly what all of this means and there are numerous confounds that have not been addressed in these studies. Children diagnosed on the autistic spectrum may be less likely than typically-developing children to attend to the actions of other individuals and this may explain why they sometimes appear better at remembering performed events (i.e., they may not be attending to actions performed by other individuals and therefore do not encode them in memory). In addition, these studies often use verbal instructions and materials which may not be appropriate with individuals in this diagnostic category. Visual tasks, like the one used in the present study, may be more appropriate in this situation. There is also speculation that a lack of self-awareness may explain many of the social and cognitive deficits in this group, specifically problems with imitation and social learning (Crane & Goddard, 2008). A task like this could be adapted to examine whether these individuals lack self-awareness. In contrast to other studies that are verbally based, a study designed for use with a non-verbal species could prove useful for examining memory in humans with language delays and impairments.

General Implications for Cognitive Theory

This series of experiments can be evaluated in terms of its broader impact within the fields of cognitive and comparative psychology. These experiments demonstrate that humans are not the only species capable of encoding episodes in memory, and they are not the only species capable of making judgments about the source of their memories for past events. These findings, taken together with other findings demonstrating that animals' memory for past episodes is influenced by the same variables (e.g., misleading post-event information) that affect human episodic recall (Schwartz, Hoffman & Evans, 2005), suggests some commonalities in memory systems across species.

Thorndike, Watson, Skinner and other behaviorists viewed animals as creatures bound by stimulus-response learning, and the notion that animals (including human animals) had mental experiences that were causal in explaining or predicting behavior was simply not relevant for scientific discussion because it was assumed that such internal processes could not be studied. However, the current study builds upon existing evidence which suggests animals are capable of responding to abstract features of their experiences, such as time and agency, qualities of events that are not easily translated into a visual image. This means that some mental representation or internal mental process is needed. There is a distinction between memories for which we are consciously aware (i.e., explicit/declarative memory) and memories which influence our behavior without awareness (i.e., implicit/procedural memory). An individual can respond to a particular stimulus based on past experiences without awareness or understanding why they are responding in that manner. Accordingly, some people might ask whether the tasks in the present study could be solved using such basic associative processes—implicit, conditioning forms of memory rather than explicit, episodic forms. The monkeys clearly used associative processing in learning the relationship between the various task icons and experimental contingencies, but they also generalized this learning to novel stimuli and different testing situations, which may suggest emergent learning from associative processes (see Rumbaugh, Washburn & Hillix, 1996).

Associative processes seem unlikely to account for how the monkeys performed on the memory task itself. In any event, this task is not fundamentally different from a recognition test or cued-recall test used with human participants, so the same associative criticism could be made against those studies. If one wants to argue that associative processes alone can account for the data in the present study, then this is also the case for numerous studies of human memory as well. However, this is not done because it becomes less parsimonious when trying to explain such complex behavior through associative processes alone. Rather, the animals and children in the present study appeared to respond flexibly to the various memory cues (what, where, when, agency or context) in a way that was consistent with the suggestion that they were remembering the stimulus episode rather than having learned a complex matrix of if-then stimulus-response associations.

The monkeys in this study did not need to integrate components in order to solve the task. At first glance, this may appear to suggest that monkeys are doing something fundamentally different from human participants when we recall past episodes. According to Tulving (2002), the autonoetic conscious awareness that we experience results directly from the integration of spatial, temporal and contextual features in memory. Following this logic, there are two initial conclusions: 1) animals do not share this mechanism for integrating event features in episodic memory and/or 2) the tasks in the present study do not assess the same memory process we experience as humans when we recall past experiences. However, an alternative interpretation exists. The monkeys may well be doing what we do as humans, using our knowledge about the world to reconstruct our experiences and fill in the gaps when we fail to encode or retrieve certain event features. We only assume that humans integrate features from past events based on our own experiences. It is never explicitly tested, for instance in the way demonstrated in the present paper and elsewhere (e.g., Skov-Rackette, Miller, & Shettleworth, 2006), because we take for granted that our memories are cohesive representations of past events. However, in reality, there are overwhelming data to suggest that our memories for past episodes are far from perfect representations that are formed by accurately integrating features in memory (see Schacter, 2001, for one extensive review). Rather, memories are reconstructive and modified by prior knowledge, subsequent experience, and expectations. If we acknowledge this fact, then monkeys' failure to integrate is not an indication that they are doing something different from humans, but that they may actually be remembering events in a way similar to humans.

Another criticism that could be leveled at this approach is that the tasks in the present study may not actually assess episodic memory. For example, some might argue that maintaining information in working memory in these tasks is a qualitatively different task than reflecting back to a past episode that happened in the distant past (e.g., last hour, last week, last month or last year). There are a number of variables (e.g., rehearsal, the presence of appropriate retrieval cues and the occurrence of similar events which can introduce interference) that influence whether information initially maintained in working memory will become a more stable memory that can be retrieved a week, month, or year later. It is likely the case that the monkeys and children will not remember specific events from this experiment for months or years to come; yet this does not mean that the mechanism that allows monkeys to perform this task is qualitatively different from the one that allows us to retrieve individual episodes years after the event in question. The working memory model proposed by Baddeley and Hitch (1974) conceptualized working memory as a process that allows us to search for information in long-term memory and bring it back into a state of active maintenance so we can use it. Baddeley (2000) expanded upon this model, arguing that an episodic buffer allows information to be temporarily bound together in working memory before being transferred to long-term memory. It is this process of temporarily binding information in working memory that is essential for episodic memory and this model supports the theoretical argument that the tasks used in the present study are examining the same underlying process that supports the encoding and retrieval of episodic memories. Indeed, it seems reasonable to suggest that short-duration tests of what/where/when memory like the one employed here may be useful for exploring the characteristics of the episodic buffer and its relation to more enduring forms of episodic memory.

More recent unistore models, such as the working memory models proposed by Cowan (2010) and Unsworth and Engle (2007) argue that there is no need to posit distinct structures or stores in memory, but still maintain that there is a portion of memory that is active (i.e., primary memory) and a portion of memory that is not currently active, but can be called upon and brought back into an active state (i.e., secondary memory). Following the logic of these models, information initially encoded in working memory and information stored in long-term memory (and brought back into active/working memory) would have to be encoded, maintained, and retrieved by the same mechanism. In this case, the distinction between long-term episodic memories and short-term episodic memories is a matter of activation rather than a qualitative difference in memory type. Accordingly, the monkeys' and children's responses on the present task are perfectly applicable to the larger literature on how human adults remember episodes over long periods of time. The findings in the present study reflect a fundamental memory system that is not a product of language or culture, but instead forms the basis of how we learn information about the world (and thus upon which language and culture may be scaffolded). It is a fundamental memory system that manifests the characteristics of episodic memory, or the articulatory loop, or procedural memory (and so forth) depending on the nature of the to-be-remembered information and the parameters of the memory test.

In learning, we initially experience novel episodes that we encode as specific past events in memory. However, after repeated exposure to similar episodes, it becomes increasingly difficult to differentiate these episodes, so contextual information about where, when or how the information was acquired can become difficult to ascertain. As a result, we refer to these general knowledge representations as semantic memories, but what we mean by this is that we have lost the source information about how, when and where the information was acquired (and the phenomenological experience that results from knowing this information). The distinction between episodic and semantic memory can perhaps better be described as a distinction between memory and knowledge. Following this reasoning, the tasks in this study are fundamentally episodic ones because they assess memory for specific past episodes and not general knowledge about the world. The fact that the tasks in the present study do not require retrieval from long-term memory does not mean that these tasks are assessing different mechanisms or processes. In fact, the episodic buffer proposed in Baddeley's working memory model (2002) posits that features from past events are initially held together in working memory before being transferred to long-term memory. Whether animals have the same mental experiences we have when we retrieve episodic memories cannot be tested, but it can also be said that we can never really know the mental experiences of other humans. The experience itself does not even have to be an integral component to episodic memory retrieval, but may be something that arises from the inferences we make when reconstructing our memories. In the future, additional research is needed to determine whether other variables that are known to affect the accuracy of human episodic memory also affect performance in children and animals. For example, the study of imagination inflation and false memory using this paradigm would prove especially useful in determining the extent to which these working memory tasks are tapping into true episodic memory, as it is commonly investigated in the laboratory.

Directions for Future Research

This study highlights the need for a more comparative approach in the field of comparative cognition. It is not always necessary or even appropriate to compare nonhuman species to human participants. However, in some situations we compare other species to what we expect we would do, without any direct comparison. As researchers studying our own species and other species, we experience a unique challenge because we have direct experience of the behavior and cognitive phenomena we are studying. Therefore, we often do not include members of our own species in comparative studies because we take for granted that humans behave in a way we expect based on our experiences. In some cases, we also require more stringent criteria to demonstrate some cognitive ability in another species than we would require for demonstrating this in our own species (e.g., episodic memory or self-awareness). However, including children or adults in comparative studies helps us ensure that the tests we have designed for animals are fair tests of cognitive abilities.

Fortunately, there have been some studies published in the past year that have used this approach by examining this ability in human adults (Holland & Smulders, 2011) and children (Hayne & Imuta, 2011) using tasks that more closely resemble tasks used with nonhuman animals. Holland and Smulders (2001) examined what-where-when memory in adult participants using a modified caching task in which participants hid coins that varied in value. The hiding occurred on two separate days and participants were asked to retrieve the coins when they returned. However, some participants had been in an active encoding condition (at the beginning of the experiment, they were told that they would get to keep coins that they hid and later retrieved) while others experienced a passive encoding condition (they were told that they were hiding the coins for someone else). They were also given an episodic memory test concerning the context or situation from each day (participants had to provide “know” or “remember” judgments and these judgments were used to measure participants’ mental experience of episodic retrieval of the context from each of the hiding events). Performance on the subjective episodic retrieval test predicted retrieval of what-where-when information for passive encoding situations, but not always for active encoding situations. The authors argued that this provided additional support for the notion that what-where-when memory tasks used with food caching species are appropriate measures of episodic memory.

However, just because human participants may have used episodic memory to solve this task, it does not mean that these types of problems can only be solved using this strategy. Even though some researchers have argued that these tasks are an ideal approach for examining integration, there are drawbacks to the food-caching and food storing tasks: 1) in order to solve this task in an efficient manner, an animal would need to integrate features if it could, but this does not mean that they would naturally do this, 2) just because an animal succeeds on this task does not mean that they could convey information about discrete features from past events (this explicit quality seems essential to the notion of self-awareness and personal experience). In addition, many food-caching studies with birds involve a series of training tasks and a probe test (to control for olfactory or visual cues). The authors argue that birds demonstrate integrated memory for what-where-when information because they tend to direct more of their searches to the appropriate location based on the delay since caching. However, the first search may provide important retrieval cues that help the animal search in subsequent locations. This may artificially inflate the number of correct searches, especially if the birds have grouped food pieces of the same type together in the environment (simply finding the first one makes it much easier to locate the other food items).

Therefore, researchers should not feel limited to using the food-caching and foraging tasks. Those tasks may be useful for answering some questions about what-where-when encoding, but like all paradigms, they have strengths and weaknesses. There are benefits to using tasks that require an animal to retrieve specific event features and make discrete responses to memory tests for each event feature. In some cases, such as with language trained chimpanzees that have a large vocabulary of symbolic lexigrams, this provides a unique opportunity that more closely resembles human recall tasks that are used with humans (Menzel, 1999; Menzel, 2005). Other approaches, like the one used to examine agency in the present study, can probe other essential aspects of event memory that have been overlooked by previous research. The awareness that one played a particular role in a past event appears to be the most difficult characteristic of episodic memory to assess in nonverbal animal species. However, the present study provides a new method for assessing this cognitive ability in animals and children and suggests that self-agency information is an important feature that is encoded with other relevant event features in working memory.

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