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MEMORY FOR “WHAT”, “WHERE”, AND “WHEN” INFORMATION BY RHESUS MONKEYS (*MACACA MULATTA*) AND ADULT HUMANS

by

MEGAN L. HOFFMAN

Under the Direction of David A. Washburn

ABSTRACT

The purpose for the present study was to examine working memory for *what*, *where*, and *when* information in rhesus monkeys (*Macaca mulatta)* and adult humans using a computerized task. In Experiment 1, monkeys and humans completed three delayed matching-to-sample (DMTS) tasks: 1) identity DMTS, 2) spatial DMTS, and 3) temporal DMTS. In Experiments 2, the identity and spatial tasks were combined so that monkeys had to report both *what* and *where* information about an event. In Experiment 3, the identity, spatial, and temporal tasks were combined in order to examine *what-where-when* memory integration. In Experiment 4, monkeys and humans were presented with two sequential events, and a memory cue indicated which event they were required to report. The rhesus monkeys and human participants were able to report all three components of the events and there was some evidence suggesting that these components were integrated in memory for the rhesus monkeys.

INDEX WORDS: Episodic memory, Episodic-like, Event memory, Temporal, What, Where, When, Nonhuman primates, Human participants

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by

MEGAN L. HOFFMAN

Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Arts

in the College of Arts and Sciences

Georgia State University

2007

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by

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Memory for "What", "Where", and "When" Information by Rhesus Monkeys (*Macaca mulatta*) and Adult Humans

INTRODUCTION

In a natural environment, many species, including nonhuman primates must remember multiple types of information, including memory for where particular foods are located in space and memory for temporal information concerning their previous foraging experiences, in order to keep track of available food sources. In the comparative literature, there are numerous impressive examples of working memory and long-term semantic memory in a variety of nonhuman species, including nonhuman primates (Beran, 2004; Beran, Pate, & Richardson, 2000; Washburn & Astur, 1998). However, few studies have explicitly examined memory for multiple components of a single past event in nonhuman primate species. In the human literature, the ability to remember multiple components of a personally experienced event is referred to as episodic memory and has been argued to be unique to humans and absent in other species including our closest living relatives, the nonhuman primates (Tulving, 1972, 1993, 2005). However, in recent years there has been increased research devoted to examining memory in nonhuman species for episodes or events (see Terrace and Metcalfe, 2005 for a review).

In contrast to other forms of memory such as working memory or long-term semantic memory, episodic memory refers to memory for a unique event from one's past in which multiple components of the event (i.e.., what, where, and when the event took place) are bound together and integrated in long-term memory (Tulving, 1972, 1993). Furthermore, for humans the retrieval of episodic memory is accompanied by an awareness of one's past and a subjective

conscious experience, in which the owner of an episodic memory feels as if he or she is mentally traveling back to the time and place where the event occurred. In contrast to semantic memory, which refers to memory for general information about the world (i.e., knowing factual information about events that you directly experienced or learned about through another source), episodic memory refers to memory for a specific past event in which spatial and temporal information concerning the event are bound together in memory. 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 event when the information was acquired (Roediger & McDermott, 2000).

The definition of episodic memory contains relatively objective behavioral elements, including the binding of several types of information in memory that can be studied in nonhuman species. However, the definition of episodic memory also contains relatively vague subjective conscious qualities that cannot be assessed in nonhuman species. It is impossible to assess the phenomenological quality of episodic retrieval in animals as they are unable to describe their mental states verbally. It is presumably the subjective quality of retrieval that has caused comparative psychologists to avoid discussion of episodic memory in nonhuman animals, as nonverbal species are unable to describe their internal mental experiences to human experimenters. However, the assumption that language is necessary to study long-term memory for past events has recently been challenged both by studies with nonhuman species that have employed behavioral definitions of *episodic-like* memory (Clayton & Dickinson, 1998, 1999; Clayton, Yu, & Dickinson, 2001; de Kort, Dickinson, & Clayton, 2005; Hampton, Hampstead, & Murray, 2005; C. Menzel, 1999, 2005; Schwartz, Colon, Sanchez, Rodriquez, & Evans, 2002; Schwartz, Hoffman, & Evans, 2005; Schwartz, Meissner, Hoffman, Evans, & Frazier, 2004;

Zentall, Clement, Bhatt, & Allen, 2001) and by studies with human infants who are in the early stages of language acquisition and are not yet able to verbalize their experiences to the same extent as human adults (Bauer, 2002; Bauer, Hertsgaard, & Dow, 1994; Bauer, Wiebe, Carver, Waters, & Nelson, 2003). In the studies with nonhuman species, the term *episodic-like* memory has been used to differentiate this behavioral definition of episodic memory that includes memory for a trial-unique event, the integration of *what*, *where*, and *when* information in memory, and retrieval from long-term memory, from the general definition of episodic memory used in the human literature.

Why Predict Similar Memory Processes in Nonhuman Species?

There is evidence that some of the brain regions implicated in the retrieval of episodic memory in humans also are essential in integrating spatial and temporal information in animals. The hippocampus, which has been implicated in episodic memory retrieval for both remote and recent past events in humans (Rekkas & Constable, 2005) appears to serve a related function in binding spatial and temporal memory in some food-caching and foraging species. Nonhuman animals with damage to the hippocampus demonstrate deficits in integrating *what*, *where*, and *when* information in memory (Colombo & Broadbent, 2000; Eichenbaum & Fortin, 2003; Ergorul & Eichenbaum, 2004). In addition to this similarity of function, the neural structure of the hippocampus has been found to be relatively 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 *what*, *where*, and *when* information about past episodes in memory. The ability to integrate multiple components of past events in memory, although not sufficient for episodic memory, does appear to be one of the prerequisites for episodic memory in humans. Therefore,

in beginning to investigate whether nonhuman species have the ability to recall specific past episodes, it is necessary to understand how humans and nonhuman species integrate information about what occurred, where the event occurred, and when it took place relative to other points in time.

Separate Studies of What, Where, and When in Nonhuman Primates

In recent years there has been an increased interest in whether animals integrate temporal and spatial information from novel events in memory in the form of episodic-like memory, but in the past these forms of memory (spatial memory, temporal memory, and object memory) have often been investigated through separate lines of research.

Spatial Memory There have been an extensive number of field and laboratory studies investigating spatial memory in nonhuman species, including nonhuman primates. Some of these investigations were 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 as an experimenter hides the food item), and after some period of delay the individual is then allowed to search for the hidden item. These studies have demonstrated that a variety of nonhuman primates, including monkey and great ape species, retain information about where food sources are located in a complex environment after both short-term and long-term memory retention intervals (Gibeault & MacDonald, 2000; Hunter, 1913; 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).

Object Memory There also have been a number of studies examining whether animals remember information about specific objects they have recently encountered. In these tasks, working memory has 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 choices are present and the animal must select the stimulus that was presented as the sample. In these laboratory studies, a variety of species have demonstrated memory for what they had experienced by selecting the previously seen stimulus at levels that are above what would be expected by chance (Colombo, Swain, Harper, & Alsop, 1997; Roitblat, Penner, & Nachtigall, 1990; Tavares & Tomaz, 2002; Washburn, Hopkins, & Rumbaugh, 1989).

Temporal Memory There is also some evidence that suggests that nonhuman species are able to retain some temporal information concerning past events. Memory for temporal information has been assessed by constructing a simulated foraging task, in which animals were given the opportunity to consume a particular food source at one of several locations, and then were reintroduced to the environment after either a short retention interval or a long retention interval. The food at the previously visited location remained depleted when the individuals were returned after a short retention interval, but the food source at the same location was replenished after a long retention interval. In order to demonstrate memory for temporal information about food sources in the environment, an animal would need to discriminate between the two retention intervals by returning to the previously visited food site only after long retention intervals (referred to as a win-stay strategy). However, when returned after a short retention interval, the animal should choose to select another location (referred to as a win-shift strategy). In one study, a species of nectar feeding bird (*Xanthomyza phrygia*) adopted a win-

shift strategy when reintroduced into the environment after a short retention interval (10 min), but adopted a win-stay strategy when reintroduced into the environment after a long retention interval (3 h; Burke & Fulham, 2003). However, this paradigm has limitations for examining temporal memory, as some species demonstrate biases in using these foraging strategies based on their natural foraging ecology. For example, some species have a diet that is primarily composed of foods that replenish fairly quickly, whereas other species have a diet that is composed of foods that take a long time to replenish (Burke, Cieplucha, Cass, Russell, & Fry, 2002; Platt, Brannon, Briese, & French, 1996). There also have been studies that have examined whether pigeons can discriminate different retention intervals using a discrimination task in which the animal was required to make one response (or in some cases inhibit responding) if the retention interval was of a particular length, and to make another response if the retention interval was a different length (Zentall, Weaver, & Clement, 2004). The temporal discriminations in these studies were between relatively short time periods (2 s vs. 8 s and 8 s vs. 16 s). The results from these studies suggest that pigeons are able to discriminate between several short temporal periods.

Experiments Examining Memory for Multiple Components of Events

Indirect Evidence for Integration of Multiple Components. There has been some indirect evidence for the integration of *what* and *where* memory in early studies of spatial memory in great apes (Menzel, 1973; Tinklepaugh, 1932). Tinklepaugh (1932) demonstrated that chimpanzees (*Pan troglodytes)* remembered multiple locations of hidden food items after relatively long delay intervals and noted that they reacted with “surprise” when a preferred food item had been surreptitiously replaced with a less desirable food item while the chimpanzees were absent during the delay, suggesting that the chimpanzees retained some memory for *what* information in addition to *where* information. In another study, E. Menzel (1973) found that

when chimpanzees searched for food items they had seen hidden in an outdoor environment, they recovered highly preferred foods (fruits) before recovering less desirable foods (vegetables), suggesting that they had some knowledge about *what* was hidden *where*.

What-Where-When Memory: The Food-Caching Paradigm. In the food-caching paradigm, developed by Clayton and Dickinson (1998, 2001), scrub jays (*Aphelocoma coerulescens)* were given the opportunity to cache perishable and nonperishable food items (e.g., mealworms and peanuts) in specific locations in sand-filled ice cube trays. The scrub jays were removed from the caching environment and returned to recover their caches after relatively long retention intervals (1 h - 24 h). Although the scrub jays had a preference for the highly perishable food (e.g., mealworms) those foods degraded after short retention intervals (1 h) whereas the less desirable food (e.g., peanuts) remained fresh after the long retention intervals (24 h). The scrub jays searched where they had cached the highly perishable food items after short retention intervals, but switched to searching locations containing less perishable foods if they were returned to the caching environment after long retention intervals.

These results indicate that the scrub jays integrated memory for *what* and *where* food items were located with memory for how much time had elapsed between their initial visit and the time when they were allowed to search. It is possible that the jays were able to accomplish this task by using familiarity cues and memory trace strength at retrieval, for example, by simply adopting the rule to search for preferred food items (that decay quickly) if the food sites were familiar or if the memory trace was vivid. However, scrub-jays maintained their high level of accuracy for novel variations in which the use of memory trace strength cues would lead to significantly reduced performance (de Kort, Dickinson, & Clayton, 2005).

Hampton et al. (2005) adapted the food-caching paradigm for use with rhesus macaques (*Macaca mulatta*). The subjects included both normal individuals and monkeys who had experienced damage to the hippocampus. The monkeys learned an arbitrary rule that a preferred food item was still fresh after a 1-hour delay, but it decayed after a 25-hour delay. If macaques retained information about what food was hidden, where it was hidden, and how much time had passed since it was hidden, one would expect them to search in the highly preferred food site after 1-hour delays, but switch to selecting the less preferred, but more stable food item after 25-hour delays. Both groups of macaques demonstrated memory for *what* and *where*, but not memory for *when*, as they continued to search for the preferred food after 25-hour delays. It is unclear why the monkeys were unable to retain information about how much time had passed since the last foraging episode. It is possible that monkeys were not able to retain *when* information in memory, but it is also possible that this task was not well suited to investigating the integration of *what*, *where*, and *when* memory in nonhuman primates. The task was modeled after a species-specific food-caching task, which may not be the best paradigm for testing laboratory animals that do not have any experience in foraging. Indeed, there have been other tasks designed to investigate episodic memory in nonhuman primates, as well as other species, that are quite different from the food-caching paradigm.

Unanticipated Memory Tests for Recently Performed Events. Zentall et al. (2001) examined episodic-like memory in pigeons (*Columbia livia*) by training pigeons to “comment” behaviorally on whether they had recently performed an action. The pigeons were trained to peck when presented with one type of color stimulus (e.g., blue), but not to peck when presented with another color stimulus (e.g., green). In a separate phase of training, the pigeons were trained to press one particular color (e.g., yellow) if they had recently pecked and to press

another color (e.g., red) if they had not recently pecked. These components were combined in unexpected tests in which the pigeons were instructed to peck or not to peck (e.g., blue or green), but after a short retention interval they were unexpectedly asked about whether they had recently performed the pecking behavior (i.e., they were given a choice between yellow or red). Although these studies do not address the binding of *what*, *where*, and *when* information in memory, the "surprise" element of these memory tests captures an essential feature of episodic memory, as these unexpected tests reduce the possibility that the pigeons were rehearsing the information in semantic memory in anticipation of being tested about that memory.

Mercado, Uyeyama, Pack, and Herman (1999) examined memory for recently performed novel events in a bottlenosed dolphin (*Tursiops truncates*) by instructing the dolphin (through the use of gestural signs) to use a particular part of her body to perform an action with specific objects located in her tank (e.g., use *tail flukes* to *hit* the *beach ball*). After some trials, the dolphin was unexpectedly presented with the sign for "repeat," instructing her to repeat the novel action she had recently performed. The dolphin successfully repeated the novel behavior at levels that were significantly above chance. These findings suggest that at least one dolphin was capable of remembering multiple components of a behavior that she recently performed when she presumably was unaware that she would be requested to repeat the behavior. However, this performance could be accomplished through procedural memory, as the dolphin only had to repeat the behavior she recently performed without necessarily having any reference to the past.

In a different paradigm using unanticipated memory tests, Skov-Rackette, Miller, & Shettleworth (2006) examined memory for what-where-when information in pigeons. The pigeons were trained on three separate tasks: 1) an identity matching-to-sample task in which the pigeon had to respond to the recently presented stimulus, 2) a spatial matching-to-sample task in

which the pigeon had to respond to the location where the stimulus was presented, and 3) a temporal discrimination task in which the pigeon had to report how much time had elapsed since the stimulus was presented (3 s vs. 6 s) by responding to one of two symbols which represented these two intervals. After being trained on these separate tasks, the pigeons were presented with a new task in which the question type varied across trials and the pigeons were not cued as to which question would be presented. If pigeons simultaneously encoded *what*, *where*, and *when* information in memory, they should have responded at above chance levels on any given trial with any question type. However, the pigeons demonstrated reduced accuracy for *when* information, but maintained high accuracy for *what* and *where* memory, suggesting that these three components were not integrated in memory.

What & Where Memory - Unprompted Recall of Events in a Chimpanzee. C. Menzel (1999) investigated recall memory for *what* and *where* information after extremely long delays in Panzee, a language-trained chimpanzee (*Pan troglodytes).* In this study, the chimpanzee viewed an experimenter hiding a particular food item in a large wooded area outside of her enclosure. In contrast to other studies of episodic memory in nonhumans, the chimpanzee spontaneously conveyed information about the type of item hidden in the woods to an experimentally blind caretaker using her large vocabulary of symbolic lexigrams. She used gestures to accurately convey information about where the item was hidden to a human caretaker who was unaware of where the food item was hidden. Panzee was highly accurate at reporting the type of food item that was hidden and where it was hidden often after very long delays of days or weeks.

Memory for What, Where, When & Who Information in a Gorilla. Schwartz et al. (2002) examined memory for *what* and *who* information about novel events in an adult western lowland gorilla (*Gorilla gorilla gorilla).* In a series of experiments, the gorilla was presented with a type

of fruit (apple, orange, banana, pear or grapes) by one of three familiar experimenters. The gorilla later was presented with a set of large wooden cards that contained pictures of the five food items and another set of cards that symbolically represented the three experimenters used in the task. The gorilla was significantly above chance at indicating both the type of fruit and the experimenter involved in the event after both short retention intervals (7 m) and long retention intervals (24 h). In another study, the gorilla was also highly accurate at reporting components of novel events involving both familiar and unfamiliar individuals (Schwartz et al. 2004).

In another study, Schwartz et al. (2005) conducted two separate studies investigating whether the gorilla was capable of remembering separate information about where an event occurred and when an event occurred relative to other events in the past. The results indicated that the gorilla was above chance at demonstrating memory for *where* information by selecting the appropriate photo of the event location, but was less accurate at reporting information concerning the temporal order of a series of three events.

What & Where Memory - Computer Tasks with Monkeys. Washburn and Gulledge (2002; Washburn, Gulledge & Martin, 2003) examined the integration of *what* and *where* memory in joystick-trained rhesus macaques (*Macaca mulatta*) using a computerized task modeled after the children's memory game, *Concentration.* The task was not designed to examine episodic memory, but to examine memory for both *what* and *where* information about past events in working memory. In this task, the monkeys were presented with an array of cards on a computer screen that they were able to "flip over" by using a joystick to reveal the picture on the card. The monkeys were trained to find the card that matched the one they had just selected. Although the data indicated that the macaques had some knowledge of *what* cards had been seen and which locations were previously visited, the monkeys made frequent perseverative

errors when required to integrate *what* and *where* information in memory (i.e., they would occasionally continue to select the pair that they had just selected despite the fact that it was incorrect). The authors speculated that this may have been due to the fact that the monkeys were unable to use language to encode information about the multiple locations and objects within the array, which may have accounted for their relatively low accuracy.

Summary

The experimental paradigms reviewed here capture essential elements of episodic memory. The experiments with food-caching scrub jays have demonstrated integrated memory for *what*, *where*, and *when* information after long-term retention intervals when familiarity and stimulus strength cues have been experimentally controlled. The unanticipated memory tests used with pigeons and dolphins address the spontaneous retrieval associated with episodic memory, and unlike the food-caching studies, refer to completed events in the past and not the present location of food in the environment. It is possible that in the food-caching tasks, successful performance may not require memory for past events, but may be accomplished through something more similar to prospective or semantic memory. The studies that have used unanticipated memory tests with pigeons and dolphins have used another method for investigating memory for past events by providing unanticipated memory tests after some of the trials. The unprompted recall studies with a language-trained chimpanzee and the recognition tests with a gorilla both demonstrate integrated memory for multiple types of information about past events after long-term delays. However, these studies have not demonstrated memory for *when* information in these great ape species. There have been few studies with nonhuman primates assessing memory for *when* in addition to *what* and *where* memory; the few studies that have been done did not find evidence for *when* memory in rhesus monkeys using an adaptation

of the food-caching paradigm (Hampton et al., 2005) or evidence for temporal sequencing of events in a gorilla (Schwartz et al., 2005). In the human literature, temporal information about when an event took place appears to be a relatively weak memory cue (Wagenaar, 1986), which may partially explain why there is evidence for integrated *what* and *where* information in nonhuman primates, but less evidence for integration of *what*, *where* and *when* information in nonhuman primates. However, it is important to note that there are too few studies examining memory for temporal information for when an event took place in nonhuman primates to draw any certain conclusions (Hampton et al., 2005; Schwartz et al. 2005).

The purpose of the present study was to examine whether rhesus monkeys are capable of integrating *what*, *where*, and *when* information in memory using a task in which monkeys were required to make discrete responses concerning each separate memory component. Although the *Concentration* task should have been easier for the monkeys, as they only had to make one response to a stimulus to indicate memory for both *what* and *where* information, the large number of spatial locations on a two-dimensional computer screen may not have been distinct enough for the monkeys to encode as unique locations. In contrast to previous studies that have only examined memory for *what*, *where*, and *when* information in one particular species without any comparison to human participants, the present study is designed to examine integration of *what*, *where*, and *when* memory in rhesus monkeys (*Macaca mulatta*) and compare their performance to the performance of human participants. In previous research, the performance of nonhuman species have typically been compared with what we assume humans would be able to do in a comparable task, but few studies (with the exception of Washburn & Gulledge, 2002) have directly compared the performance of humans and nonhuman primates.

It was predicted that the rhesus monkeys would be significantly above chance at indicating object information, spatial information, and temporal information about past events, but that human participants would perform at higher levels than the rhesus monkeys. The human participants were expected to perform better than rhesus monkeys, and the reason for this difference in accuracy could be: 1) the ability to rehearse information verbally in working memory may facilitate performance in humans, or 2) human participants may just be more accurate at reporting information from past events, even when verbal rehearsal is controlled. These two possible explanations were tested by comparing performance of human participants in a control group with participants who were required to perform a distracting verbal task (an articulatory suppression task) while simultaneously engaged in the memory tasks. It was predicted that human participants in the control condition would be more accurate than participants in the articulatory suppression condition. Taken together these findings would suggest that although species differences may also be present, verbal rehearsal in humans facilitates memory.

However, I predicted that the pattern of results for both rhesus monkeys and human participants would demonstrate similar trends and that accuracy in both groups would be influenced by similar variables (e.g., the length of delay between presentation and test and the type of information that must be recalled). Specifically, both humans and rhesus monkeys should be less accurate when tested after long retention intervals than when tested after short retention intervals. In addition, I predicted that both humans and rhesus monkeys should be less accurate at reporting *when* an event took place, than reporting the *what* or *where* component of the event, as the human literature suggests that memory for *when* information is a less salient retrieval cue than the other types of information.

EXPERIMENT 1

In this experiment rhesus monkeys (*Macaca mulatta*) and human participants were presented with three separate delayed matching-to-sample (DMTS) tasks to assess independent memory for *what*, *where*, and *when* information: 1) an *identity* delayed matching-to-sample task, 2) a *spatial* delayed matching-to-sample task, and 3) a *symbolic-temporal* delayed matching-to-sample task. The identity DMTS task required the subject to remember *what* stimulus was presented, the spatial DMTS task required the subject to remember *where* the photo stimulus was presented, and the temporal DMTS task required the subject to remember *when* the stimulus was presented (either 1-s or 10 s in the past).

Method

Participants In this study, rhesus monkeys (N = 4) and human participants (N =40) were tested. The rhesus monkeys that participated in the study were joystick-trained, adult males, housed at the Language Research Center. The rhesus monkeys (Gale, Murph, Willie, & Chewie) had participated in numerous cognitive studies using the computerized testing system developed at the Language Research Center. In addition, some of these individuals had participated in previous computerized delayed matching-to-sample tasks and spatial memory tasks (e.g., Washburn & Gulledge, 2002; Washburn, et al., 2003; Washburn & Astur, 2003). The monkeys were never food- or water-deprived for research purposes. Each monkey participated in the research on a voluntary basis, receiving supplemental food rewards in exchange for participation. Each monkey had a computerized test system in its home cage and had the opportunity to work on the task at any time. The human participants (N = 40) were recruited from undergraduate psychology courses at Georgia State University and received course credit for their participation.

The participants were randomly assigned to one of two conditions, an articulatory suppression condition (n = 20) and a control condition (n = 20).

General Procedure In the DMTS tasks, the rhesus monkeys and human participants were presented with a brief event, in which a photo appeared at one location on the computer screen. The event was followed by a "question" in which the participant was presented with a choice between two alternatives (photos, locations, or temporal symbols, depending on the DMTS task) and had to select the stimulus corresponding to the event. The rhesus monkeys completed the tasks while working on the test systems in their home cage. The tasks were presented during 4-h testing sessions, which were presented 3 to 5 days each week. The total number of trials each monkey completed was determined by their motivation to participate in the task. In each task, monkeys were reinforced for correct responses with positive auditory feedback and the presentation of a 97-mg banana flavored Noyes primate chow pellet, delivered by an automatic pellet dispenser. After incorrect responses, monkeys were presented with negative auditory feedback (a brief low tone). However, monkeys were not given any timeout for incorrect responses and were allowed to proceed immediately to the next trial.

The human participants were also tested individually, in a similar fashion to the monkeys, each in their own room test room with a computer system. The participants completed comparable tasks, with the exception that they were provided with brief verbal instructions. The purpose of providing humans with explicit verbal instructions was to ensure that they reached criterion on these tasks, and that we could compare their performance on subsequent tasks with the rhesus monkeys. In contrast to the monkeys, who had thousands of trials to learn the tasks, the human participants had less than an hour to complete all of the tasks. In pilot testing with

human participants, some of the tasks were not clear to the participants (especially the temporal DMTS task).

As the principle purpose of the study was to examine memory processes, and not learning processes, I decided to provide the humans with verbal instructions to ensure that they understood the objective of the task. Although human participants did not receive any food reinforcement for correct responses, they did receive the same auditory feedback for correct and incorrect responses as did the rhesus monkeys. The participants in the articulatory suppression condition (n = 20) and control condition (n = 20) received the same instructions, with the exception that participants in the articulatory suppression condition were told that they would be required to repeat the word "the" aloud while completing the tasks. In order to ensure that they completed the articulatory suppression task, the participants were told that they would be monitored (using a baby monitor) to ensure that they were engaged in the task. The purpose of the articulatory suppression task was to examine whether the inability to verbally rehearse information about past events affected accuracy.

Identity Delayed Matching-to-Sample The identity delayed matching-to-sample task was used to assess memory for *what* information in rhesus monkeys and human participants. In this task, the photo stimulus was randomly selected on each trial from a set of 80 clipart photos of different items (e.g., fruits, vegetables, monkeys, animals, and objects). The sample photo randomly appeared at one of the four corners of the computer screen and flashed every second for a total of three seconds. The photo disappeared and was followed by a 1-s delay in which the computer screen remained blank. The subjects then were presented with a choice between two alternatives, the previously presented sample photo and an alternate photo that had not been presented (see Figure 2.1). The monkeys received feedback concerning their response, followed

by a brief intertrial interval (1 s). The monkeys completed this task when they reached a criterion of 75% correct over the last 100 trials. The human participants were presented with the same general task, but were given verbal instructions and completed a smaller number of trials (10 trials). The human participants in both conditions were told that they would be presented with a brief event on the computer screen and would have to report information about *what* had been presented.

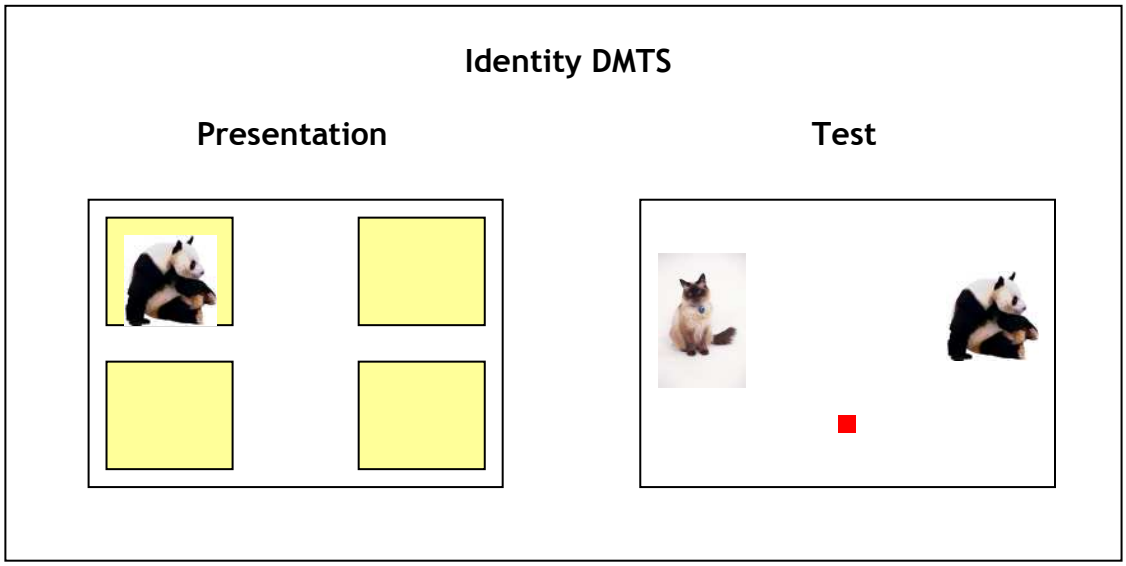

Figure 2.1 Identity Delayed Matching-to-Sample.

Spatial Delayed Matching-to-Sample The rhesus monkeys and human participants were presented with a spatial delayed matching-to-sample task after being trained on the identity delayed matching-to-sample task. In this task, the number of response locations was reduced from four to two locations, as pilot testing with the rhesus monkeys revealed that with four locations the monkeys' performance never exceeded chance levels. In addition, the response location boxes were filled with a light yellow background to make the locations more visually distinctive (see Figure 2.2). In this task, the photo stimulus (a photo of strawberry) remained the

same on every trial, but the location where the photo appeared was randomly selected on each trial. The strawberry photo appeared at one of the two locations on the computer screen and flashed every second for a total of three seconds. The photo disappeared and was followed by a one second delay in which the computer screen remained blank. The subjects then were presented with a choice between the two response locations. This was followed by a brief intertrial interval (1 s). The monkeys completed this task when they reached a criterion of 75% correct in a block of 100 trials. The human participants completed a smaller number of trials (10 trials) and were told that they would be presented with a brief event on the computer screen and would have to report information about where they had seen the event.

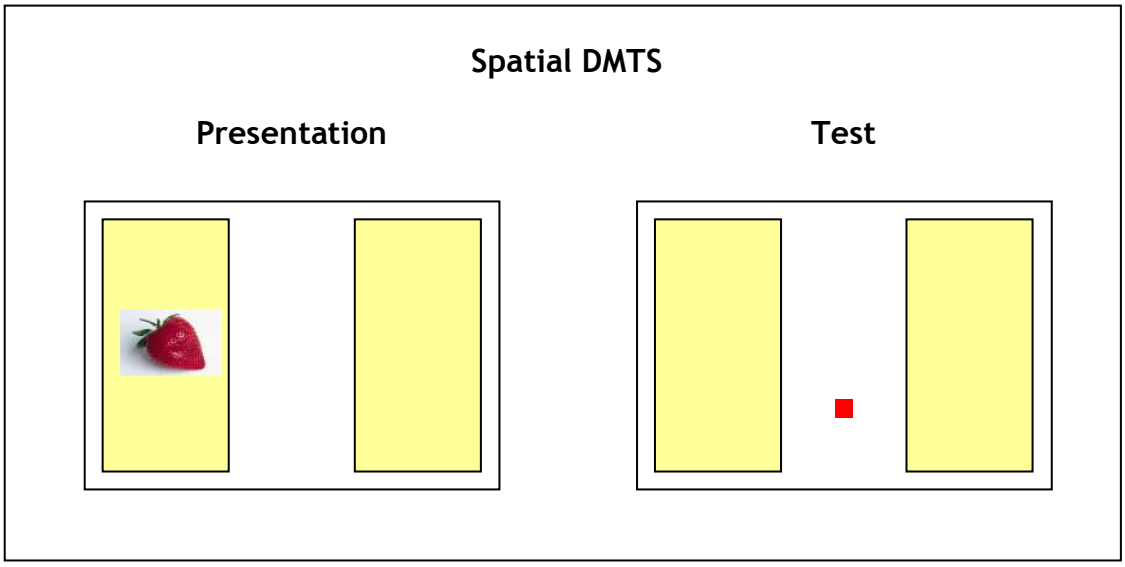

Figure 2.2 Spatial Delayed Matching-to-Sample.

Temporal Delayed Matching-to-Sample The rhesus monkeys and human participants then were presented with a symbolic delayed-matching-to-sample task in order to assess memory for temporal information. In this task, subjects were required to indicate delay length between the presentation of the event and subsequent memory test using temporal symbols. In this task, a

photo appeared in the center of the screen and then disappeared after a brief interval (3 s). The disappearance of the photo was followed by either a short retention interval (1 s) or a long retention interval (10 s), which was randomly determined on each trial. After the delay, the subjects were presented with a choice between two arbitrary stimuli (a purple triangle and a black circle). If the delay between the presentation and test was short (1 s), reinforcement was given for selecting the purple triangle. In contrast, if the delay between the presentation and test was long (10 s), subjects were reinforced for selecting the black circle (see Figure 2.3). In this task, the rhesus monkeys had to learn to select the purple circle if the event was presented recently, but select the black circle if the event was presented in the more distant past (after a 10-s delay). Some of the monkeys first completed a simpler version of the task, in which the purple triangle and black circle were always positioned in the same locations on each trial. These monkeys were then presented with a more advanced version of the task, in which the locations of the temporal symbols was randomly determined on each trial. In this version, the task could not be solved by simply moving the cursor to the left if the delay was short or moving the cursor to the right if the delay was long, but instead required an understanding of the temporal symbols. The monkeys completed this task when they reached a criterion of 75% correct over the last 100 trials.

The human participants completed a smaller number of trials (10 trials) and were told that they would be presented with a brief event on the computer screen and would have to report how long ago the event was presented. They were told that if the delay was short they were to select one symbol (the purple triangle) but if the delay was long they were to select another symbol (the black circle). These specific instructions were given, as pilot testing revealed that participants did not understand the task requirements when no verbal instructions were presented. As the

purpose of the study was to compare memory processes in nonhuman primates and human participants, and not learning of arbitrary task rules, I felt it was necessary to ensure that the human participants understood what the symbols represented rather than allow them to learn those rules over many trials.

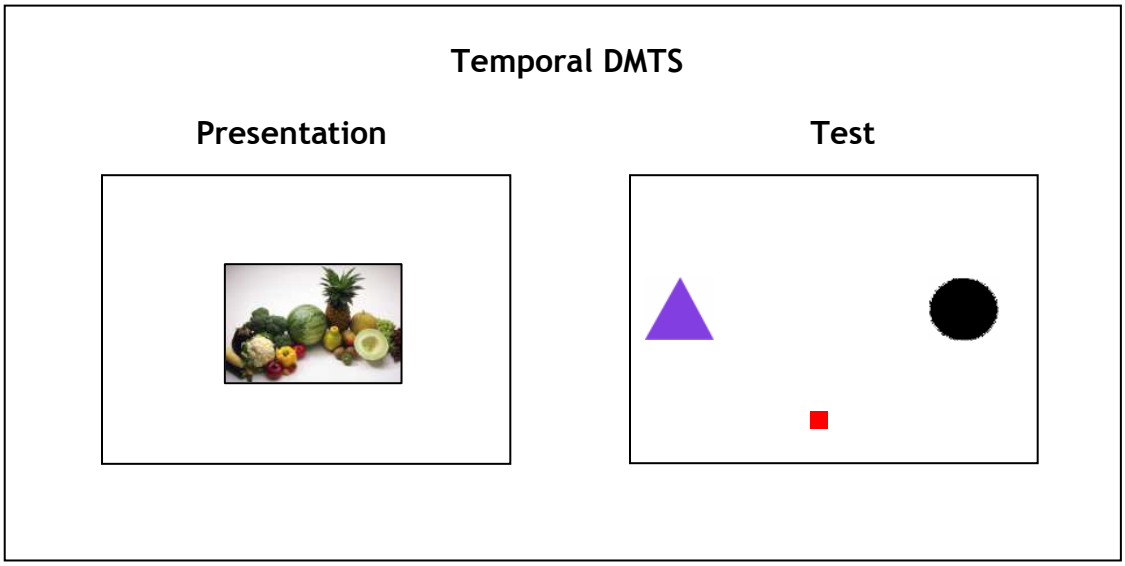

Figure 2.3 Temporal Delayed Matching-to-Sample.

Hypotheses I predicted that both rhesus monkeys and human participants would be highly accurate on all three of the DMTS tasks (at levels significantly above chance performance). However, I expected that human participants in the articulatory suppression condition would be less accurate than participants in the control condition on all of the DMTS tasks. In addition, it was predicted that the length of retention interval would affect *when* accuracy in both the monkeys and human participants (i.e., performance would be significantly better for short retention interval trials compared to long retention interval trials).

Results

Identity Delayed Matching-to-Sample The rhesus monkeys and human participants in both conditions were significantly above chance (50%) on the identity DMTS task, as analyzed a binomial test, $p < .001$ (see Table 2.1 for descriptive statistics). The difference in accuracy between the control condition and the articulatory suppression condition was not significant, as determined by a chi-square difference test, $\chi^2(1, N= 400) = 0.34$, $p > .10$.

Table 2.1 The percent correct for the identity, spatial, and temporal DMTS tasks.

	Identity DMTS			*Spatial DMTS*			*Nonsymbolic Temporal DMTS*			*Symbolic Temporal DMTS*		
Monkeys	Trials	Correct		Trials	Correct		Trials	Correct		Trials	Correct	
Gale	7,394	90%	*	16,374	87%	*	5,326	81%	*	11,433	87%	*
Murph	23,966	97%	*	21,587	93%	*	-------	-------		10,901	91%	*
Willie	4,459	89%	*	9,834	73%	*	25,866	92%	*	22,045	89%	*
Chewie	7,553	85%	*	8,653	77%	*	2,927	89%	*	1,798	91%	*
Humans												
Control	200	99%	*	200	100%	*	-------	-------		200	95%	*
AS	200	100%	*	200	100%	*	-------	-------		200	92%	*

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .001$

The rhesus monkeys completed a larger number of trials than the human participants. The percent correct during the first 100 trials was compared to the last 100 trials completed to determine whether accuracy increased as a result of experience with the task (see Table 2.2). Although only two of the monkeys, Murph and Willie, performed at levels significantly above chance during the first 100 trials, all of the monkeys were significantly above chance during the last 100 trials, as determined by a binomial test, $p < .001$. For the two monkeys who were not initially above chance during the first 100 trials (Gale and Chewie), the increase in accuracy

during the last 100 trials compared to the first 100 trials was significantly different, as determined by a chi-square difference test, Gale, $\chi^2(1, N = 200) = 23.58$, $p < .001$; Chewie, $\chi^2(1, N = 200) = 23.58$, $p < .001$.

Table 2.2 Accuracy during the first 100 and last 100 trials on each DMTS task.

	Identity DMTS				*Spatial DMTS*				*Nonsymbolic Temporal DMTS*				*Symbolic Temporal DMTS*			
	First		Last		First		Last		First		Last		First		Last	
Gale	56%		87%	*	43%		96%	*	50%		89%	*	75%	*	90%	*
Murph	92%	*	93%	*	43%		99%	*	----		----		49%		100%	*
Willie	78%	*	90%	*	47%		63%	*	50%		87%	*	69%	*	95%	*
Chewie	40%		74%	*	53%		96%	*	51%		100%	*	71%	*	90%	*

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .01$.

Spatial Delayed Matching-to-Sample The rhesus monkeys and human participants in both conditions were significantly above chance (50%) on the spatial DMTS task, as analyzed a binomial test, $p < .001$ (see Table 2.1 for descriptive statistics). The difference in accuracy between the control condition and the articulatory suppression condition was not significant, as determined by a chi-square difference test, $\chi^2(1, N = 400) = 1.00$, $p > .01$.

The rhesus monkeys completed a larger of number of trials than the human participants. The percent correct during the first 100 trials was compared to the last 100 trials completed to determine whether accuracy increased as a result of experience with the task (see Table 2.2). The rhesus monkeys all performed at chance levels during the first 100 trials, but were significantly above chance during the last 100 trials completed, as analyzed by a binomial test, $p < .001$. There difference in accuracy between the first 100 and last 100 trials was significant for three individuals, , Gale, $\chi^2(1, N = 200) = 66.26$, $p < .001$; Murph, $\chi^2(1, N = 200) = 76.15$, $p < .001$; Chewie, $\chi^2(1, N = 200) = 48.66$, $p < .001$.

Temporal Delayed Matching-to-Sample In this task, three monkeys first completed a simple nonsymbolic temporal DMTS training task, in which the temporal response symbols always remained in the same positions. After reaching criterion (75%) correct on this task, the monkeys were presented with the symbolic-temporal DMTS task, in which the left and right positions of the symbols were randomly determined on each trial. In order to determine whether this training task was necessary to learn the symbolic discrimination, one monkey, Murph, did not complete the first training task and began immediately on the symbolic-temporal DMTS task.

Nonsymbolic DMTS Training The rhesus monkeys were all significantly above chance (50%) on the nonsymbolic DMTS task, as determined by a binomial test, $p < .001$ (see Table 2.1). In comparing accuracy for the first 100 trials and the last 100 trials, it was found that all of the monkeys performed at chance levels during the first 100 trials, but were significantly above chance during the last 100 trials, as determined by a binomial test, $p < .001$ (see Table 2.2). The increase in accuracy during the last 100 trials compared to the first 100 trials was significant for each individual, Gale, $\chi^2(1, N = 200) = 35.88$, $p < .001$; Willie, $\chi^2(1, N = 200) = 31.72$, $p < .001$; Chewie, $\chi^2(1, N = 200) = 64.90$, $p < .001$.

Symbolic-Temporal DMTS The rhesus monkeys and human participants were all significantly above chance (50%) on the symbolic DMTS task, as determined by a binomial test, $p < .001$ (see Table 2.1). The monkeys who had previous experience working on the nonsymbolic training version of the task were above chance during the first 100 trials completed, as determined by a binomial test, $p < .01$, but the monkey that did not have any previous experience with the nonsymbolic version of the task (Murph) performed at chance levels during the initial 100 trials. However, this individual, along with the other monkeys, demonstrated above chance performance during the last 100 trials completed, as determined by a binomial test,

$p < .001$ (see Table 2.2). The monkey that did not have prior experience with the nonsymbolic training task demonstrated errorless performance during the last 100 trials completed, suggesting that although helpful in initial task acquisition, the training task was not necessary to learn the symbolic discrimination. The increase in accuracy from the first 100 trials completed to the last 100 trials completed was significant for all four monkeys, as determined by a chi-square difference test, Gale, $\chi^2(1, N = 200) = 7.79$, $p = .005$; Murph, $\chi^2(1, N = 200) = 68.46$ $p < .001$; Willie, $\chi^2(1, N = 200) = 22.9$, $p < .001$; Chewie, $\chi^2(1, N = 200) = 11.5$, $p = .001$.

Table 2.3 Accuracy after short and long delays on the symbolic temporal DMTS task.

	All Trials				First 100 Trials				Last 100 Trials			
	Short		*Long*		*Short*		*Long*		*Short*		*Long*	
Monkeys												
Gale	83%	*	90%	*	76%	*	75%	*	81%	*	100%	*
Murph	90%	*	91%	*	52%		47%		100%	*	100%	*
Willie	88%	*	90%	*	76%	*	63%		91%	*	100%	*
Chewie	93%	*	90%	*	85%	*	56%		84%	*	96%	*
Humans												
Control	96%	*	93%	*	----		----		----		----	
AS	91%	*	92%	*	----		----		----		----	

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .001$.

The rhesus monkeys and human participants were significantly above chance on both short retention interval trials and long retention interval trials, as analyzed using a binomial test, $p < .001$ (see Table 2.3). An analysis of the last 100 trials completed revealed that, for three of the monkeys, accuracy was significantly better for long retention interval trials than short retention intervals (Gale, $\chi^2(1, N = 200) = 10.26$, $p = .001$; Willie, $\chi^2(1, N = 200) = 4.48$, $p = .034$; Chewie, $\chi^2(1, N = 200) = 4.27$, $p = .039$. However, the length of the retention interval did

not significantly affect performance for the human participants in either condition [control, $\chi^2(1, N = 200) = 1.14$, $p > .05$; articulatory suppression, $\chi^2(1, N = 200) = 0.04$, $p > .05$].

Discussion

The rhesus monkeys and human participants were above chance on each of the separate DMTS tasks, as predicted, suggesting that both monkeys and humans were able to retrieve these separate memory components from working memory after brief retention intervals. The role of verbal rehearsal did not affect performance on any of the separate DMTS tasks, as participants in the articulatory suppression group did not perform significantly different than participants in the control condition. The rhesus monkeys completed a larger number of trials than the human participants, and accuracy did improve as experience with the task increased, suggesting that the monkeys' memory for these components can be facilitated through increased task experience. However, the prediction that monkeys and humans would be better when tested after short retention intervals than long retention intervals was not supported. In fact, the rhesus monkeys performed better when tested after long retention intervals compared to short retention intervals. It is possible that long retention intervals (10 s) were more aversive to the rhesus monkeys than short retention intervals, and that the aversive quality of the delay may have made the event more salient.

EXPERIMENT 2

The rhesus monkeys were able to perform each of the separate DMTS tasks at levels significantly above chance, but Experiment 2 was designed to examine whether monkeys were able to report two components (*what* and *where* information) from the same event. In this experiment, the monkeys were presented with the same type of event on the computer screen, but then were required to report *where* the photo had been presented, and *what* photo had been

presented. The questions were asked in this order on all trials to avoid any interference effects. That is, if the identity question were presented first, the monkey would have to make a match-to-sample response to a location on the screen (which may or may not correspond to the location of the event) before making a response to the event location. It is possible that the monkeys would become confused by the task and select the location that they had just selected using the joystick cursor, not the location where the event was shown.

Method

Participants The same four rhesus monkeys that were trained on the separate DMTS and tasks in Experiment 1 served as subjects in this experiment. The human participants did not participate in this experiment, as the purpose of this experiment was to determine whether monkeys would be able to understand the task of reporting more than one component from the same event. The identity and spatial components were chosen for this task, under the assumption that if the monkeys were able to understand this format, the temporal question could be added to the sequence of questions in the next experiment.

Procedure The monkey had to move the joystick cursor to a start box in the center of the screen in order to start a trial. A stimulus photo was randomly selected (from a set of 80 photos) on each trial and was randomly assigned to appear in one of two locations on the screen (see Figure 3.1). The photo flashed in the location once per second, lasting three seconds in total. The photo then disappeared and was followed by retention interval (1 s, 5 s, 10 s, or 20 s). After the retention interval, the monkey was presented with a choice between the two response locations (i.e., the spatial question).

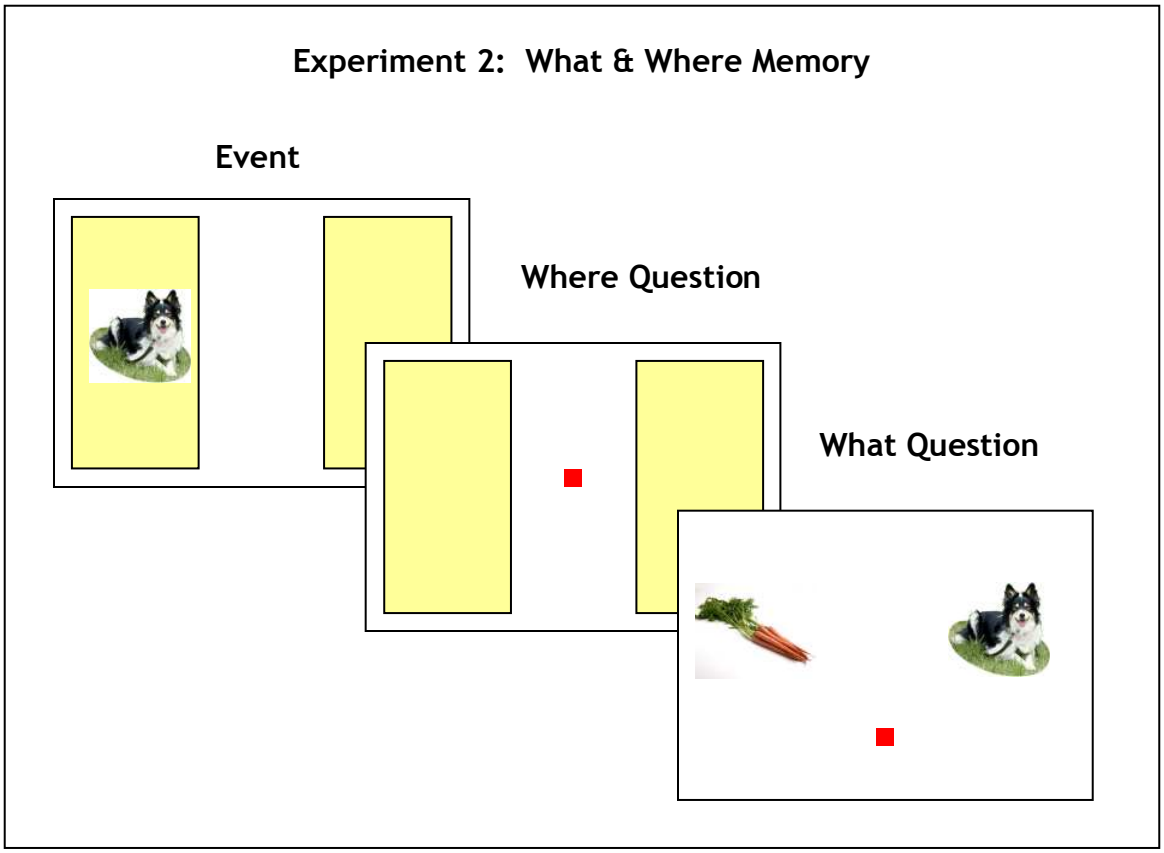

Figure 3.1 What & Where Memory Task

If correct, the monkey received positive sound feedback and a fruit-flavored pellet. However, if the spatial-memory response was incorrect, a brief low tone was presented. The monkey was then presented with a choice between the sample photo and a distractor photo, each in random positions on the screen (i.e., the identity question). Again, if the monkeys were correct they received positive sound feedback and a fruit-flavored pellet, but heard a low buzz on errors. There was a brief intertrial interval (1 s) before the next trial was available to the monkey. The monkeys were initially presented with 1-s retention intervals, but progressed to a longer retention interval (5 s) when they reached criterion (75% correct). Similarly, after reaching criterion on the 5-s retention intervals, the animals were tested with 10-s retention intervals. This continued until the monkeys reached 20-s retention intervals.

Hypotheses It was predicted that the monkeys would be significantly above chance for each of the retention intervals (1 s, 5 s, 10 s, 20 s). However, it was expected that there would be a general trend of decreasing accuracy for each of the retention interval lengths.

Results

The rhesus monkeys were each significantly above chance (50%) at reporting *what* information and *where* information for each of the retention intervals (1 s, 5 s, 10 s, 20 s), as analyzed by a binomial test, $p < .001$ (see Table 3.1). The initial accuracy (the first 100 trials) was compared to the final accuracy (the last 100 trials) to determine if initial performance was above chance and whether increased experience with the task facilitated performance.

Table 3.1 Accuracy for 1-s, 5-s, 10-s, and 20-s retention intervals.

		Trials	*Where*		*What*	
1-s Retention Interval						
	Gale	588	80%	*	83%	*
	Murph	466	97%	*	92%	*
	Willie	24,568	84%	*	88%	*
	Chewie	9,862	96%	*	78%	*
5-s Retention Interval						
	Gale	4,584	77%	*	88%	*
	Murph	8,087	88%	*	93%	*
	Willie	28,355	63%	*	86%	*
	Chewie	8,955	92%	*	79%	*
10-s Retention Interval						
	Gale	5,917	82%	*	93%	*
	Murph	9,654	91%	*	93%	*
	Willie	9,455	63%	*	89%	*
	Chewie	8,654	85%	*	78%	*
20-s Retention Interval						
	Gale	4,034	74%	*	91%	*
	Murph	768	76%	*	89%	*
	Willie	3,971	58%	*	88%	*
	Chewie	781	77%	*	75%	*

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .001$

1-s Retention Interval The rhesus monkeys were each significantly above chance during the first 100 trials of the first task (1-s retention intervals), suggesting that the task of reporting multiple components was not difficult for the monkeys, $p < .01$. For some individuals, accuracy increased significantly from the first 100 trials to the last 100 trials. Specifically, one monkey (Chewie) was significantly more accurate at reporting *where* information during the final 100 trials of the task than during the initial 100 trials, $\chi^2(1, N = 200) = 14.20$, $p < .001$. Two individuals (Chewie and Gale) were significantly more accurate at reporting *what* information during the last 100 trials compared to the first 100 trials, Chewie , $\chi^2(1, N = 200) = 13.67$, $p < .001$, and Gale, $\chi^2(1, N = 200) = 5.10$, $p = .024$ (see Table 3.2).

5-s Retention Interval In this task, the monkeys were required to respond after a longer retention interval, and this task (specifically the task of having to report spatial information after a delay) was initially difficult for the monkeys, as they were not above chance at reporting *where* information during the first 100 trials completed, as analyzed by a binomial test, $p > .05$. However, increased experience with the task facilitated performance, as there was a significant increase in accuracy for *where* information during the last 100 trials compared to the first 100 trials for each of the monkeys, Gale $\chi^2(1, N = 200) = 33.68$, $p < .001$; Murph, $\chi^2(1, N = 200) = 51.43$, $p < .001$; Willie, $\chi^2(1, N = 200) = 6.17$ $p = .013$; Chewie, $\chi^2(1, N = 200) = 31.23$, $p < .001$. In contrast, the monkeys were immediately accurate at reporting *what* information after the delay, demonstrating significantly above chance accuracy for reporting *what* information during the first 100 trials of the task (see Table 3.2).

10-s Retention Interval After the monkeys had experience responding after a longer delay (5 s), they were able to proceed to the next retention interval (10 s) with minimal difficulty, as performance was significantly above chance during the first 100 trials of the 10 s retention

interval task, $p < .01$. The increase in accuracy for reporting where information during the last 100 trials compared to the first 100 trials was significant for one monkey, Gale, $\chi^2(1, N = 200) = 22.84$, $p < .001$. However, the increase in accuracy for reporting what information during the last 100 trials compared to the first 100 trials was not significant for any of the monkeys (see Table 3.2).

Table 3.2 Accuracy for each retention interval during the first and last 100 trials.

	First 100				Last 100			
	Where		What		Where		What	
1-s Retention Interval								
Gale	85%	*	77%	*	92%	*	89%	*
Murph	98%	*	88%	*	93%	*	93%	*
Willie	75%	*	86%	*	77%	*	89%	*
Chewie	80%	*	66%	*	97%	*	88%	*
5-s Retention Interval								
Gale	56%		83%	*	92%	*	91%	*
Murph	55%		94%	*	98%	*	91%	*
Willie	54%		81%	*	71%	*	84%	*
Chewie	61%		90%	*	94%	*	82%	*
10-s Retention Interval								
Gale	64%	*	90%	*	92%	*	83%	*
Murph	88%	*	91%	*	90%	*	94%	*
Willie	66%	*	86%	*	69%	*	87%	*
Chewie	86%	*	68%	*	87%	*	76%	*
20-s Retention Interval								
Gale	60%		87%	*	69%	*	91%	*
Murph	87%	*	93%	*	74%	*	85%	*
Willie	64%	*	90%	*	55%		87%	*
Chewie	67%	*	78%	*	83%	*	75%	*

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .01$

20-s Retention Interval The monkeys were all significantly above chance at reporting *what* information during the first 100 of the 20-s retention interval task, but only three of the

monkeys were above chance at reporting *where* information during the first 100 trials, suggesting that the increase in delay was difficult for one of the monkeys. The increase in accuracy for reporting where information during the last 100 trials compared to the first 100 trials was significant for two of the monkeys, Murph $\chi^2(1, N = 200) = 5.83$, $p = .02$, and Chewie, h $\chi^2(1, N = 200) = 6.83$, $p = .009$. However, the increase in accuracy for reporting what information during the last 100 trials compared to the first 100 trials was not significant for any of the monkeys (see Table 3.2).

Discussion

In the previous tasks, the monkeys had not been required to make multiple responses after the event presentation, so one might predict that the purpose of the task would not be immediately apparent. However, the monkeys acquired an understanding of the task immediately, and were able to report both *what* information and *where* information after varying retention intervals. The results confirm that rhesus monkeys are able to retain and report multiple components of past events using this paradigm. However, this study was not designed to test whether multiple components are bound together in memory (which is assessed in Experiment 3). The purpose of this study was to ensure that monkeys were able to understand the paradigm and the specific format for reporting multiple components, as well as to ensure that the monkeys would be able to report information after varying delays. In the next experiment, however, the integration of *what*, *where*, and *when* was tested explicitly in both rhesus monkeys and human participants.

EXPERIMENT 3

In this experiment, rhesus monkeys and human participants were required to report all three components of the event (*what, where, when)* after presentation of the event. In another

task, both monkeys and humans were required to report only one component of the event (that was randomly selected on each trial). In this task, participants could not anticipate which response they would be required to make because they were not aware which question they would receive.

Method

Participants The same rhesus monkeys and human participants that were initially trained on the three separate DMTS tasks also participated in this experiment. Therefore, all of the participants had experience with each of the separate tasks before being required to report multiple components from the same event. In addition, the rhesus monkeys also had experience in reporting both *where* and *what* components in Experiment 2, in order to determine whether they would be capable of understanding the task and report multiple components (*what* and *where* information) from past events.

Reporting All Three Components Sequentially In this task, a randomly selected photo randomly appeared at one of the two locations. The presentation was followed by either a short retention interval (1 s) or a long retention interval (10 s), which was randomly determined on each trial. Then, the rhesus monkeys were presented with the *where* question, the *what* question, and the *when* question sequentially (see Figure 4.1). The questions were presented in the order stated above to minimize interference (e.g., if one were to ask the *what* or *when* question first, the animal must make a response to a location on the screen, and this may interfere with the memory for *where* the actual event took place). If the monkey responded correctly to one of the questions, it received positive auditory feedback and a fruit flavored pellet. If the monkey responded incorrectly to one of three questions, it received negative auditory feedback and no

pellet reinforcement. However, all three questions were presented even if the participant responded incorrectly to one of the questions in the sequence.

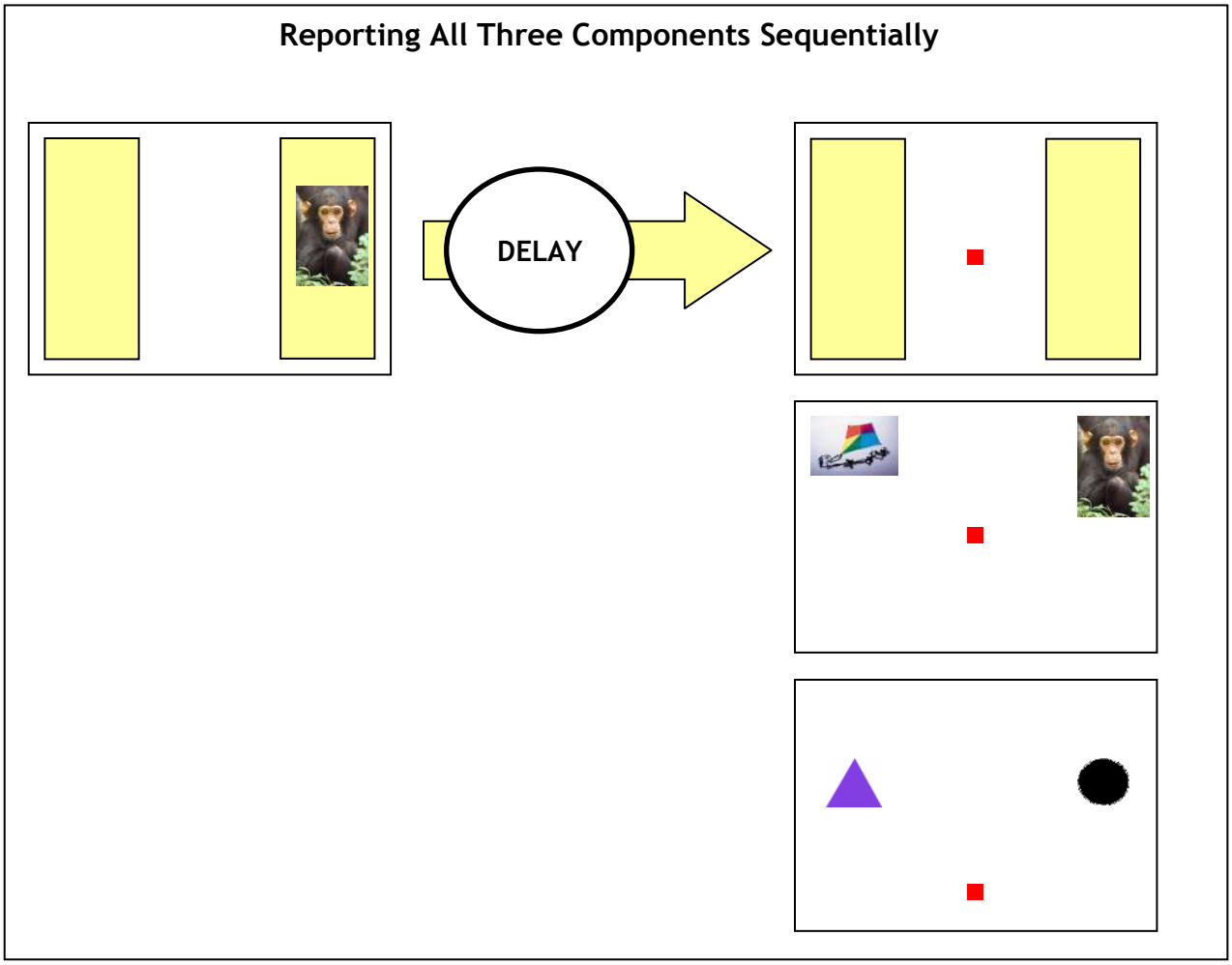

Figure 4.1 Reporting All Three Components Sequentially

Unanticipated Question Type Although the experiment described above is one method of assessing whether *what*, *where*, and *when* information is integrated in memory, it was also be necessary to present this same task in which only one question is randomly selected for presentation on each trial in order to assess whether interference or decay processes interfere with retrieval. For example, asking the questions sequentially may interfere with the ability to remember the event itself, or the question may no longer be straightforward (e.g., asking the

individual to determine *when* the event occurred becomes complicated if the individual must answer several questions beforehand, as the time it takes to respond to these questions increases the amount of time since the event). In this task, the monkeys and human participants were unaware of which question they would be asked, as the question type was randomly selected on each trial (see Figure 4.2). If *what*, *where*, and *when* information is concurrently available in memory, the monkeys and humans should be significantly above chance at recalling any of the components, even when they are unaware of which question will be presented.

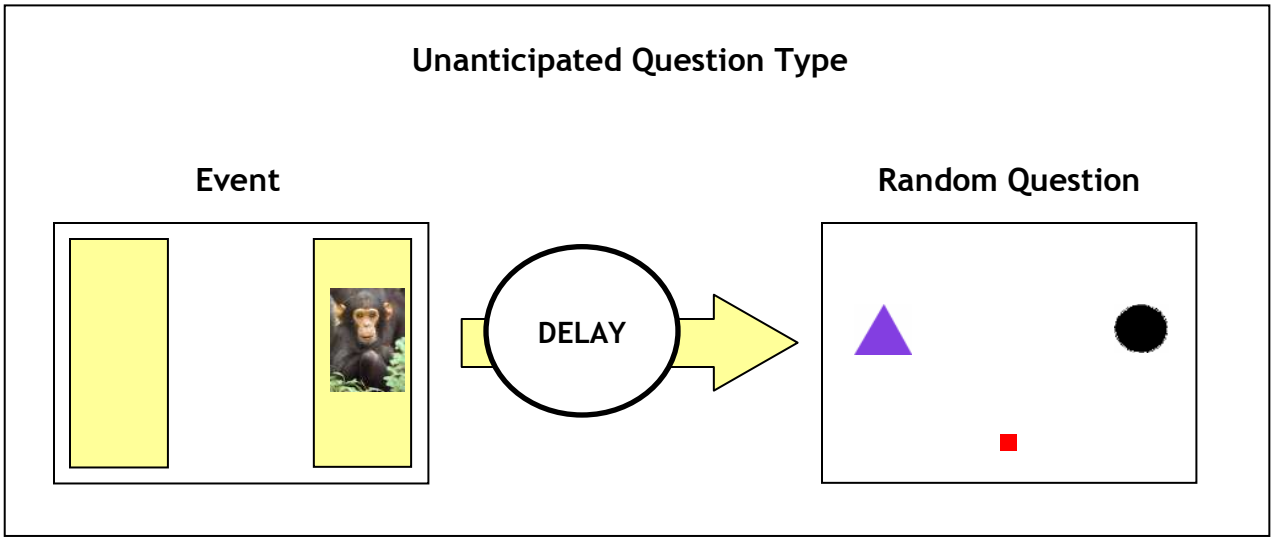

Figure 4.2 Unanticipated Question Type

The rhesus macaques in this study (N = 4) were presented with both tasks: 1) presentation of the *where*, *what*, and *when* questions in sequential order and 2) random presentation of one of the questions on any given trial. If a monkey reached a criterion of 75% correct in a block of 100 trials on the sequential order task, the animal was then presented with the random question task. As stated previously, however, the sequential question task may cause various interference effects; therefore, if a monkey failed to reach criterion after 5,000 trials, the animal was still tested on the unanticipated question task.

The human participants also were presented with both tasks (the sequential question task and the random question task) in the same order presented to the rhesus monkeys. The human participants were informed that the task would require them to remember a past event and report information concerning the event (specifically what, where, and when the event occurred). As with Experiment 1, the participants were assigned to one of two conditions, an articulatory suppression condition and a control condition. If verbal rehearsal facilitates the integration of *what*, *where*, and *when* information in memory, the participants who were required to perform the articulatory suppression task should be less accurate than the participants who were not prevented from rehearsing during the retention interval.

Hypotheses It was predicted that both rhesus monkeys and human participants would demonstrate simultaneous memory for *what*, *where*, and *when* information, and that there would be evidence of what-where-when integration in both monkeys and human participants. The human participants were expected to do better than the rhesus monkeys, and the participants in the control condition were expected to do better than those in the articulatory suppression condition. It was also predicted that accuracy for *what* and *where* information would be higher than accuracy for *when* information in both humans and monkeys. I also expected both monkeys and humans would perform better when presented with short retention interval trials than when presented with long retention interval trials.

Results

Reporting All Three Components Sequentially The rhesus monkeys were significantly above chance (50%) at reporting *what* information and *where* information, and two monkeys were also significantly above chance at reporting *when* information, as analyzed using a binomial test, $p < .001$ (for descriptive statistics, see Table 4.1). The human participants in both the

control condition and the articulatory suppression condition were significantly above chance at reporting *what* information, *where* information, and *when* information from the event, as analyzed using a binomial test, $p < .001$ (see Table 4.1).

Table 4.1 The percentage correct for what, where, and when information.

		Where		What		When	
Reporting All Three Components							
Rhesus Monkeys							
Gale	3,218	85%	*	93%	*	57%	
Murph	2,771	93%	*	96%	*	50%	
Willie	6,536	69%	*	84%	*	63%	*
Chewie	1,163	89%	*	82%	*	63%	*
Human Participants							
Control	400	100%	*	100%	*	95%	*
AS	400	100%	*	100%	*	94%	*
Unanticipated Question Type							
Rhesus Monkeys							
Gale	1,091	86%	*	97%	*	80%	*
Murph	2,209	92%	*	96%	*	75%	*
Willie	1,803	68%	*	90%	*	85%	*
Chewie	2,193	88%	*	84%	*	89%	*
Human Participants							
Control	400	100%	*	100%	*	94%	*
AS	400	98%	*	100%	*	96%	*

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .001$

The conditional probabilities of accuracy were analyzed to determine whether the rhesus monkeys and human participants were more likely to be correct on any given question type, given correct performance on the preceding question type(s). If working memory for *what* and *where* information were bound together, the conditional probability of correctly responding to the *what* question, given correct performance on the *where* question, should be higher than the overall accuracy for *what* information (i.e., accuracy for *what* information independent of

performance on *where*). However, there was no difference in accuracy between conditional probabilities of *what given correct performance on where* and actual percent correct for *what* information in both the rhesus monkeys and human participants. In addition, if working memory for *what, where,* and *when* information are bound together, the conditional probability of correctly responding to the *when* component, given correct performance on both *what* and *where* questions, should be significantly higher than the probability of correctly responding to the *when* question (independent of whether previous responses were correct or incorrect). There were differences between the conditional probabilities of *when given correct performance on what and where* and the actual percent correct for rhesus monkeys, but these differences were not significant, Gale, $\chi^2(1, N = 3{,}218) = 0.49$, $p > .05$; Murph, $\chi^2(1, N = 2{,}771) = 1.41$, $p > .05$. There was also no difference between the conditional and actual percent correct for the human participants (see Table 4.2).

The conditional probabilities were also analyzed using binomial logistic regression to determine whether accuracy on one question predicted accuracy on subsequent questions. The results indicated that *where* accuracy predicted *what* performance for one monkey, Willie, $\chi^2(1, N = 6536) = 8.78$, $Exp(B) = 0.81$, $p < .01$. The odds ratio (Exp(B)) refers to the increase in the dependent variable (i.e., correctly reporting the *what* component of the event) that is associated with each unit increase in the independent variable (i.e., correctly reporting the *where* component of the event). The odds of Willie correctly reporting *what* information increased by a factor of 0.81 if he had correctly reported the *where* component of the event. The results also indicated that accuracy on *what* and *where* questions predicted *when* accuracy for two monkeys, Gale, $\chi^2(1, N = 3{,}218) = 4.29$, $Exp(B) = 1.20$, $p < .05$; Murph, $\chi^2(1, N = 2{,}771) = 24.70$, $Exp(B) = 1.89$, $p < .001$. If Gale had correctly reported the *what* and *where* components of the event, the odds of

him reporting the *when* component of the event increased by a factor of 1.2. If Murph had correctly reported the *what* and *where* components of the event, the odds of him reporting the *when* component of the event increased by a factor of 1.89. It was impossible to conduct a binomial logistic regression analysis to determine whether *where* accuracy predicted *what* accuracy for human participants in both conditions because each group demonstrated 100% accuracy for one of the memory components. However, it was possible to determine whether *what* and *where* accuracy predicted *when* accuracy, but the results were not significant for both groups, $\chi^2(1, N = 400) = 0.00$, $p < .05$.

Table 4.2 The conditional probabilities of being correct on one question given correct performance on the preceding question(s).

	What		When	
	Conditional (correct where)	overall percent correct	conditional (what + where)	overall percent correct
Monkeys				
Gale	93.23%	93.04%	55.75%	56.68%
Murph	96.57%	96.43%	47.94%	49.58%
Willie	85.26%	84.36%	62.72%	62.81%
Chewie	81.77%	81.51%	63.58%	63.28%
Humans				
Control	99.75%	99.75%	94.74%	94.75%
AS	100.00%	100.00%	93.48%	93.50%

The accuracy levels for short retention interval trials and long retention interval trials (from the last 100 trials completed) were compared to determine whether the length of delay affected accuracy for reporting the three memory components (see Table 4.3). There was a trend for some monkeys to perform better on both the *what* and *where* questions after short retention intervals. Specifically, two monkeys (Gale and Murph) were more accurate at reporting *what* information on short interval trials, [Gale, $\chi^2(1, N = 200) = 4.78$, $p < .05$, and Willie, $\chi^2(1, N =$

200) = 7.41, $p < .01$], and one monkey (Chewie) was more accurate at reporting *where* information on short retention interval trials, $\chi^2(1, N = 200) = 7.71$, $p < .01$. In contrast, for the *when* question, the opposite pattern was observed; some monkeys were more accurate on long retention intervals compared to short retention intervals. These monkeys were the individuals who performed at chance levels on the temporal component (Gale and Murph). These individuals were only above chance on long retention intervals.

Table 4.3 The accuracy for all components on short RI trials and long RI trials. The table displays accuracy for the last 100 trials completed for the monkeys and accuracy for all trials completed for the human participants.

	Where		What		When	
	Short	Long	Short	Long	Short	Long
Reporting All Three Components						
Rhesus Monkeys						
Gale	94%	89%	98%	87%	37%	63%
Murph	100%	93%	93%	98%	0%	100%
Willie	76%	64%	95%	76%	76%	62%
Chewie	100%	85%	77%	83%	62%	77%
Human Participants						
Control	100%	100%	100%	99%	95%	94%
AS	100%	99%	100%	100%	95%	92%
Unanticipated Question Type						
Rhesus Monkeys						
Gale	96%	74%	100%	98%	89%	73%
Murph	96%	89%	100%	96%	93%	91%
Willie	88%	57%	95%	88%	94%	79%
Chewie	93%	75%	80%	80%	81%	94%
Human Participants						
Control	100%	100%	100%	100%	92%	96%
AS	100%	96%	100%	100%	99%	94%

It is possible that, for those two individuals, the time required to answer each question before reaching the *when* question may have increased the delay length since the original event

presentation, making it difficult for the monkeys to respond to this question. If this was the case, we would expect to find a bias in selecting the long delay symbol for these individuals. An analysis of all trials completed revealed that one of the monkeys (Murph) was indeed significantly more likely to select the long delay symbol (97%) than the short delay symbol (3%) as determined by a binomial test, $p < .001$. The other monkey (Gale) also demonstrated this bias, but to a lesser and nonsignificant extent, selecting the long delay symbol (55%) more often than the short delay symbol (45%). The human participants in both groups performed equally well on both short and long retention intervals. Specifically, there was no difference in accuracy for *what* or *where* information for short and long delays. In addition, the difference in accuracy for *when* information after short delays and long delays was not significant, $\chi^2(1, N = 127) = 0.36$, $p > .05$.

The rhesus monkeys completed more trials than human participants. In order to determine whether experience with the task affected performance in the rhesus monkeys, a chi-square difference test was used to determine whether accuracy was significantly higher during the last 100 trials compared to the first 100 trials (for descriptive statistics, see Table 4.4). The rhesus monkeys were all significantly above chance at correctly indicating *what* information and *where* information during the first 100 trials of the task, as analyzed using a binomial test, $p < .01$, but none of the monkeys were above chance at reporting *when* information during these initial 100 trials, $p > .05$. However, an analysis of the last 100 trials completed revealed that in addition to being above chance at reporting *what* and *where* information, two of the monkeys had also reached significantly above chance performance for reporting the *when* component of the event, $p < .001$ (see Table 4.4). The monkeys were not significantly better at reporting *what* information during the last 100 trials than during the initial 100 trials of the task, $p > .05$.

However, three monkeys did perform significantly better on the *where* question during the last 100 trials compared to the first 100 trials, as analyzed using a chi-square difference test, Gale, $\chi^2(1, N = 200) = 11.48$, $p = .001$; Murph, $\chi^2(1, N = 200) = 18.98$, $p < .001$; Chewie, $\chi^2(1, N = 200) = 11.48$, $p = .001$. In addition, two monkeys performed significantly better on the *when* question during the last 100 trials than the first 100 trials, as analyzed using a chi-square difference test, Willie $\chi^2(1, N = 200) = 6.81$, $p = .009$; Chewie, $\chi^2(1, N = 200) = 10$, $p = .002$.

Table 4.4. The rhesus monkeys accuracy during the first 100 and last 100 trials.

	Where				What				When			
	First		Last		First		Last		First		Last	
Reporting All Three Components												
Gale	74%	*	92%	*	95%	*	93%	*	54%		49%	
Murph	74%	*	96%	*	94%	*	96%	*	51%		54%	
Willie	64%	*	71%	*	85%	*	86%	*	52%		70%	*
Chewie	74%	*	92%	*	77%	*	80%	*	48%		70%	*
Unanticipated Question Type												
Gale	90%	*	84%	*	96%	*	99%	*	71%	*	80%	*
Murph	91%	*	92%	*	91%	*	98%	*	71%	*	92%	*
Willie	67%	*	72%	*	88%	*	92%	*	73%	*	95%	*
Chewie	92%	*	83%	*	82%	*	80%	*	86%	*	87%	*

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .01$

Unanticipated Question Type The rhesus monkeys were all significantly above chance for all three trial types (*what*, *where*, and *when* trials) when the question type was randomly selected on each trial, as analyzed by a binomial test, $p < .01$ (see Table 4.1). The human participants in both conditions were also significantly above chance on *what*, *where*, and *when* trials, as analyzed by a binomial test, $p < .001$

The percentage correct for each of the three trial types were compared using chi-square difference tests to determine whether the question types varied in difficulty. The rhesus monkeys demonstrated individual differences concerning the difficulty levels for the three

question types (see Table 4.5). For two monkeys, accuracy on *what* trials was significantly higher than accuracy on *where* trials [Gale, $\chi^2(1, N = 200) = 25.97$, $p < .001$; Murph, $\chi^2(1, N = 200) = 8.84$, $p = .003$] and accuracy on *where* trials was significantly higher than accuracy on *when* trials [Gale, $\chi^2(1, N = 200) = 5.65$, $p = .017$; Murph, $\chi^2(1, N = 200) = 78.44$, $p < .001$]. Another monkey, Willie, was significantly more accurate on *what* trials than *when* trials, [$\chi^2(1, N = 200) = 6.11$, $p = .013$] and on *when* trials than *where* trials [$\chi^2(1, N = 200) = 48.01$, $p < .001$]. Chewie demonstrated a different pattern; he was equally accurate on *when* trials and *where* trials [$\chi^2(1, N = 200) = 0.03$, $p > .05$], but he was significantly more accurate on *where* trials than *what* trials [$\chi^2(1, N = 200) = 5.35$, $p = .021$], and *when* trials than *what* trials [$\chi^2(1, N = 200) = 8.04$, $p = .005$]. The human participants in both groups were less accurate on *when* trials than *what* and *where* trials, but the difference was not significant [control group, $\chi^2(1, N = 252) = 0.1$, $p > .05$; articulatory suppression, $\chi^2(1, N = 262) = 0.01$, $p > .05$].

There were differences in accuracy for short retention interval trials and long retention interval trials for the rhesus monkeys, but not the human participants (see Table 4.3). One monkey (Chewie) was significantly more accurate at reporting *when* information on short retention interval trials compared to long retention interval trials, $\chi^2(1, N = 100) = 4.04$, $p < .05$. Three monkeys (Gale, Willie, and Chewie) were more accurate at reporting *where* information when the delay was short than when the delay was long, Gale, $\chi^2(1, N = 100) = 8.61$, $p < .01$; Willie, $\chi^2(1, N = 100) = 11.83$, $p = .001$; Chewie, $\chi^2(1, N = 100) = 6.19$, $p < .05$. In contrast, the human participants in both conditions did not perform significantly different on short retention interval trials than long retention interval trials, as analyzed using a binomial test, $p > .05$.

Table 4.5 The rank order of difficulty for each trial type.

		Accuracy				
		High ----------				Low
Rhesus Monkeys						
	Gale	What	>	Where	>	When
	Murph	What	>	Where	>	When
	Willie	What	>	When	>	Where
	Chewie	Where	=	When	>	What
Human Participants						
	Control	What	=	Where	=	When
	AS	What	=	Where	=	When

The rhesus monkeys completed more trials than human participants. In order to determine whether experience with the task affected performance for the rhesus monkeys, a chi-square difference test was used to determine whether accuracy was significantly higher during the last 100 trials compared to the first 100 trials (see Table 4.4). Each of the monkeys was significantly above chance on *what* trials, *where* trials, and *when* trials during the first 100 trials and maintained this performance during the last 100 trials completed, as analyzed by binomial tests, $p < .001$. There was a significant increase in accuracy for *what* trials for one monkey (Murph) during the last 100 trials compared to the first 100 trials [$\chi^2(1, N = 200) = 4.71, p < .05$] as well as a significant increase in accuracy for *when* information for two individuals, Murph, $\chi^2(1, N = 200) = 14.62, p < .001$ and Willie, $\chi^2(1, N = 200) = 18.01, p < .001$.

Discussion

The rhesus monkeys and human participants demonstrated memory for *what*, *where*, and *when* information when they were unaware of which question they would be presented on any given trial, suggesting that all three types of information were concurrently available in working memory. In addition, some monkeys were able to report all three components sequentially after each event. There was some evidence that *what*, *where*, and *when* information were integrated in working memory, as accuracy on both the *what* and *where* questions predicted performance on

the *when* question. Specifically, two of the monkeys were more likely to be correct on the temporal question if they had been correct at reporting the object component and spatial component, suggesting that memory for *when* an event occurred was bound to memory for *what* and *where* the event occurred. It is important to note that although there was no evidence of *what-where-when* integration in the remaining two rhesus monkeys and the human participants, the fact that both groups were highly accurate on all three questions types may have made it difficult to detect binding of information in memory. In fact, the monkeys who demonstrated evidence of binding were the monkeys who were not significantly above chance at reporting the temporal component of the past event.

The monkeys and human participants were highly accurate on all of the question types, but there were individual differences with regard to how easily the types of information were retrieved. There was a general trend that memory for *what* information was most accurate, followed by memory for *where* and *when* information. However, one monkey actually performed better on both *where* and *when* information than *what* information. Although Chewie demonstrated higher accuracy for *when* information in this experiment, he actually performed the smallest number of trials on the nonsymbolic (N = 2,591) and symbolic DMTS tasks (N = 1,645) compared to other monkeys. In addition, he completed a larger number of identity and spatial DMTS trials than temporal DMTS trials. These results suggest that there may be individual differences in the extent to which a monkey attends to the temporal component of the event, as well as which components are most salient to the individual.

These results suggest that rhesus monkeys and human participants are able to report multiple components from the same event. However, it is possible that this task can be accomplished by simply selecting the most recent or familiar stimulus (and not a specific past

episode). In the next experiment, rhesus monkeys and human participants were prevented from using familiarity cues in responding, as they were required to select the most recent stimulus on half of the trials and the less familiar stimulus on half of the trials, and this was randomly determined on each trial, so that the individual did not know which question they would be asked about until they were given the cue.

EXPERIMENT 4

The purpose of Experiment 3 described above was to: 1) determine whether rhesus monkeys and adult humans are capable of using temporal symbols to "comment" about the length of time that has elapsed since an event, 2) determine whether temporal knowledge of the amount of time that has elapsed is integrated with spatial information concerning the location of the event and the properties of the event itself and 3) compare the results of rhesus monkeys and adult humans. However, knowing whether a short delay (1 s) or a long delay (10 s) has elapsed since an event does not provide evidence that an individual understands *when* the event occurred relative to other events in the past. In addition, it does not demonstrate that the individual is responding to particular past event, as the individual could be responding to just the most recent event. The purpose of Experiment 4 was to determine whether rhesus monkeys use the temporal symbols to comment on which events are relatively "recent" compared to events that are "remote," and to compare the monkeys' performance with the results from adult human participants. Specifically, in this task I examined whether the identity of these symbols (purple triangle and black circle) were indeed associated with the correct temporal properties, and whether subjects were able to use these symbols to comment on the relative temporal properties of past events.

Method

Participants The same rhesus monkeys and human participants that participated in the previous experiments also participated in this experiment. Therefore, all of the participants had experience with each of the previous tasks.

Procedure In contrast to the previous experiment in which only one event was presented, two different events were presented sequentially on the computer in this experiment. One event will be referred to as the remote event and one event will be referred to as the recent event. Each event was unique, occurring at a particular point in time (the temporal component) and containing a separate randomly selected photo (the *what* component) and location (the *where* component). The interval between the first event and the questioning phase (10 s) and the second event and the questioning phase (1 s) was consistent with monkeys' previous training with the temporal symbols. On each trial, one of the events was randomly selected as the "test event," so that the individual would not be able to anticipate which event they would be asked to report. The presentation of the events was followed by the presentation of a cue from one of the events (an object cue, a spatial cue, or a temporal cue) to indicate which event the individual must report. In the case of the *object cue*, the subject was be presented with a photo from the test event (the *what* cue), followed by the *where* and *when* questions The subject was reinforced for selecting the spatial location where the photo was presented and the temporal symbol corresponding to when the photo was presented. In the case of the *spatial cue*, the subject was presented with the spatial location from the test event (the *where* cue), followed by the *what* and *when* questions. The subject was reinforced for selecting the object presented in this spatial location and the temporal symbol corresponding to when the event took place in this spatial location. In the case of the *temporal cue*, the subject was presented with the temporal symbol

corresponding to the test event (the *when* cue), followed by the *what* and *where* questions. In this task, the subject was required to indicate *what* and *where* information about the recent or remote event (see Figure 5.1).

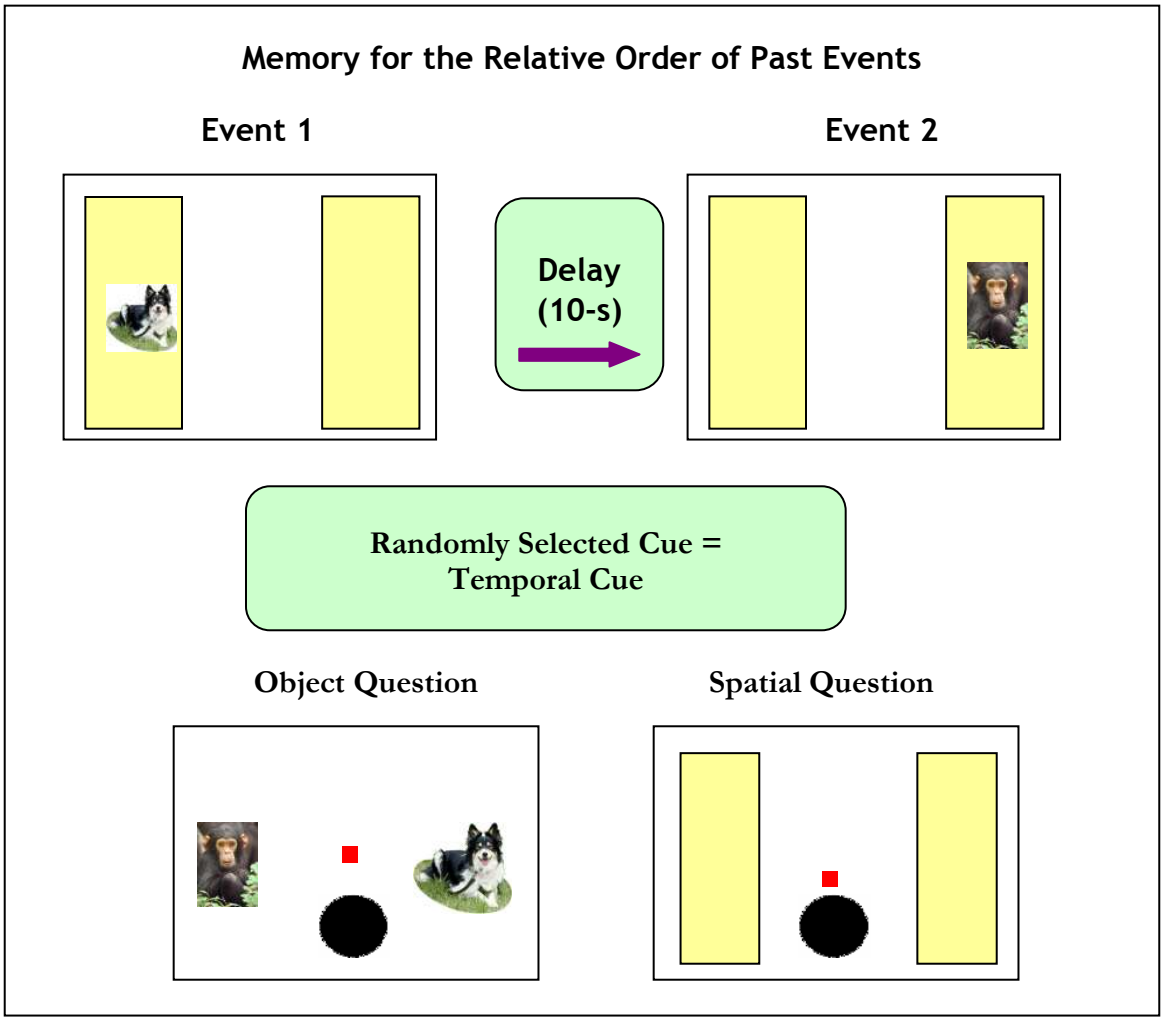

Figure 5.1 Memory for the Relative Order of Past Events

It is important to note that the event that the subjects were tested on was randomly determined on each trial and therefore the subject could not anticipate whether they would be required to report information from the most recent event or the remote event. Therefore, this task required reference to a particular past event among other past events, and accuracy on this

task could not be accomplished by adopting a simple rule such as “always select the most familiar item” or “respond to the item and location that has the strongest memory trace.” In trials in which the remote event was selected as the to-be-remembered event, responding to the most recent location and photo would lead to decreased accuracy.

Hypotheses It was predicted that the rhesus monkeys and human participants would be able to use all three memory cues to report the appropriate event. However, it was expected that: 1) human participants in the control condition would perform better than participants in the articulatory suppression condition, and 2) the temporal cue would have the highest accuracy in both humans and monkeys.

Results

The rhesus monkeys were presented with a training task in order to familiarize them with attending to two sequentially presented events and then responding on the basis of a temporal, spatial, or object cue from one of the events. In this training task, the monkeys were first trained on the long retention interval symbol as a cue (in this case the monkey was to select the photo and spatial location of the first event that was presented). In the last 100 trials, two monkeys were above chance at selecting the photo from the first event, $p < .001$, but none of the monkeys reached above chance performance for reporting the spatial component from the first event, $p > .05$. Next, the monkeys were trained on the short retention interval symbol as a cue (in this case the monkey was to select the photo and spatial location of the second event that was presented). In the last 100 trials, the same two monkeys were above chance at selecting the photo from the second event, $p < .001$, but once again none of the monkeys were above chance at selecting the spatial component from the second event, $p < .001$ (see Table 5.1).

Table 5.1 The rhesus monkeys' accuracy on the memory cue training tasks.

		All Trials			First 100 Trials			Last 100 Trials		
	Trials	Where	What		Where		What	Where	What	
Long Temporal Cue										
Gale	6779	50%	70%	*	47%		40%	47%	78%	*
Murph	3452	53%	58%		62%	*	41%	51%	73%	*
Willie	2963	52%	46%		47%		43%	58%	48%	
Chewie	1731	53%	45%		55%		39%	56%	48%	
Short Temporal Cue										
	N	Where	What		Where		What	Where	What	
Gale	6882	51%	52%		67%	*	34%	44%	83%	*
Murph	1918	47%	50%		43%		33%	47%	85%	*
Willie	1660	59%	49%		51%		49%	67%	* 56%	
Chewie	1038	49%	53%		37%		49%	56%	56%	

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .01$

Temporal Cue Task In this task the monkeys were required to select the appropriate photo and spatial location corresponding to the randomly chosen temporal cue on each trial. There was evidence that one monkey, Murph, was able to report both the *what* and *where* components corresponding to the temporal cue, at levels significantly above chance, as determined by a binomial test, $p < .001$. Two other monkeys were significantly above chance for one type of component, but not both. Specifically, Gale was significantly above chance at reporting the *what* component and Willie was significantly above chance at reporting the *where* component, as analyzed by a binomial test, $p < .001$ (see Table 5.2). The human participants in both the control and aritculatory suppression group were significantly above chance at indicating both *what* and *where* information corresponding to the temporal cue, as analyzed by a binomial test, $p < .001$ (see Table 5.2). There were no significant group differences in accuracy for *where*

information [$\chi^2(1, N = 800) = 2.13$, $p > .05$] or *what* information, [$\chi^2(1, N = 800) = 0.05$, $p > .05$].

Table 5.2 Accuracy for the temporal, object, and spatial cue tasks.

			First Event				Second Event			
Temporal			Where		What		Where		What	
Monkeys										
	Gale	6973	51%		49%		49%		72%	*
	Murph	2720	75%	*	41%		85%	*	79%	*
	Willie	3558	45%		51%		66%	*	50%	
	Chewie	1164	53%		49%		50%		53%	
Humans										
	Control	400	95%	*	97%	*	95%	*	98%	*
	AS	400	92%	*	97%	*	93%	*	98%	*
Object			Where		When		Where		When	
Monkeys										
	Gale	2943	50%		44%		52%		59%	*
	Murph	3058	48%		67%	*	71%	*	46%	
	Willie	3793	52%		39%		51%		62%	*
	Chewie	1138	48%		53%		47%		53%	
Humans										
	Control	400	94%	*	93%	*	97%	*	95%	*
	AS	400	99%	*	97%	*	97%	*	99%	*
Spatial			What		When		What		When	
Monkeys										
	Gale	1805	54%		54%	*	49%		45%	
	Murph	2418	52%		61%	*	53%		37%	
	Willie	2154	51%		46%		55%	*	52%	
	Chewie	1208	42%		59%	*	62%	*	40%	
Humans										
	Control	400	94%	*	94%	*	92%	*	88%	*
	AS	400	95%	*	94%	*	99%	*	96%	*

Note: An asterisk indicates above chance performance, as analyzed by a binomial test, $p < .01$

However, when accuracy is analyzed as a function of trial type, comparing performance for short retention interval trials and long retention interval trials, the results indicate that, in general, monkeys were not equally accurate for both trial types. The monkeys that had been

above chance at indicating *what* or *where* information were actually only above chance when the cue prompted them to report information from the most recent event. However, there was one exception; Murph was equally accurate at indicating spatial information on both trial types. In contrast to the rhesus monkeys, the human participants were above chance at reporting both types of information on trials in which they had to select the location and photo from the first event (long retention interval cue) and trials in which they had to select the location and photo from the second event (short retention interval cue).

Object Cue Task The rhesus monkeys performed at chance levels, with the exception of Murph who was significantly above chance at reporting *where* information and *when* information, as determined by a binomial test, $p < .001$ (see Table 5.2). An analysis of performance by trial type (comparing trials in which the object cue was from the first event and trials in which the object cue was from the second event) revealed that Murph was only above chance at reporting *where* information when he was required to select the location from the most recent event, $p < .001$. It was also found that Murph was only above chance at reporting *when* information if he was presented with the object cue from the first event (the less familiar event), $p < .001$.

In contrast to the rhesus monkeys, human participants in both conditions were significantly above chance at reporting *where* information and *when* information from the event corresponding to the object cue, as determined by a binomial test, $p < .001$ (see Table 5.2). There was a significant difference in group performance for *where* information, $\chi^2(1, N = 800) = 4.99$ $p < .05$, and *when* information $\chi^2(1, N = 800) = 7.55$, $p < .01$. Specifically, participants in the articulatory suppression condition performed significantly better than participants in the control condition. The human participants in both conditions were above chance at reporting

both types of information on trials in which they had to select the location and photo from the first event (long retention interval cue) and trials in which they had to select the location and photo from the second event (short retention interval cue).

Spatial Cue Task An analysis of all trials completed revealed that the rhesus monkeys performed at chance levels, with the exception of Murph and Willie who were significantly above chance at reporting *what* information corresponding to the spatial cue (see Table 5.2). However, their accuracy was relatively low (53%) and was only significantly above chance due to the large number of trials that they completed. An analysis of the last 100 trials completed (a more stringent test of significance) revealed that they were not above chance. (In all of the results described thus far, the monkeys who were significantly above chance on all trials completed had also met the stringent criteria of being correct on the last 100 trials completed.)

In contrast to the rhesus monkeys, human participants in both conditions were significantly above chance at reporting *what* information and *when* information from the event corresponding to the spatial cue, as determined by a binomial test, $p < .001$ (see Table 5.2). There was a significant difference in group performance for *what* information, $\chi^2(1, N = 800) = 5.16$, $p < .05$, and *when* information $\chi^2(1, N = 800) = 3.89$, $p < .05$. Specifically, participants in the articulatory suppression condition performed significantly better than participants in the control condition. The human participants in both conditions were equally accurate when the spatial cue prompted them to report information from the first event and when the spatial cue prompted them to report information from the second event.

Discussion

The rhesus monkeys were not able to use the spatial and object cues to report information from the corresponding event, and there was only minimal evidence that they were able to use

the temporal cue appropriately for both short and long delay trials (only for one monkey and one question type). The monkeys were able to learn to select the photo that was seen most recently or the photo that was less familiar in the training tasks, but when the temporal symbol was randomly chosen on each trial, performance in general deteriorated, with the exception of one monkey who was able to use the temporal symbols appropriately to report spatial information.

Table 5.3 The hypotheses and results from each experiment.

Experiment	Hypotheses	Monkeys	Humans
Experiment 1	Independent evidence of object, spatial, and temporal memory	Yes	Yes
	Accuracy for short retention intervals > long retention intervals	No	No
	Accuracy for control condition > articulatory suppression	----------	No
Experiment 2	Memory for *what* and *where* information (1 s, 5 s, 10 s, 20 s)	Yes	Not Tested
	General trend of accuracy decreasing as retention interval increases	Some	Not Tested
Experiment 3	Reporting all three components (*what, where,* and *when)*	Yes	Yes
	Integration of *what-where-when* in working memory	Some	No
	Unanticipated question type (randomly selected)	Yes	Yes
	Memory for what & where > memory for when	Some	No
	Accuracy for short retention intervals > long retention intervals	No	No
	Accuracy for control condition > articulatory suppression	----------	No
Experiment 4	Use of a temporal cue to report *recent* or *remote* event	Some	Yes
	Use of an object cue to report *recent* or *remote* event	No	Yes
	Use of a spatial cue to report *recent* or *remote* event	No	Yes
	Accuracy for control condition > articulatory suppression	----------	No

The human participants were able to use all three types of cues appropriately. The participants in the control condition did not perform better than participants in the articulatory suppression condition, as originally predicted. In fact, it appeared that participants in the articulatory suppression condition performed slightly better than participants in the control

condition, suggesting that the articulatory suppression task actually facilitated performance. It is possible that the articulatory suppression task may have actually made participants more aware of rehearsal strategies, and they may have compensated for their inability to verbally rehearse by using other nonverbal rehearsal strategies. In order to summarize the hypotheses and results from all of the experiments, including the present experiment, the specific predictions from each experiment and the results are presented in Table 5.3.

General Discussion

These experiments provide evidence of simultaneous memory for *what*, *where*, and *when* information in a nonhuman primate species. These data complement data that have been obtained from pigeons using a similar paradigm (Skov-Rackette et al., 2005) and suggest that the paradigm is well suited to investigating memory in a variety of nonhuman species. In contrast to the pigeons that did not demonstrate integration of *what*, *where*, and *when* information in memory, three of the rhesus monkeys did show evidence of integration of these components in memory. It is important to note that the high level of accuracy in both the monkeys and humans may have obscured additional evidence of integration. It is possible that future research using more difficult memory tasks would reveal even more evidence of integration.

In much of the previous research with nonhuman primates (Schwartz et al., 2005; Menzel, 1999; Hampton et al., 2005), the focus has been on the long-term memory component of episodic memory and not specifically the integration of *what-where-when* components in memory. The present set of experiments provides the first systematic analysis of *what-where-when* integration in nonhuman primates. Although it is true that episodic memories are often retrieved from long-term memory, it has been argued that they are typically encoded first in working memory, through the use of an episodic buffer that temporarily binds information

together before it is transferred to long-term memory (Baddeley, 2000). Therefore, it seems that whether they are retrieved from working memory or long-term memory, the essential element that makes episodic memories distinct is the integration of multiple components to represent a past event in memory.

In contrast to the study that examined what-where-when memory in rhesus monkeys and did not find memory for temporal information (Hampton et al., 2005), these findings suggest that rhesus monkeys can report information about the temporal properties of an event. However, it is important to note that the Hampton et al. (2005) study used long retention intervals and a modified food-caching task, both of which may explain why the results were different than the findings of the present experiments. However, the present study does provide evidence that nonhuman primates can use temporal symbols to report on temporal properties of an event. Although the symbols represented discrete temporal intervals (1 s and 10 s) the monkeys often had to use these symbols to comment on past events after completing intervening tasks, which most likely required them to have an understanding that the temporal symbols represented relative temporal intervals (short vs. long) and not discrete intervals. In addition, evidence from the sequential training tasks suggests that some monkeys were able to use the temporal symbols as cues to report information from a recent event or remote event, which suggests that monkeys may have some understanding that the symbols referred to relative temporal discriminations.

In the nonhuman primate literature, there has not been any evidence to indicate that monkeys or apes can communicate about past events using temporal symbols. For example, even language-trained chimpanzees that have an extensive vocabulary of lexigrams (symbols that represent foods, people, locations, and activities) do not use the lexigrams for *yesterday* and *today* in their daily interactions to comment about past events. In future research, this paradigm

can be extended to examine memory for relative temporal durations in rhesus monkeys and chimpanzees.

It is not surprising that human participants performed at generally higher levels than the rhesus monkeys in all of the experiments (see Table 6.1 for list of predictions and results from each experiment). The human participants received verbal instructions to ensure that they would understand the task. If instructions had not been provided the human participants would have likely been less accurate on all of the tasks than the rhesus monkeys due to the large number of trials the rhesus monkeys had completed to learn the tasks. However, in contrast to the prediction that the articulatory suppression task would decrease accuracy, for the most part it had no effect, and in some cases the articulatory suppression task actually facilitated performance, suggesting that participants may have been using some form of nonverbal rehearsal to compensate. It is possible that engaging in the suppression task made participants more aware of potential rehearsal strategies.

On the surface, these results would seem to suggest a species difference between rhesus monkeys and human participants because humans generally performed better than rhesus monkeys even when they were prevented from using verbal rehearsal strategies.
However, this conclusion would be based on the assumption that the articulatory suppression actually did prevent rehearsal, but the fact that the articulatory suppression condition performed better than the control condition in the last experiment suggests that the group was using some form of nonverbal rehearsal strategy. Taken together with the fact that human participants were given verbal instructions in response to early pilot testing, I would argue that it is difficult to determine whether these differences are due to a species difference in memory. I speculate that the human participants in the articulatory suppression condition may have engaged in some other

form of nonverbal rehearsal in order to compensate for the verbal task they were engaged in. In future research, this could be explored by examining *what-where-when* memory as participants complete concurrent visual tasks and concurrent verbal tasks and compare the accuracy of the two groups.

The results were somewhat consistent with the prediction that the length of retention interval and information type (what, where, or when) would affect accuracy in both rhesus monkeys and human participants. Specifically, it was predicted that accuracy would be higher on short retention interval trials than long retention interval trials, and that accuracy for *what* and *where* information would be higher than accuracy for *when* information. The length of retention interval did affect accuracy to some extent for the rhesus monkeys, but not for the human participants. In addition, it was not always the case that accuracy for short retention interval trials was higher than accuracy for long retention interval trials. In fact, monkeys were more accurate at reporting temporal information after long retention intervals than short retention intervals. It is possible that the long delay between the presentation and test was aversive to the monkey, and the human literature demonstrates that particularly emotional events (positive or negative) tend to be more salient.

Although the literature suggests that memory for *when* an event occurred is a less salient cue than *what* occurred or *where* it occurred, these experiments suggest that there are individual differences in the salience of the temporal properties of an event. Specifically, the type of information to be reported (what, where, or when) affected accuracy for the rhesus monkeys, but there were individual differences in which types of information were more difficult. There was some support for the prediction that *when* information would be more difficult to recall (two monkeys demonstrated this pattern). However, the fact that one monkey was most accurate at

reporting *when* information and that this difference could not be readily explained by the individual's training history, suggests that there are individual differences in the salience of the temporal properties of past events. It is also important to note that the temporal cue may have been more salient for this individual because the delays were relatively short compared to delays that have been studied in the human literature (autobiographical memory for events). Therefore, more research is needed to determine whether individual differences in temporal memory remain when longer temporal discriminations are used.

It is important to acknowledge the limitations of this study. Although the rhesus monkeys and human participants demonstrated memory for *what*, *where*, and *when* information, the retention intervals used in this study were not long-term memory delays, but working memory delays. In order to be considered episodic memory, it has been argued that information must be retrieved from long-term memory (Tulving, 1993). Information may be temporarily integrated in working memory, through the use of an episodic buffer (Baddeley, 2000) before being transferred to long-term memory, but true episodic memory, as defined in the human literature refers to memories that are retrieved after relatively long delays. Therefore, an ideal test of episodic memory would examine both integration and the long-term memory component of episodic memories. In future research, modifications of this paradigm that have been used successfully using working memory delays can be extended to examine memory for multiple components of events after long-term memory retention intervals.

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