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Memory for “What”, “Where”, and “When” Information in Rhesus Monkeys (*Macaca mulatta*)

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Abstract

The present study examined working memory for *what*, *where*, and *when* information in rhesus monkeys (*Macaca mulatta*) using a computerized task. In Experiment 1, monkeys completed three delayed matching-to-sample (DMTS) tasks: (1) identity DMTS, (2) spatio-temporal DMTS, and (3) temporal DMTS. In Experiment 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 to examine *what-where-when* memory integration. The rhesus monkeys reported all three components of the events, and there was some evidence suggesting that these components were integrated in working memory.

Keywords

episodic memory; episodic-like; event memory; nonhuman primates; rhesus monkeys

In a natural environment, many species, including nonhuman primates, must remember multiple types of information. For example, they must remember where particular foods are located in space and temporal information concerning their previous foraging experiences, to keep track of available food sources (Garber, 1997; Healy & Hurly, 1995; Janson, 1998). In the human literature, the ability to remember multiple components of a personally experienced event is referred to as episodic memory, and some researchers have argued that this ability is unique to humans (Tulving, 1972, 1993, 2005). The definition of episodic memory contains relatively objective behavioral elements that can be studied in nonhuman species (the binding of what, where, and when information in long-term memory), but it is also said to be accompanied by an awareness of one's past and a subjective conscious experience, which is difficult to assess in nonverbal species. However, the assumption that language is necessary to study long-term memory for past events has been challenged by studies with nonhuman species that have employed behavioral definitions of *episodic-like*

memory (Clayton & Dickinson, 1998, 1999; Hampton, Hampstead, & Murray, 2005; C. R. Menzel, 1999, 2005; Schwartz, Hoffman, & Evans, 2005; 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).

Recently, 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. Separate lines of research have investigated these forms of memory (spatial memory, temporal memory, and object memory). Various nonhuman primates, including monkey and great ape species, retain spatial 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). In addition, various species are able to remember what stimulus has been presented in a matching-to-sample format (Colombo, Swain, Harper, & Alsop, 1997; Roitblat, Penner, & Nachtigall, 1990; Tavares & Tomaz, 2002; Washburn, Hopkins, & Rumbaugh, 1989). Nonhuman species also keep track of temporal information (Burke, Cieplucha, Cass, Russell, & Fry, 2002; Platt, Brannon, Briebe, & French, 1996; Zentall, Weaver, & Clement, 2004).

Despite demonstrations of individual memory capacities for what, where, or when information, more relevant tasks pertaining to the occurrence of episodic memory in animals must involve integration of multiple types of information. In a 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 they returned to recover their caches after relatively long retention intervals (4–124 hrs.). Although the scrub jays preferred the highly perishable food (e.g., mealworms) those foods remained fresh at short retention intervals (4 hrs.), but had degraded by long retention intervals (124 hrs.) whereas the less desirable food (e.g., peanuts) remained fresh after the long retention intervals (24 hours). The scrub jays searched where they had cached the highly perishable food items after short retention intervals, but they switched to searching locations containing less perishable foods if they were returned to the caching environment after long retention intervals. These results indicated that 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 was 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). Additional research using similar paradigms has shown that rats (Babb & Crystal, 2005) also

remembered what, where, and when information and rhesus monkeys demonstrated memory for *what* and *where*, but not memory for *when*, as they continued to search for the preferred food after 25-hr delays (Hampton et al., 2005). 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. 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.

Schwartz et al. (2002) examined memory for *what* and *who* information from 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 was significantly above chance at indicating with symbols both the type of fruit and the experimenter involved in the event after both short retention intervals (7 minutes) and long retention intervals (24 hours). The gorilla was also highly accurate at reporting components of novel events involving both familiar and unfamiliar individuals (Schwartz et al., 2004) and remembering separate information about where an event occurred, but was less accurate at indicating when an event occurred relative to other events in the past (Schwartz et al., 2005). 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.

Washburn and Gullledge (2002; Washburn, Gullledge & 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 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).

Skov-Rackette, Miller, and 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 seconds vs. 6 seconds) 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. The pigeons performed at above chance levels on all three tasks, suggesting they encoded what, where, and when information from the events. However, the data did not suggest that these components were integrated in memory.

In much of the previous research with nonhuman primates (Hampton et al., 2005; Menzel, 1999; Schwartz 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. We investigated whether rhesus monkeys could report *what*, *where*, and *when* information using a computerized task similar to the task used by Skov-Rickette et al. (2006). Although 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). Comparative research has also demonstrated short-term to long-term memory transfer in rhesus monkeys (Wright, 1998). Therefore, in beginning to investigate whether nonhuman species have the ability to recall specific past episodes, it is useful to first understand how they encode *what*, *where*, and *when* information in working memory. It is important to note that the term *working memory* here refers to the temporary storage of information in memory. This is somewhat different from the way the term has been used in the comparative literature, which refers to the retrieval of trial specific information independent of delay interval (Shettleworth, 1998). The distinction is important, as the present study uses a working memory task to examine memory for trial specific information, but it also uses working memory delay intervals to assess storage of *what*, *where*, and *when* information in the working memory system, as it is defined in the human literature.

Experiment 1

Rhesus monkeys (*Macaca mulatta*) 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. The symbolic-temporal DMTS task required the subject to remember *when* the stimulus was presented (either 1 second or 10 seconds in the past) and select one comparison stimulus if the delay was short (1 second) and another if it was long (10 seconds).

Method

Subjects—Four joystick-trained, adult male rhesus monkeys were tested (Gale, Murph, Willie, and Chewie). The monkeys 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 & Astur, 2003; Washburn & Gulledge, 2002; Washburn et al., 2003). Each monkey had a computerized test system in its home cage

and had the opportunity to work on the task at any time. Each monkey participated in the research on a voluntary basis, receiving supplemental food rewards in exchange for participation.

Procedure—To begin a trial, the rhesus monkeys had to select a start box in the center of the screen. This was followed by 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 monkey was presented with a choice between two alternatives (photos, locations, or temporal symbols, depending on the DMTS task), and it had to select the stimulus corresponding to the event. The tasks were presented during 4-hr testing sessions that were presented 3 to 5 days each week. The total number of trials each monkey completed during a session was determined by their motivation to participate in the task. The monkeys reached criterion on each task when they demonstrated at least 75% accuracy across a minimum of three testing sessions.¹ Although each monkey received roughly the same number of sessions, some monkeys completed a much larger number of trials within a given session, resulting in some monkeys completing a much larger total number of trials than other individuals. In each task, monkeys were reinforced for correct responses with positive auditory feedback (ascending tones) 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 buzz tone). Monkeys were not given any timeout for incorrect responses and were allowed to proceed to the next trial after a 1-s intertrial interval.

Identity delayed matching-to-sample—The identity delayed matching-to-sample task was used to assess memory for *what* information. In this task, a 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 monkey then was presented with a choice between two alternatives, the previously presented sample photo and an alternate photo that had not been presented (see Figure 1). The monkey received feedback after each response, followed by a brief intertrial interval (1 second).

Spatial delayed matching-to-sample—In this task, the number of response locations was reduced from four to two locations. In addition, the response location boxes were filled with a light yellow background to make the locations more visually distinctive (see Figure 1). 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 1-s delay in which the computer screen remained blank. The monkey then was presented with a

¹In some cases monkeys completed more than the minimum three sessions at criterion because experimenters were not always available to review performance immediately after each session (e.g., because of absences from the lab).

choice between the two response locations. This was followed by a brief intertrial interval (1 second).

Temporal delayed matching-to-sample—In this task, monkeys were required to indicate delay length between the presentation of the event and subsequent memory test using temporal symbols. A photo appeared in the center of the screen and then disappeared after a brief interval (3 seconds). The disappearance of the photo was followed by either a short retention interval (1 second) or a long retention interval (10 seconds) that was randomly determined on each trial. After the delay, the monkey was 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 second), reinforcement was given for selecting the purple triangle. In contrast, if the delay between the presentation and test was long (10 seconds), the monkey was reinforced for selecting the black circle (see Figure 1). 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. All monkeys then were presented with a more advanced version of the task, in which the locations of the temporal symbols were 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 that the monkeys associate each of the two response icons with a specific delay interval.

Results

For all three tasks, all monkeys met the established criterion. The individual percentages and total number of trials completed for each task for each monkey are displayed in Table 1.

Identity delayed matching-to-sample—There was evidence of learning as individuals became more experienced with the task; accuracy during the last 100 trials ($M = 86\%$) was significantly higher than accuracy during the first 100 trials ($M = 67\%$), $\chi^2(1, N = 200) = 10.04, p < .01$.

Spatial delayed matching-to-sample—There was evidence of learning as individuals became more experienced with the task; accuracy during the last 100 trials ($M = 89\%$) was significantly higher than accuracy during the first 100 trials ($M = 47\%$), $\chi^2(1, N = 200) = 40.53, p < .001$.

Nonsymbolic temporal delayed matching-to-sample—There was evidence of learning as individuals became more experienced with the task; accuracy during the last 100 trials ($M = 92\%$) was significantly higher than accuracy during the first 100 trials ($M = 50\%$), $\chi^2(1, N = 200) = 42.84, p < .001$.

Symbolic temporal delayed matching-to-sample. The rhesus monkeys that had previous experience with the nonsymbolic temporal task were significantly above chance (50%) on the symbolic temporal delayed matching-to-sample task ($M = 88\%$), as determined by a binomial test, $p < .001$. The one individual that did not have previous experience with the nonsymbolic task performed at a comparable level (90%), $p < .001$. 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 non-symbolic temporal task was not necessary to learn the symbolic discrimination.

Discussion

Rhesus monkeys indicated independent memory for *what*, *where*, and *when* information using separate delayed matching-to-sample tasks. These results were consistent with the literature demonstrating that nonhuman primates are able to remember these separate memory components after brief delays. In addition, these findings were consistent with results that have been obtained from pigeons using a similar computerized delayed matching-to-sample paradigm (Skov-Rackette et al., 2006). The results also indicated that rhesus monkeys were capable of learning to discriminate temporal intervals and using arbitrary icons to indicate memory for the temporal delay since an event had occurred. However, the primary objective was not to examine whether rhesus monkeys were able to use different delayed matching-to-sample tasks to report *what*, *where*, and *when* information separately, but rather to determine whether these three types of information were integrated in working memory. This was assessed in Experiment 2.

Experiment 2

The purpose of this experiment was to examine whether rhesus monkeys could report more than one component from the same event and whether they could do this after varying retention intervals (1 second, 5 seconds, 10 seconds, 20 seconds). In this experiment, the monkeys were presented with the same type of event on the computer screen, but they were required to first report *where* the photo had been presented, and then *what* photo had been presented. 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.

Method

Participants—The same four rhesus monkeys (Gale, Murph, Willie, and Chewie) that participated in Experiment 1 served as subjects in this experiment. The monkeys had all completed the delayed matching-to-sample training in Experiment 1 before participating in this experiment.

Procedure—A monkey had to move the joystick cursor to a start box in the center of the screen 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. The photo flashed in the location once per second for a total of three seconds. The photo then disappeared and was followed by a retention interval (1 second, 5 seconds, 10 seconds, or 20 seconds). After the retention interval, the monkey was presented with a choice between the two response locations (i.e., the spatial question from Experiment 1). 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 then was presented with a choice between the sample photo and a distractor photo, each in random positions on

the screen (i.e., the identity question from Experiment 1). Again, if the monkey was correct it received positive sound feedback and a fruit-flavored pellet, but it heard a low buzz on errors. The questions were asked in this order on all trials to avoid any interference effects. If the identity question had been presented first, the monkey would have had to make an identity matching response to a location on the screen (which may or may not have corresponded to the location of the event) before making a response to the event location. After the monkey responded to the identity question, there was a brief intertrial interval (1 second) before the next trial was available to the monkey. The monkeys were initially presented with 1-s retention intervals, but they progressed to a longer retention interval (5 seconds) when they reached criterion (75% correct on both questions). After reaching criterion on the 5-s retention intervals, the animals were tested with 10-s retention intervals and then 20-s retention intervals.

Results

The individual percentages and total number of trials completed for each monkey at each delay interval are displayed in Table 2.

One-second retention interval—The rhesus monkeys were significantly above chance (25%) at correctly reporting both components during the first 100 trials ($M = 68\%$) as analyzed using a binomial test, $p < .001$, which suggests that the task of reporting multiple components was not difficult for the monkeys. The individual percentages and total number of trials completed for each monkey are displayed in Table 2. There was evidence of learning as individuals became more experienced with the task; accuracy for reporting both components during the last 100 trials ($M = 82\%$) was significantly higher than accuracy during the first 100 trials ($M = 68\%$), $\chi^2(1, N = 200) = 5.23, p < .05$. To determine if the components were integrated in memory, a binomial logistic regression was used to determine if accuracy on the first question (*where*) predicted accuracy on the second question (*what*). Although there was no evidence that performance on the first question predicted performance on the second question during the first 100 trials completed, $\chi^2(1, N = 400) = 1.96, \text{Exp}(B) = 0.64, p > .05$, there was evidence for this during the last 100 trials completed, $\chi^2(1, N = 400) = 4.04, \text{Exp}(B) = 0.42, p < .05$.

Five-second retention interval—In this task, the monkeys were significantly above chance (25%) at correctly reporting both components during the first 100 trials ($M = 49\%$) as analyzed using a binomial test, $p < .001$. There was evidence of learning as individuals became more experienced with the task; accuracy for reporting both components during the last 100 trials ($M = 78\%$) was significantly higher than accuracy during the first 100 trials ($M = 49\%$), $\chi^2(1, N = 200) = 18.14, p < .001$. A binomial logistic regression indicated that there was no evidence that performance on the first question predicted performance on the second question during the first 100 trials completed, $\chi^2(1, N = 400) = 0.24, \text{Exp}(B) = 1.16, p > .05$ or during the last 100 trials completed, $\chi^2(1, N = 400) = 2.15, \text{Exp}(B) = 0.55, p > .05$.

Ten-second retention interval—The monkeys were significantly above chance (25%) at correctly reporting both components during the first 100 trials ($M = 64\%$) as analyzed using a binomial test, $p < .001$. In contrast to the monkeys' performance on the previous

tasks, there was no significant improvement from the first 100 trials ($M = 64\%$), to the last 100 trials ($M = 78\%$), $\chi^2(1, N = 200) = 1.471, p > .05$. There was no evidence that performance on the first question predicted performance on the second question during the first 100 trials completed, $\chi^2(1, N = 400) = 0.58, \text{Exp}(B) = 0.79, p > .05$ or during the last 100 trials completed, $\chi^2(1, N = 400) = 0.25, \text{Exp}(B) = 1.23, p > .05$.

Twenty-second retention interval—The monkeys were significantly above chance (25%) at correctly reporting both components during the first 100 trials ($M = 63\%$) as analyzed using a binomial test, $p < .001$. As with the monkeys' performance with 10 second retention intervals, there was no significant difference in performance from the first 100 trials ($M = 63\%$) to the last 100 trials ($M = 59\%$), $\chi^2(1, N = 200) = 0.164, p > .05$. However, performance on the first question did predict performance on the second question during the first 100 trials completed, $\chi^2(1, N = 400) = 6.68, \text{Exp}(B) = 0.46, p = .01$, but this effect was no longer significant during the last 100 trials, $\chi^2(1, N = 400) = 0.02, \text{Exp}(B) = 1.04, p > .05$.

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 apparently understood the response requirements of the task immediately because they accurately reported both *what* information and *where* information after varying retention intervals. The results from the binomial logistic regressions suggested that, although accuracy on the first question did not successfully predict accuracy on the second question during the shorter retention interval trials, it was a successful predictor of accuracy when the monkeys were initially presented with the longer 20-s delays. This suggested that binding of what and where information had occurred.

Experiment 3

The integration of *what*, *where*, and *when* information was examined by presenting monkeys with two tasks; in one task the monkeys had to report all three types of information on each trial and in the other task the monkeys were presented with one randomly determined question on each trial. The purpose of the second task was to assess the extent to which interference or decay processes interfered with retrieval. 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 all three question types beforehand as the time it takes to respond to these questions increases the amount of time since the event). In the second task, presumably all three type of information would still need to be available for monkeys to succeed on this task, as they 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 participated in this experiment.

General procedure—The rhesus macaques 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 each trial. The monkeys first were presented with the sequential task. If a monkey performed at the level of 75% correct during the last 100 trials, it then was presented with the random question task. As stated previously, however, the sequential question task could cause various interference effects; therefore, if a monkey failed to reach criterion after 5,000 trials on the sequential task, it then was tested on the unanticipated question task.

Reporting all three components sequentially—In this task, a randomly selected photo appeared at one of the two locations. The presentation was followed by either a short retention interval (1 second) or a long retention interval (10 seconds), 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 in the same manner as was done in the previous experiments. The questions were presented in the order stated above to minimize interference (e.g., if the *what* or *when* question was asked first, the animal would have had to make a response to a location on the screen, and that may have interfered with the memory for *where* the actual event took place). All three questions were presented even if the participant responded incorrectly to any of the questions in the sequence, and each response was given individual feedback in the form of reward for correct responses or buzz tones for incorrect responses.

Unanticipated question type—In this task, the procedure was identical to the procedure described above, except that monkeys were only presented with one question after the event. The question type was randomly selected on each trial so that monkeys were unable to anticipate which question would be presented. All other aspects were identical to those already outlined.

Results

Reporting all three components sequentially—The rhesus monkeys were significantly above chance (50%) at reporting *what* information ($M = 89\%$) and *where* information ($M = 79\%$), and two monkeys also were significantly above chance at reporting *when* information ($M = 63\%$) as determined using a binomial test, $p < .001$. The individual percentages and total number of trials completed for each monkey are displayed in Table 3. To determine whether monkeys became more accurate over time, 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. The rhesus monkeys were all significantly above chance at correctly indicating *what* information ($M = 88\%$) and *where* information ($M = 72\%$) 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 ($M = 51\%$) 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* ($M = 89\%$) and *where* ($M = 88\%$) information, two of the monkeys had also reached significantly above chance performance for reporting the *when* component ($M = 61\%$) of the event, $p < .001$.

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 no differences between the conditional probabilities of *when* given correct performance on *what* and *where* and the actual percent correct for rhesus monkeys, Gale, $\chi^2(1, N = 3,218) = 0.49, p > .05$; Murph, $\chi^2(1, N = 2,771) = 1.41, p > .05$.

The conditional probabilities also were 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, $\chi^2(1, N = 6536) = 8.78, \text{Exp}(B) = 0.81, p < .01$. The odds ratio ($\text{Exp}(B)$) 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 probability 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, $\chi^2(1, N = 3,218) = 4.29, \text{Exp}(B) = 1.20, p < .05$; Murph, $\chi^2(1, N = 2,771) = 24.70, \text{Exp}(B) = 1.89, p < .001$. If Gale had correctly reported the *what* and *where* components of the event, the probability 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 probability of him reporting the *when* component of the event increased by a factor of 1.89.

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. 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.

It is important to note that the amount of time required to answer each question before reaching the *when* question increased the delay length since the original event presentation, which may have made 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), however, did not

demonstrate this bias as there was no significant difference ($p > .05$) in the percentage of responses to the long delay symbol (55%) versus the short delay symbol (45%).

Unanticipated question type—The rhesus monkeys were all significantly above chance on *what* ($M = 91\%$), *where* ($M = 84\%$), and *when* (83%) trials, as analyzed by a binomial test, $p < .01$. The individual percentages and total number of trials completed for each monkey are displayed in Table 3. The monkeys were significantly above chance on each trial type during the first 100 trials (*what*, $M = 89\%$; *where*, $M = 85\%$; *when*, $M = 83\%$), and they maintained this high level of performance during the last 100 trials completed for each trial type (*what*, $M = 92\%$; *where*, $M = 83\%$; *when*, $M = 89\%$).

The percent correct for each of the three trial types was 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. 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, $\chi^2(1, N = 200) = 78.44, p < .001$]. 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 [$\chi^2(1, N = 200) = 48.01, p < .001$].² 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 [$\chi^2(1, N = 200) = 8.04, p = .005$].

There were differences in accuracy for short retention interval trials and long retention interval trials. 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, $\chi^2(1, N = 100) = 6.19, p < .05$.

Discussion

The rhesus monkeys demonstrated memory for *what*, *where*, and *when* information when they could not anticipate the specific 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, although this clearly was a more difficult task. 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 for some monkeys.

²It is interesting to note that Willie has demonstrated similar low levels of accuracy in comparison to other monkeys on other spatial memory tasks (Washburn & Gullledge, 2002; Washburn, Gullledge, & Martin, 2003).

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 other two monkeys, the fact that the monkeys 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.

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.

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-Rickette et al., 2005) and suggest that the paradigm is well suited to investigating memory in multiple nonhuman species. In contrast to the pigeons that did not demonstrate integration of *what*, *where*, and *when* information in memory, two 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 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 contrast to the Clayton and Dickinson (1998) study in which integration of components was inferred from behavior at cache recovery (where the individual had one opportunity to demonstrate memory for all three components), the present study assessed memory for all three components using discrete tasks. We analyzed integration by examining the probability of getting one question right as a function of correctly answering the previous questions. However, unlike the food-caching paradigm, the present study used working memory delays instead of long-term memory delays. Therefore, the present data are not sufficient for an episodic memory interpretation using the criteria set forth by Clayton and Dickinson (1998), but the data do provide a more in depth analysis of *what-where-when* integration in working memory than has been obtained using other testing paradigms.

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), the present findings indicate 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. The present study does provide evidence that nonhuman primates can use arbitrary icons to report on temporal properties of an event. Although the icons represented discrete temporal intervals (1 second and 10 seconds) the monkeys often had to use these icons to comment on past events after completing intervening tasks, which most likely required them to have an understanding that the icons represented relative temporal intervals (short vs. long) and not discrete intervals.

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) have not been trained to understand the meaning of the lexigrams representing the temporal concepts of *yesterday* and *today* (for a study of chimpanzees' long-term retention of lexi-grams see Beran, Pate, Richardson, & Rumbaugh, 2000; Rumbaugh & Washburn, 2003). In future research, perhaps this paradigm can be extended to examine memory for relative temporal durations in rhesus monkeys and chimpanzees.

Although the literature indicates that memory for *when* an event occurred is a less salient cue than *what* occurred or *where* it occurred (Wagenaar, 1986), these experiments indicate 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 was more difficult to recall (two monkeys demonstrated this pattern). However, one monkey was most accurate at reporting *when* information, and this could not be readily explained by the individual's training history. Thus, there are individual differences in the salience of the temporal properties of past 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 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. To be evidence of episodic memory, it has been argued that recalled 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. The present test, however, is adequate and useful for probing the working memory capacity and binding aspects of such memory in nonhuman animals, and the successful performance of these monkeys supports the view that they may be capable of more episodic-like memories that rely on such integration.

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Figure 1.

The identity, spatial, and temporal DMTS tasks. The identity task assessed memory for *what* information (i.e., the monkey had to select the photo that had been shown). The spatial task assessed memory for *where* information (i.e., the monkey had to select the location where the photo had been shown). The temporal task assessed memory for *when* information (i.e., the monkey had to select the symbol that was associated with the length of delay).

Table 1

Performance on Separate DMTS Tasks

Temporal DMTS											
Identity DMTS				Spatial DMTS				Nonsymbolic			
Trials	Correct	*		Trials	Correct	*		Trials	Correct	*	
Gale	7,394	90%	*	16,374	87%	*		5,326	81%	*	
Murph	23,966	97%	*	21,587	93%	*		—	—	*	
Willie	4,459	89%	*	9,834	73%	*		25,866	92%	*	
Chewie	7,553	85%	*	8,653	77%	*		2,927	89%	*	
M	10,843	90%	*	14,112	83%	*		34,119	87%	*	

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

Table 2

What & Where Information

	N	Where	What
1-s retention interval			
Gale	588	80% *	83% *
Murph	466	97% *	92% *
Willie	24,568	84% *	88% *
Chewie	9,862	96% *	78% *
M	8,871	89% *	85% *
5-s retention interval			
Gale	4,584	77% *	88% *
Murph	8,087	88% *	93% *
Willie	28,355	63% *	86% *
Chewie	8,955	92% *	79% *
M	12,495	80% *	87% *
10-s retention interval			
Gale	5,917	82% *	93% *
Murph	9,654	91% *	93% *
Willie	9,455	63% *	89% *
Chewie	8,654	85% *	78% *
M	8,420	80% *	88% *
20-s retention interval			
Gale	4,034	74% *	91% *
Murph	768	76% *	89% *
Willie	3,971	58% *	88% *
Chewie	781	77% *	75% *
M	2,389	71% *	86% *

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

Table 3

What, Where, and When Information

	<i>N</i>	Where	What	When
What, where, & when				
Gale	3,218	85%	* 93%	* 57%
Murph	2,771	93%	* 96%	* 50%
Willie	6,536	69%	* 84%	* 63%
Chewie	1,163	89%	* 82%	* 63%
<i>M</i>	3,422	84%	89%	58%
Random question				
Gale	1,091	86%	* 97%	* 80%
Murph	2,209	92%	* 96%	* 75%
Willie	1,803	68%	* 90%	* 85%
Chewie	2,193	88%	* 84%	* 89%
<i>M</i>	1,824	84%	92%	82%

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