Anim Cogn (2002) 5 : 85–90
DOI 10.1007/s10071-002-0132-0

ORIGINAL ARTICLE

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Single-trial learning of "what" and "who" information in a gorilla (*Gorilla gorilla gorilla*): implications for episodic memory

Received: 11 October 2001 / Revised: 12 April 2002 / Accepted: 13 April 2002 / Published online: 25 May 2002

Abstract Single-trial learning and long-term memory of "what" and "who" information were examined in an adult gorilla (*Gorilla gorilla gorilla*). We presented the gorilla with a to-be-remembered food item at the time of study. In Experiment 1, following a retention interval of either approximately 7 min or 24 h, the gorilla responded with one of five cards, each corresponding to a particular food. The gorilla was accurate on 70% of the short retention-interval trials and on 82% of the long retention-interval trials. In Experiment 2, the food stimulus was provided by one of two experimenters, each of whom was represented by a card. The gorilla identified the food (55% of the time) and the experimenter (82% of the time) on the short retention-interval trials. On the long retention-interval trials, the gorilla was accurate for the food (73%) and for the person (87%). The results are interpreted in light of theories of episodic memory.

Keywords Primates · Gorillas · Memory · Episodic memory · Single-trial learning

Introduction

The ability to remember specific events is taken for granted in humans. Numerous studies have shown that, based on single events, humans can retrieve a rich assortment of details from that event. Tulving (1983, 1993, 2002) considered the term episodic memory to refer to the human capacity to recollect individual events of one's personal life and attribute them to the past. Schwartz and Evans (2001) defined episodic memory in terms of remembering specific events, attributed to the past. For example, episodic memories might include one's memory of the moment one's first child was born, witnessing a bank robbery, the menu of this morning's breakfast, or the words presented on a list in a memory experiment 24 h ago. What is common to these events is that memories may be formed based on a single exposure to a stimulus, and that they are attributed by the rememberer to the past.[1] Thus, a memory may be episodic and autobiographical (remembering one's child's birth), but another memory may be autobiographical but not episodic (knowing one's own birthday). According to Tulving (1983, 1993, 2002), episodic memory involves mental time travel – or a reexperiencing of the earlier event. This is not a general characteristic of autobiographical memory (Conway and Pleydell-Pearce 2000). There is a frequent assumption that an episodic memory is unique to humans (Suddendorf and Corballis 1997; Tulving 1983, 2002). Memory following single-trial learning over long retention intervals has occurred in non-human animals (see Dewsbury 2000; Terrace 1993; Tomasello and Call 1997). However no researcher has ever documented if non-human animals can consciously attribute these events to the psychological past, presumably because of the immense difficulties in demonstrating this experimentally. Chimpanzees, gorillas, and orangutans have demonstrated long-term memory after single-trial learning (MacDonald 1994; MacDonald and Agnes 1999; Menzel 1999; Gibeault and MacDonald 2000; see Schwartz and Evans 2001 for a review), suggesting the possibility of episodic memory. Even stronger findings have been documented with some birds (Clayton and Dickinson 1998, 2000; Clayton et al. 2001), suggesting episodic-like memory.

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[1] Episodic memory only refers to memory for specific events and is not synonymous with autobiographical memory. Autobiographical memory includes both memory for specific events and general knowledge we have about ourselves (Conway and Pleydell-Pearce 2000).

Clayton and her colleagues (e.g., Clayton and Dickinson 1998; Griffiths and Clayton 2002) operationally defined episodic-like memory as the memory components (e.g., what, where, when, and with whom) an animal remembers from a specific event. Griffiths and Clayton (2002) argued that episodic memory should encompass some combination of these four questions (what, where, when, and who) to entail the creation of a representation of an entire event. In humans, Wagenaar (1986) showed that people are capable of remembering what, where, with whom, and to some extent, when for ordinary events for years after the initial event. Following this reasoning, in the current study, we addressed single-trial learning of "what" information in experiment 1 and of both "what" and "who" information in experiment 2 with a western lowland gorilla.

Clayton and her colleagues (Clayton and Dickinson 1998, 2000; Clayton et al. 2001) found similar evidence for episodic-like memory in scrub jays (*Aphelocoma coerulescens*). In a series of studies, Clayton showed that these birds, based on a unique learning event, recognized which of two foods were stored in which of two locations at which of two different times (measured in hours). Clayton et al. (2001) included a unique configuration of a Lego structure to enhance the unique status of each trial. Although Clayton et al. (2001) did not argue that this form of cache memory is identical to human episodic memory, they argued that it must be considered episodic-like because the birds have learned "what," "where," and "when" information.

Menzel (1999) examined single-trial learning of unique stimuli over long retention intervals in a common chimpanzee (*Pan troglodytes*). In his study, single-trial learning of both "where" information and "what" information was tested (and he used a recall format to test retrieval). A symbol-competent chimpanzee witnessed the hiding of foods in an outdoor enclosure. Later, the chimpanzee used a visual-graphic keyboard to identify the hidden food and used manual pointing to suggest that she had knowledge of the location of the hidden food. Relevant in this study is that many of the recall trials were self-initiated by the chimpanzee and that they often occurred at long intervals after the witnessed event (up to 16 h). Our study was similar, but we tested a gorilla with a lesser degree of symbolic competence.

Previous research demonstrated that gorillas are capable of single-trial learning of the "where" question. In a study designed to investigate spatial, not episodic, memory, MacDonald (1994) and Gibeault and MacDonald (2000) showed that gorillas remembered the location of baited sites up to 24 h later after a single learning trial. In MacDonald's task, a gorilla was allowed to search for food hidden in four of eight sites. Later, the food was rehidden in the same sites. The gorilla was significantly better than chance at returning to the locations that had previously been baited. On the next trial, the baited sites were switched, but the gorilla required only one search attempt to remember the new locations. These data can be interpreted in terms of the relative familiarity of specific locations. Nonetheless, they do show long-term memory based on single-trial learning, a necessary precursor of episodic-like memory.

Many studies of non-human animals show single-trial learning over short retention intervals, such as the performance seen in delayed match-to-sample studies (see Buchanan et al. 1981; Dewsbury 2000). Most of these studies, however, had retention intervals measured in seconds or, at most, 2 or 3 min, most likely in the domain of short-term memory. What is particularly significant about Clayton et al.'s (2001) study of scrub jays, Menzel's (1999) study of chimpanzees, and MacDonald's (1994) study of gorillas is that the memories are maintained over long periods of time based on a single learning episode.

In the current study, following Menzel (1999), we wanted to address the issue of single-event memory and symbolic communication in a great ape species. Our subject was a gorilla with some symbolic competency. We avoided testing "where" because it has been done previously (MacDonald 1994); we avoided testing "when" because of the difficulties of getting the gorilla to communicate this information. Instead, we focused on "what" and "who" because the gorilla was capable of symbolically communicating this information. Two specific hypotheses were addressed. First, we suspected that gorillas are capable of single-trial learning of both what (specific foods) and who (person who gave food) information. We tested this by examining a gorilla's memory after individual feeding events. We hypothesized our subject would be above chance at reporting both what and who information. Second, we suspected that the gorilla would be capable of doing so at both relatively short (7 min) and long (24 h) retention intervals.

Methods

Subject

The subject, King, a male western lowland gorilla (*Gorilla gorilla gorilla*), was 30 years old at the time of the experiment. King was born in the wild in Cameroon but was raised in a circus in the United States. At the age of 10, he was moved to Monkey Jungle in Miami, Florida, where he has lived for the last 20 years. At the time of the study, King weighed approximately 205 kg and was approximately 1.5 m tall. Observations of King from his trainers suggested that he does not engage in regurgitation/reingestion behaviors. He has been the subject of an investigation on mirror self-recognition (Swartz and Evans 1994) and has participated in enrichment programs with his trainers, but he had not participated in memory experiments prior to this one.

Prior to testing in the current study, as part of ongoing enrichment, King had been taught by his trainers to associate certain objects and English words with wooden cards, upon which a drawing or name appeared. Thus, at the time of testing, he had already learned to associate each of the five fruits used as stimuli with one of five wooden cards with a drawing of the fruit. Thus, if shown a banana, he returned the card with a banana drawn on it. Furthermore, in response to the word banana, he returned the banana card, even if no banana was actually present. During a 10-day baseline test period in August 2000, in which he was given cards and allowed to return them in exchange for the food that they represented, he showed no preferences for particular foods or cards. None of his card/food preferences differed from what was predicted by a chance model ($\chi^2<3.84$). During this period, he was 86% accurate when asked in spoken English for the appropriate card, which was significantly above chance (20%). He was 91% accurate when shown the fruit and asked for the corresponding card, also significantly above chance (20%).

Environment and stimuli

King was housed in an indoor–outdoor facility. At the time of testing, construction was taking place to enlarge considerably King's outdoor space. He also had an air-conditioned sleeping room, which was accessible to him during the day. During testing, he had full access to his entire area, and if he did not wish to participate, he could move to another area in his cage. Testing was always done in one corner of his cage, the corner he preferred for eating. King was provided with a daily diet of chow, vegetables, leaves, and fruit. The food provided for him in the experiment was integrated into his normal diet to prevent excess weight gain. He was not food deprived during trials or during any time during these experiments.

Test objects were five food types (apple, banana, grapes, orange, pear). King used five wooden cards to respond, one for each food type. On each card was a colored drawing of one of the fruits. The cards were 20×20×1.5 cm. In the drawings, the apple was red, and the grapes and the pear were green. Test apples, pears, and grapes were both red and green. For experiment 2, three new cards were used. These cards were the same size as the food cards, but each had a name written on the card in large bold letters. The names corresponded to the three experimenters who presented King with food in Experiment 2 (B.L.S., I.C.S., and M.R.C.).

Design and analyses

Retention interval was defined as the amount of time that passed after King finished eating the test food and when he returned a card to the trainer. In experiment 1, the short retention interval averaged 7.3 min, but varied from 5 to 65 min. In experiment 2, the short retention interval averaged 9.3 min and varied from 5 to 33 min. Because King was not constrained and could choose when or if to participate on any given trial, we could not keep the retention interval constant from trial to trial. Thus, in some cases, he chose not to cooperate until some time had passed after he had been given the response cards. The long retention interval varied from 24 h to 96 h in experiment 1 but was always 24 h (plus or minus a few minutes) in experiment 2. In experiment 1, there were 112 trials at the short retention interval and 17 at the long retention interval. In experiment 2, there were 111 trials at the short retention interval and 15 at the long retention interval.

We statistically analyzed the short and long retention interval separately because of the different number of trials in each experiment. The binomial test was used to determine if King's response for a specific feeding differed from chance. In experiment 1, chance performance was considered 20% because he had five cards with which to respond, one for each food. In experiment 2, chance performance was considered 20% for the choice of the correct food card and 50% for the choice of the experimenter.

Procedure

We describe the procedure used in experiment 1, followed by the changes made for experiment 2. King was initially handed an apple, a banana, a pear, an orange, or a bunch of grapes. The food was handed through the bars of the cage by one of three experimenters. Fruits to be presented to King were chosen in a semi-random order (the foods were chosen randomly, but we did not allow the same food to be given twice in a row for the short retention-interval trials). The experimenters removed any residue (peels, grape vines, etc.) before testing occurred. After King had eaten the food and the retention interval was complete, the trainer returned to the testing area and the experimenter left the training area. The trainer was blind to the food presented to King. In experiment 1, the trainer then passed the five response cards through the bars and asked him, in English, "What did you eat?"[2] Because the trainer did not know what the food was, she could not cue him. King was expected to pick out the card that corresponded to the last food he had eaten. The four incorrect cards served as distractors. King looked through his set of cards to find the card with which he wanted to respond. King then passed the card through the bars of the cage, and the response was recorded.[3] In both experiments, King needed no training to respond appropriately when the to-be-tested event was given the previous day. In both experiments 1 and 2, he responded correctly on the first trial and needed no training or practice trials. Because of this, we inferred that, at some level, King's choices indicated that he was referring to foods given by experimenters during sessions with them at both short and long retention intervals.

After King had responded, the trainer called out King's response. The experimenters, who were out of view of both King and the trainer, replied if King's response was correct. If King was correct on a trial, he was given verbal praise, physical contact, or both from the trainer. Then the trainer would solicit the return of the remaining cards. If King was initially incorrect, the trainer would again ask "What did you eat?" If King responded with the correct card on his second card, he was then rewarded. The trainer would then ask King to return the remaining cards. If King was not correct on the second card return, he was asked to return the remaining cards, which included the correct card. He was not rewarded when the return of the correct card came at this point. Once all of the cards had been retrieved, the trainer would leave the area. If King had been correct, an experimenter would then immediately re-enter and give King the next food as soon as the trainer left the area. If King was incorrect, the experimenters waited for a 1- to 3-min time-out period before giving him the next food for the next trial.

On any given day, we ran three to eight trials at the short retention interval and then ended by giving him a trial with salient stimuli (e.g., two bananas or a large bunch of grapes), upon which he was not tested. On some days, he was only given one type of food in advance of a 24-h retention interval. In these cases, the first food presented was the one he was expected to remember over the long interval. During long retention intervals, the trainer was also blind to the specific food to be tested. With respect to the long retention interval, King was able to answer correctly on the first trial in each experiment. At some level, he recognized that he was being queried about food that the experimenters were giving him and not his usual diet and regimen. Thus, despite all the food he may have eaten over a 24-h period, King responded appropriately (as the results will bear out) from the last experimental session.

Because of the constraints of doing research in a zoo environment, it was impossible for us to monitor his food intake during the long retention interval. King was never food deprived, and during this interval, his trainers gave him large quantities of food, some of which corresponded to test foods. Given that all of the foods in the test set are part of his daily diet in large quantities, it is likely that on most long-term trials he received both the to-be-tested food and all of the distractor foods during the retention interval. However, record-keeping procedures at Monkey Jungle did not allow us to verify this.

In experiment 1, three people served as experimenters, including the first (B.L.S.) and second author (M.R.C.) and experimenter

[2]Through whatever learning mechanism, King immediately responded appropriately that the desired response was the most recently eaten food and only the most recently eaten food in the experimental context. We are not contending that King understands the English commands, just that he has learned to respond appropriately. We are currently conducting studies to address what verbal commands King responds to.

[3]Some trials were recorded on videotape and are available to other researchers.

I.W. Because of various constraints associated with testing in a non-laboratory environment, the trials that each experimenter conducted were neither counter-balanced nor randomized. King was familiar and comfortable with all three of the experimenters. The trainer who performed the testing (T.C.) had worked with King for 10 years as his primary trainer and caretaker. Twenty-two days of testing took place in June and July of 2000.

Several procedural changes occurred for experiment 2. First, for several weeks prior to the study, King was trained with three new cards, each to be associated with one of the three experimenters who would be conducting this experiment (B.L.S., I.C.S., and M.R.C.). King learned to associate each card with both the spoken name and the presence of that experimenter. The study did not begin until King could produce the correct card 90% of the time when cued with the experimenter's name.

In experiment 2, one experimenter handed the food through the bars of the cage to King. The experimenter who provided food to King on any given trial was selected in a semi-random manner, with the provision that the same experimenter not be the feeder on more than three trials in a row on any particular day. I.C.S. was present during all trials, either with B.L.S. or with M.R.C. Experimenters B.L.S. and M.R.C. never tested together. Therefore, even though I.C.S. presented foods most often, a strategy of always responding with her card would not have been adaptive for King, as during any particular session, there was only a 50% chance that she would be the one to give the food. Both experimenters were present during the exchange of food, but only the to-be-remembered experimenter handed the food to King. The distractor card was always the other person present during the food-presentation trial.

At the time of the test, the trainer asked King in English, "what did you eat?" and "who gave you the food?" During testing, King was given two additional cards, in addition to the five food cards. Each additional card represented one of the two experimenters present during the presentation. The trainer served as tester. She did not know either the food given to King or the experimenter who had handed him the food.

If King was correct on both the what and who responses on a trial, he was given verbal praise, physical contact, or both from the trainer. A food reward was also given only if he was correct on both what and who information. If he was correct on only one a food reward was not provided, but no time-out was given. If he got both wrong, no food was given and a 1- to 3-min time-out occurred before he was given the next stimulus food. Testing in experiment 2 took place during 24 sessions from September through December 2000.

Results

Experiment 1

At the short retention interval, 112 trials were recorded, and the mean retention interval was 7.3 min. King responded correctly on 78 of these trials, for an accuracy rate of 70%, which was significantly above chance (20%), z=13.1, P<0.05.

We correlated the retention interval (which varied from 5 to 65 min) with the probability of correctness for the first responses. Because correctness was a dichotomous variable, non-parametric correlation statistics were used to examine this correlation. Using a point-biserial correlation, we found that the correlation did not differ from zero. Thus, accuracy of the memory report did not vary as a function of the length of the retention interval in the short retention-interval condition.

For the long retention interval (24 h or more), King showed above-chance accuracy. He was correct on 14 of the 17 trials, for an accuracy rate of 82%, z=6.42, P<0.05. We did not have enough trials to examine the correlation between retention interval and accuracy.

Because of the zoo environment and the particular subject tested, we could not control several variables, which may have influenced the outcome of the study. Therefore, we conducted several analyses to rule out differential responding based on non-mnemonic factors. First, we did a series of chi-square analyses to determine if King was statistically better at remembering any particular food than others. His accuracy rate for any particular food did not statistically differ from his overall accuracy rate (all χ^2<1.96). We also examined if King was more accurate when certain experimenters were presenting the food. We compared the accuracy rate for each experimenter relative to the overall accuracy rate. King was significantly less accurate when experimenter M.R.C. (55%) was testing, χ^2=5.95 (df=1, n=45), P<0.05. We do not know why accuracy was lower with M.R.C. We also were concerned that over time, King may have adapted strategies to ensure his memory of the correct food, such as hiding an orange peel. Thus, we compared his performance over the first 56 trials with his performance over the second 56 trials. Although numerically his mean was higher for the second half (0.73) than for the first half (0.66), this difference was not significant (z<1.96).

Experiment 2

At the short retention interval, 111 trials were recorded, and the mean retention interval was 9.3 min. With regard to his memory for food, King responded correctly on 61 of these trials, for an accuracy rate of 55%, which was significantly above chance (20%), z=9.22, P<0.05.

King was asked to remember who gave him the food. On any given trial, the food could have been given by one of two experimenters (thus, chance was assumed to be 50% in these analyses). King correctly identified who gave him the food on 82% of all trials, significantly above chance, z=6.27, P<0.05. Thus, King could identify "who" information as well as "what" information.

We also examined King's memory as a function of whether he remembered both aspects of the event correctly. That is, a response was only considered correct if he remembered both the experimenter and the food item. He remembered both correctly on 43% of the trials (chance was 10%), which was statistically significant, z=11.7, P<0.05. His memory performance for "who" did not decrease for trials in which he got the food correct (79%) relative to his overall performance for "who" information.

Point-biserial correlations were also used to examine the correlation between retention interval and correct performance for both food information and person information. Neither correlation was statistically different from zero. Thus, variation in retention interval did not affect the outcome of this study.

We also conducted 15 trials with a 24-h retention interval. With the long retention-interval trials, King was asked to retrieve what he had eaten the previous day and who had given it to him. He correctly remembered the food on 73% of trials (11 of 15), which was significantly better than chance, z=2.26 P<0.05. He correctly remembered who gave that food to him 87% (13 of 15) of the time, which was also significantly better than chance, z=2.83, P<0.05. On the 11 trials in which he remembered "what" correctly, he remembered "who" correctly on 10 trials (91%).

We also did additional analyses as manipulation checks. King was equally accurate for each experimenter, for each type of food, and when each experimenter was present.

Discussion

In experiment 1, we found that King recognized the correct food 70% of the time after an approximately 7-min retention interval and over 80% of the time at a 24-h retention interval. In experiment 2, we found that, at the short retention interval, King correctly remembered both the food (55%) and the experimenter (82%) who gave him that food at better than chance levels. At the long retention interval, this increased to 73% and 87%, respectively. These studies show that gorillas are capable of remembering "what" and "who" information, based on single-trial learning.

Four procedural issues must be ruled out before the issue of episodic memory can be discussed. We attempted to rule out all sources of non-mnemonic cueing. First, because the trainer was experimentally blind to the food given in all trials, and the experimenters were not present at testing, King's memory responses could not be a function of subtle cueing from the trainer. Second, great care was taken to remove physical evidence of his last food from his cage because this too could have caused responding based on non-mnemonic factors. Third, the testing was outdoors, so odors were not likely to linger. However, we cannot rule out that odor or tastes still lingered, and that it influenced his short retention-interval performance. In experiment 2, however, his performance on remembering people could not have been influenced by these factors. Fourth, observations failed to detect any regurgitation/reingestion in King's eating habits.

Another non-episodic explanation for King's memory responses may come from priming of particular responses. King may have made his responses based on an implicit representation of memory "strength," with the most recent food incurring the strongest value. Although this can account for his performance at the short retention interval in which the last food eaten is the one for which he is being tested, it cannot explain his performance at the long retention interval. In those trials, King ate many foods, including some that were in the test set, during the retention interval between stimulus presentation and test. Thus, priming of a representation of the most recently eaten food cannot account for the data.

Another possible interpretation of the short retention-interval data is that King is mentally rehearsing the correct food item in one way or another throughout the retention interval. Although King often engaged in play with either the experimenter or the trainer during the retention interval, rehearsal and maintenance in short-term memory remain a concern. However, it is improbable that King would continuously rehearse the correct response for a 24-h period, especially as he slept during this interval. Thus, long-interval trials clearly represent a case of retrieval from long-term memory without any possibility of non-mnemonic cueing.

Differences among conditions

In both experiments, we observed a higher percent correct performance during the long retention-interval trials than during the short retention-interval trials. This was not predicted a priori, but there are several potential explanations. First, we suspected it was because double portions were given in experiment 1 to promote a more memorable event. Thus, in the second study, the amount of food given to him at the long retention intervals was identical to the food given for the short retention-interval trials. However, performance was still better at the long retention interval. Second, it is possible that, during the short retention-interval trials, interference took place between the different responses on any given day. Thus, King may have incorrectly responded with the card from a previous trial. To test this we did a post-hoc analysis across both experiments comparing percent correct on the first trial of any session and later trials. There was no difference between the means, and thus, it is unlikely that interference was a major reason for the lower recognition in the short retention-interval trials. However, a subsequent unpublished pilot study showed interference between adjacent presented items. That King was better at the longer retention interval is counterintuitive, and, as of now, we do not have an adequate explanation.

Also of interest is why his performance in experiment 2 was lower than that in experiment 1 in retrieval of "what" information at the short retention interval. It is likely that the task became more difficult when King was required to remember two components ("what" and "who") of the experience in experiment 2. For our purposes, however, the absolute difference in performance is less important than the observation that King was able to remember successfully both "what" and "who" information. We also found that King showed a higher percentage correct for "who" than "what" information. Because the base rates (50% vs 20%) were different, we do not know if this difference was due to differences in memorability or simply a higher likelihood of guessing "who" correct.

Issues of episodic memory

Clayton et al. (2001) and Menzel (1999) argued that one necessity of episodic memory is that it must maintain memories of "what," "who," "where," and "when" information based on a unique event. Our study demonstrated memory for both "what," and "who" in an adult male gorilla after single-trial learning. We claim that our study replicates Clayton and Dickinson's uniqueness criterion. Every testing trial involved the test for a specific one-time event. Because testing was done outside, each trial was done against a backdrop of different constellations of weather, temperature, clouds, light, and so forth. This naturally mimics the Lego structures used by Clayton et al. (2001) to ensure trial-unique learning.

The long-term retention interval data suggests that King was able to discriminate a particular memory of eating from other memories of eating that took place more recently in time. This follows because King was able to remember specific events associated with the testing after 24-h retention intervals, even though he ate often in between eating the test stimuli and the time of the test. Thus, the testing event was a specific memorable event for him that stood out from his other feedings. The experimental feeding event may have been salient because food is not normally given to him by people other than his trainers. This may explain why King was able to remember one eating event among many over a 24-h period. We will not speculate on how King responded correctly after a 24-h retention interval, but the data clearly show that, at a behavioral level, he was able to indicate correctly the specific food and person associated with a unique event a full day later and discriminate this from other similar episodes.

In sum, although other explanations are possible, we posit that episodic memory can account for the present data. We have not shown that King is mentally re-experiencing the event when he makes his memory response, so the study does not show full human-like episodic memory. We have not shown that King can even retrieve all of the components postulated by Clayton and Dickinson (1998) for episodic-like memory. However, we have shown that he can remember multiple components based on a unique event. We also have shown that at least one gorilla is capable of retrieving information about events and communicating them to people in a symbolic manner.

Acknowledgements The research was partially funded by the Grants-in-aid Program from the Florida International University College of Arts and Sciences. Monkey Jungle and the DuMond Conservancy provided logistical support for the project. We are grateful to Monkey Jungle for access to King and for employees' time. The authors thank Dr. Leslie Frazier, Dr. Lisa Son, and several anonymous reviewers for comments on preliminary drafts of this paper. The authors thank Ilanna Walden for assistance in testing and Robert Castillo for constructing stimuli. We thank Sharon Du Mond and Steve Jacques of Monkey Jungle for their encouragement, cooperation, and assistance. We especially thank Tina Casquarelli of Monkey Jungle for her devotion, time, and expertise.

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