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Michael J. Beran
Georgia State University, mberan1@gsu.edu

Emily D. Klein

Theodore A. Evans
Georgia State University, taevans@gsu.edu

Betty Chan

Timothy M. Flemming

See next page for additional authors

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Authors
Michael J. Beran, Emily D. Klein, Theodore A. Evans, Betty Chan, Timothy M. Flemming, Emily H. Harris, David A. Washburn, and Duane M. Rumbaugh

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DISCRIMINATION REVERSAL LEARNING IN CAPUCHIN MONKEYS (*CEBUS APELLA*)

Michael J. Beran, Emily D. Klein, Theodore A. Evans, Betty Chan, Timothy M. Flemming, Emily H. Harris, and David A. Washburn
Georgia State University

Duane M. Rumbaugh
Georgia State University and Great Ape Trust of Iowa

Learning styles in capuchin monkeys were assessed with a computerized reversal-learning task called the mediational paradigm. First, monkeys were trained to respond with 90% accuracy on a two-choice discrimination (A+B–). Then the authors examined differences in performance on three different types of reversal trials (A–B+, A–C+, B+C–), each of which offered differing predictions for performance, depending on whether the monkeys were using associative cues or rule-based strategies. Performance indicated that the monkeys mainly learned to avoid the B stimulus during training, as the A–C+ condition produced the best performance levels. Therefore, negative stimuli showed greater control over responding after reversal and reflected a more associative rather than rule-based form of learning.

Reports of cognitive abilities in a variety of animal species have surged in recent years (e.g., Wasserman & Zentall, 2006). Many of these reports emerged from studies with nonhuman primates, and attendant explanations for such abilities center on the large brains, complex social groups, and foraging behaviors of these species (e.g., Byrne & Whiten, 1988; Maestripieri, 2003; Rumbaugh & Washburn, 2003). However, much of what we understand about why organisms behave the way that they do comes from conditioning paradigms designed to assess the role of stimulus-response (S-R) associations between stimuli and the extent to which such processes led to generalized forms of learning (Hull, 1943; Spence, 1937).

Thorndike (1911) believed that common associative processes could

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All authors are affiliated with the Language Research Center at Georgia State University, and Timothy M. Flemming, Emily H. Harris, and David A. Washburn are also with the Department of Psychology at that institution.
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Address correspondence to Michael Beran, Language Research Center, Georgia State University, P.O. Box 3965, Atlanta, Georgia 30302. E-mail: mjberan@yahoo.com

account for most, if not all, learning in animals and human beings. Although Thorndike recognized that there were important performance differences between species, he believed that these differences were caused by quantitative differences in associative learning processes. Thus, if a monkey could learn a symbolic matching-to-sample task faster than a pigeon, it was because the monkey could form associations faster than a pigeon, not because the monkey was more cognitive than the pigeon. However, Harlow (1949) showed that rhesus monkeys given a large number of novel two-choice discrimination problems in succession showed significant improvement in their acquisition rates. Indeed, after several hundred problems, the monkeys needed only one trial to determine which stimulus was correct and which stimulus was incorrect and could respond correctly on almost all subsequent trials with those same stimuli. Harlow argued that animals that established learning sets were, in effect, learning how to learn the rules that provided for efficient responding during a two-choice discrimination task, where criterional performance on one pair of stimuli led to the introduction of two new stimuli, with each pair containing a randomly determined positive discriminative stimulus (S+) and negative discriminative stimulus (S–). Such increases in efficiency could not result from specific pairings of stimuli and responses (and outcomes) because of the novelty of stimuli across problems, and therefore associative principles could be discounted as accounting solely for the learning that occurred (see Murray & Gaffan, 2006, for a prospective memory account of learning sets).

Rumbaugh (1971) devised a testing paradigm, which he called the mediational paradigm, for differentiating associative and rule-based interpretations for reversal learning in nonhuman animals. The task is a reversal-learning task, in which animals must first learn which of two stimuli is paired with food reward (and which is not) and then learn that the outcomes for selecting the different stimuli had been reversed. The specifics of the task provided different predictions for how animals might respond, depending on whether they were learning through S-R associative processes such as those posited for more general learning phenomena (Hull, 1943; Spence, 1937) or whether they learned about relations between stimuli through the attendant rule learning that accompanies logical task structuring.

In the mediational paradigm, animals first are trained to a criterion of 9 of the last 10 trials correct in a two-choice discrimination (A+B–). Next, the reward contingencies of the two stimuli are reversed for a single A–B+ reversal trial (i.e., the former S+ becomes the S– for this single trial, and the former S– becomes the S+). Then one of three different conditions is presented for an additional 10 trials. In the A–B+ condition, the 10 additional trials are presented with this now reversed contingency. In the B+C– condition, the A stimulus is replaced with a new stimulus (C) that acts as the S– for 10 trials. In the A–C+ condition, the B stimulus is replaced with a new stimulus (C) that acts as the S+ for the additional 10 trials. Then, a new A+B– problem is presented in the next block of trials.

A comparison of performance in these three conditions provides evidence for the basis of the learning that occurs. The relative difficulty of the B+C– and A–C+ conditions allows an assessment of the extent to which animals learn only to approach the original S+ (the A stimulus) or avoid the original S– (the B stimulus). If this type of associative learning underlies performance during the training phase of each problem, performance should differ between these two conditions and the control (A–B+) condition. If an animal

has learned only to approach the A stimulus, the B+C– condition should produce high performance levels, because there is no need to extinguish approach responses to stimulus A, since it is no longer present. If an animal has learned only to avoid the B stimulus, the A–C+ condition should produce high performance levels because there is no need to overcome inhibition of responding to stimulus B. If the animal has learned both to avoid the B stimulus and to approach the A stimulus, performance should be poorest on the control (A–B+) condition, because both associative processes (approach and inhibition) remain. In addition, if an animal shows a preference for novel stimuli, it should perform at very high levels for the A–C+ condition but at very low levels for the B+C– condition.

A more cognitive, rule-based approach to the task, freed somewhat from the constraints of inhibitory and excitatory associations formed between specific stimuli and responses, would allow the organism to learn all that it needed to know from the first reversal trial. That trial provides information that now the B stimulus is the correct stimulus, and the subsequent introduction of the C stimulus would not disrupt performance. In the B+C– condition, the organism could respond on the basis of the information presented in the first reversal trial that B is now the correct response. In the A–C+ condition, the organism could respond on the basis of learning that the A stimulus is no longer the correct response, and thus the C stimulus should be selected. Finally, the control condition (A–B+) would simply require a continuation of the win-stay, lose-shift rule that emerges from the first reversal trial (see Rumbaugh & Pate, 1984a, 1984b).

To date, a number of nonhuman primate species have been tested with this paradigm. Rumbaugh (1971) originally tested gorillas, gibbons, and talapoins and found that there were qualitative differences in learning processes among these species, with the larger-brained ape species exhibiting more rule learning, compared with the more associative (S-R) learning exhibited by the other species. Specifically, Rumbaugh found that whereas gorillas performed equally well in all conditions, the talapoins performed significantly worse in the A–B+ control condition, and the gibbons showed a strong bias to select the C stimulus in the A–C+ and B+C– conditions. These species differences were evident despite the groups having shown no differences in meeting the training criteria for the problems. That is, they differed not in their capacity to learn but rather in the nature of that learning.

Subsequent tests with additional primate species confirmed that smaller-brained species tended to learn in an associative manner, whereas larger-brained species utilized task-based rules (e.g., Rumbaugh, 1997; Rumbaugh & Pate, 1984a). Associative learners performed more poorly on the A–B+ condition than on the other conditions, whereas relational learners performed comparably across conditions. These data matched those from other reversal learning paradigms, such as the Transfer Index (Rumbaugh, 1970, 1997) that examined performance in relation to brain size.

Some species seemed to show characteristics of both associative learners and rule learners. For example, Washburn and Rumbaugh (1991) reported that rhesus monkeys performed as well on the A–B+ problem as they did on the other two problems, indicating rule learning. However, Essock-Vitale (1978) reported that macaques performed more like associative learners when given the mediational paradigm, because their performance was higher when the original S– was removed for the postreversal trials. Increased exposure

to the discrimination task (i.e., more training with new problems) led to performance more indicative of simple rule learning regarding selection of new stimuli over old stimuli after reversal.

Capuchin monkeys have been reported to show cognitive patterns of responding in some contexts designed to assess capacities such as tool using, numerical cognition, and concept learning (e.g., D'Amato & Colombo, 1988; Evans & Westergaard, 2004; Judge, Evans, & Vyas, 2005; McGonigle, Chalmers, & Dickinson, 2003; Wright, 1999; Wright & Katz, 2006), but they show less cognitive patterns of responding in others (e.g., Schino, Spinozzi, & Berlinguer, 1990; Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995). Data from capuchin monkeys on other reversal learning tasks such as the Transfer Index (Rumbaugh, 1970, 1997) also place them into a gray area between associative learners and rule learners, and a test of the mediational paradigm using a manual apparatus indicated that capuchins performed below the levels shown by great apes (De Lillo & Visalberghi, 1994). Capuchins sometimes show an initial preference for the novel stimulus, leading to higher performance in the A–C+ condition and lower performance in the B+C– condition. Individual differences also have been reported, but De Lillo and Visalberghi concluded that overall, capuchins most clearly showed signs of associative learning. However, there are no data from computerized tests with capuchin monkeys using this task. As noted, with rhesus monkeys there is some evidence that the testing paradigm (manual vs. computerized) may lead to different behavioral outcomes (Essock-Vitale, 1978; Washburn & Rumbaugh, 1991), perhaps as a function of the amount of experience. Therefore, additional data from capuchin monkeys on a computerized version of the mediational paradigm that allows for the presentation of a large number of trials are important in further assessing the basic reversal learning tendencies of this species.

The goal of this study was to examine the learning style of capuchin monkeys. All capuchins that we observed in this experiment had shown that they were capable of forming learning sets. During joystick training, one of the training tasks involved two-choice discrimination learning in which each pair of stimuli was presented for only six trials. To meet the criterion for that task, a monkey had to perform at greater than 80% correct for 50 consecutive problems, ensuring that the animal was learning how to respond after the first trial with each new pair of stimuli. All monkeys succeeded with that training task, indicating that they were proficient at two-choice discrimination learning.

Method

Participants

Five capuchins were tested: Liam (male, 2 years old), Wren (female, 3 years old), Nala (female, 4 years old), Gabe (male, 8 years old), and Griffin (male, 8 years old). All five animals had been trained to respond to computer-generated stimuli but had not participated in any formal tests beyond this computer training.

Training consisted of learning to move the cursor into contact first with stationary objects on the screen and then into contact with moving objects on the screen (see Richardson, Washburn, Hopkins, Savage-Rumbaugh, &

Rumbaugh, 1990; Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989; Washburn & Rumbaugh, 1991). Finally, the monkeys were trained to perform an identity matching-to-sample task followed by a two-choice discrimination task, which formed the basis for the present experiment. As noted, all animals showed evidence of learning set during training whereby performance was very high after the first trial with each new pair of stimuli presented.

Apparatus

Trials were presented on a Compaq DeskPro with an attached 17-inch color monitor. Joystick responses were made with a Logitech Precision digital joystick mounted vertically to the cage. The test program was written in Visual Basic for Windows. Correctly completed trials were automatically rewarded by the computer with single 45 mg Bio-Serv pellets through use of an automated pellet dispenser. (For more details of the computerized apparatus, see Richardson et al., 1990.) All stimuli consisted of clip-art images downloaded from the Internet and from commercially available software.

Design and Procedure

All animals were tested individually while physically and visually isolated from all other animals in their social group. Testing occurred between 9:00 a.m. and 12:00 noon, with test sessions usually occurring over the course of 1.5 to 2 hours. All animals worked only when they wanted, and they had constant access to water. Additionally, all animals were given a full meal of vegetables and fruits in the afternoon, no matter how many trials they completed in the experiment.

For each new problem (i.e., series of trials using the same stimuli) that was presented, two arbitrary clip-art images were randomly drawn from a collection of more than 150 images, and one image was randomly assigned as the S+ and the other was assigned as the S–. These training trials are hereafter called A+B– trials. On each trial, the two stimuli were placed into the two upper corners of the screen, with side position randomly assigned across trials. Monkeys responded by moving the joystick to produce movement of a cursor on the computer screen. This cursor had to be guided into contact with one of the two stimuli to register a selection.

If the selected stimulus was the S+, the monkey received a single food pellet while a melodic tone was played, and there was a 1 s intertrial interval (ITI) before the stimuli were presented again. If the selected stimulus was the S–, there was no food reward and a buzz tone sounded. The ITI after incorrect selections was 5 s.

All monkeys continued in the training (A+B–) phase with a discrimination problem until they had selected the S+ on 9 of the last 10 trials. At that point, a single reversal trial, of the type A–B+, was presented. After this reversal trial, 10 additional reversal trials were presented to complete the problem in one of three different conditions. In the A–B+ condition, the 10 additional trials continued to have the same reversed contingency as in the single reversal trial. In the B+C– condition, the A stimulus was replaced with a new stimulus that acted as the S– for the additional 10 trials. In the A–C+ condition, the B stimulus was replaced with a new stimulus that acted as the S+ for the additional 10 trials (Table 1). After 10 trials were presented from one of these

conditions, a new problem was presented with a new A+B– discrimination. For each block of 3 problems, each of the three conditions was presented one time in random order, and the dependent measure was the number of correct responses made after reversal trial 1 of each problem. Individual clip-art images were used in only one problem in a given experimental session.

Table 1
Mediational Learning Paradigm

Acquisition (9/10 correct)	Reversal Trial (trial 1)	Reversal Problem (trials 2–11)
A+B–	A–B+	A–B+ (control)
		B+C– (novel S–)
		A–C+ (novel S+)

All animals worked on this task for approximately 2 weeks, accumulating a large number of trials and completing a large number of problems. Griffin completed 5,928 trials and 215 problems; Liam completed 7,536 trials and 314 problems; Nala completed 5,801 trials and 240 problems; Wren completed 5,676 trials and 251 problems; and Gabe completed 5,235 trials and 140 problems.

Results

Given the small number of animals in the experiment, we analyzed the performance of each animal separately to generate quantitative and qualitative profiles of each monkey's learning process. Here, the critical data came from performance on reversal trial 2 and trial 3. These trials indicate the clearest difference in performance as a function of condition. Given the rapid speed of learning new two-choice discriminations (A+B– phase), it was important to look for differences that might occur immediately after the reversal trial (and before the monkeys could relearn the S+ and S– across the 10 reversal trials that followed the first reversal trial of each problem). However, we also assessed differences across all reversal trials to provide a full account of performance.

The performance of each capuchin monkey is presented in Figure 1. As expected, performance on the first reversal trial was very low and did not differ across conditions for any of the monkeys, Griffin, χ^2 (2, N = 215) = .157, p = .92; Liam, χ^2 (2, N = 314) = 1.174, p = .56; Nala, χ^2 (2, N = 224) = 2.17, p = .34; Gabe, χ^2 (2, N = 140) = .13, p = .93; and Wren, χ^2 (2, N = 251) = 1.70, p = .43.

Gabe's performance did not differ among the three conditions for the second or third reversal trial. However, overall performance on reversal trials differed as a function of condition, F (2, 137) = 12.38, $p < .01$. Post hoc analyses (Tukey honestly significant difference [HSD] test) indicated significantly better performance on reversal trials 2–11 in the A–C+ condition, compared with the other two conditions ($p < .05$), but no difference between the A–B+ condition and the B+C– condition.

Wren's performance differed on the second reversal trial as a function of condition, χ^2 (2, N = 251) = 106.2, $p < .01$, with performance on the A–C+ condition exceeding performance on the other two conditions and performance on the A–B+ condition exceeding performance on the B+C– condition. This same pattern was true for Wren's performance on the third reversal trial, χ^2 (2, N = 251) = 20.1, $p < .01$, and her overall reversal performance differed across conditions on trials 2–11, F (2, 251) = 20.37, $p < .01$. Post hoc analyses (Tukey HSD) indicated significantly better performance on reversal trials 2–11 in the

A–C+ condition, compared with the other two conditions (p < .05), but no difference between the A–B+ condition and the B+C– condition.

Nala's performance differed on the second reversal trial as a function of condition, χ^2 (2, N = 224) = 56.86, $p < .01$, with performance on the A–C+ condition exceeding performance on the other two conditions. This result was confirmed for overall reversal performance on trials 2–11, F (2, 221) = 9.87, $p < .01$. Post hoc analyses (Tukey HSD) indicated significantly better performance on reversal trials 2–11 in the A–C+ condition, compared with the other two conditions ($p < .05$), but no difference between the A–B+ condition and the B+C– condition.

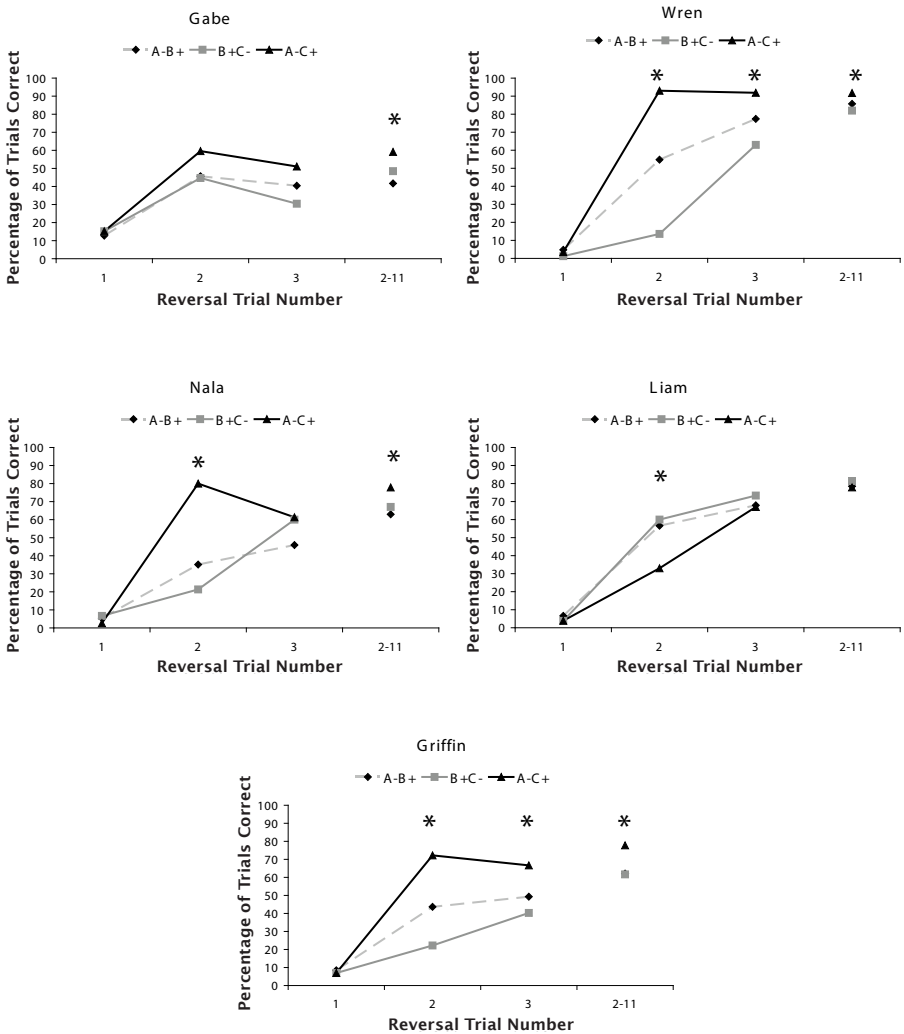

Figure 1. Performance of each capuchin monkey on each condition after reversal. Asterisks indicate significantly different performance across conditions (see text for details).

Liam's performance differed on the second reversal trial as a function of condition, χ^2 (2, N = 314) = 17.94, $p < .01$, with performance on the A–C+ condition significantly lower than performance on the other two conditions. Overall reversal performance on trials 2–11 indicated no difference as a function of condition, F (2, 311) = 11.66, $p = .31$.

Griffin's performance differed on the second reversal trial as a function of condition, χ^2 (2, N = 215) = 36.47, $p < .01$, with performance on the A–C+ condition exceeding performance on the other two conditions and performance on the A–B+ condition exceeding performance on the B+C– condition. Griffin's performance also differed on the third reversal trial as a function of condition, χ^2 (2, N = 215) = 10.38, $p < .01$, with performance on the A–C+ condition exceeding performance on the other two conditions. This result was confirmed for overall reversal performance on trials 2–11, F (2, 212) = 14.18, $p < .01$. Post hoc analyses (Tukey HSD) indicated significantly better performance on reversal trials 2–11 in the A–C+ condition, compared with the other two conditions ($p < .05$), but no difference between the A–B+ condition and the B+C– condition.

Discussion

Given the clear predictions offered by Rumbaugh (1971) for how animals would perform on the mediational paradigm as a function of associative versus rule learning processes, we offer the following interpretations of the data that we have collected:

Four of five capuchin monkeys produced the highest performance levels on the A–C+ problems. Two monkeys (Griffin and Wren) also showed significantly poorer performance on the B+C– problem (on early test trials within the 10-trial reversal block) compared with the other two problems. For these two animals, it is likely that they were biased toward responding to novel stimuli, a response pattern that would produce highest performance on A–C+ problems and lowest performance on B+C– problems. This pattern also was reported for gibbons (Rumbaugh, 1971), other capuchin monkeys (De Lillo & Visalberghi, 1994), and some rhesus monkeys (see Trial 2 performance reported in Table 1 of Washburn and Rumbaugh [1991]). However, a strategy for responding to the novel stimulus was not used by the other three monkeys. If it had been, performance would have been poorest for the B+C– problems. However, that was not true.

In the early reversal trials, the youngest capuchin monkey, Liam, had the greatest difficulty with the condition at which all of the other animals excelled (A–C+). He may have been somewhat neophobic and biased against the new C stimulus. However, had this been true, one would have expected his performance to be particularly high on the B+C– problems, but it was not. Therefore, his performance stands as an anomaly for this sample of animals. However, it is true that human children also sometimes show very different performance levels on learning set tasks as a function of age (e.g., Berman, Rane, & Bahow, 1970; Cameron, 1979). Rhesus monkeys also show changes in learning set performance as a function of age (e.g., Harlow, Harlow, Rueping, & Mason, 1960; Mason, Blazek, & Harlow, 1956; but also see Zimmerman, 1969, for a report where age did not influence performance), and Japanese monkeys show different performance levels on the Transfer Index depending on the age of the animals (Kinoshita, Ohta, & Matano, 1997). Therefore, perhaps performance on the mediational paradigm may change across development in monkeys as well.

Given that the A–C+ problems led to the highest performance in 4 of 5 subjects, what can we conclude about the learning process that occurs during reversal of reward contingencies in two-choice discrimination? According to Rumbaugh (1971), high performance on this problem indicates that inhibition accrues to the B stimulus during training, and the subsequent removal of the B stimulus after reversal produces high performance because this inhibition disappears. The question is why this inhibition accrues. The simplest explanation is that incorrect responses during training (with their attendant time-out periods) are more salient for the monkeys than are the reward pellets. If this is true, one would predict that monkeys would be more likely to make errors on reversal trials involving the B stimulus when they had made more errors during the training phase than when they had made fewer errors (and there was greater inhibition to the B stimulus as a result of this increased number of errors).

We conducted a series of post hoc *t* tests using the outcome on reversal trial 2 (correct or incorrect) as the grouping variable for each monkey, but we found no significant differences in how many training trials were required to meet criterion as a function of the outcome on reversal trial 2. This was true not only for the A–C+ condition but for all conditions.

In a further post hoc attempt to determine whether the number of rewarded or nonrewarded trials during the training phase influenced the likelihood of responding correctly on reversal trial 2, we examined performance across all conditions on the basis of the number of rewarded trials and the number of total training trials required to meet criterion with the A+B– discrimination (i.e., the prereversal training). This series of *t* tests also failed to produce any evidence that the monkeys' performance on reversal trial 2 was influenced by how many training trials they completed during the training phase of each problem, how many trials led to reward during the training phase, or how many trials led to time-outs during the training phase. Finally, we examined performance on reversal trial 3, but we still found no evidence that reversal performance was related to how many training trials were required, how many training trials were completed correctly (and were rewarded), or how many training trials were completed incorrectly (leading to time-outs).

The above analyses indicate that performance on reversal trials was not related to how many reinforcements or time-outs were obtained during training. However, the data indicate that inhibition that accrued to the B stimulus was the primary force behind reversal performance. During training, inhibition accrued to the B stimulus and response strength increased for the A stimulus. However, during the first reversal trial (A–B+), responding to A was penalized. Thus, after this reversal, the animal had several negative experiences with B (from the training phase of the problem), one recent negative experience with A, and no experience with C. This inhibitory learning explains performance across all three conditions as exhibited by the majority of the monkeys. For A–C+ trials, the organism can avoid both inhibitory stimuli and perform at a high level. At the same time, A–B+ and B+C– are roughly similar. A–B+ elicits some inhibition to the A stimulus on the basis of reversal trial 1 and continued strong inhibition to the B stimulus, whereas B+C– elicits inhibition to the B stimulus alone. From this perspective, we would predict that the B+C– condition might produce somewhat lower performance levels, because removal of the A stimulus leaves only inhibition for the B stimulus and thus a bias toward selecting C. This pattern was reported for 3 of the 5 animals that we tested.

None of the monkeys showed the lowest performance for the A–B+ condition. Both rhesus monkeys observed by Washburn & Rumbaugh (1991) performed at the lowest levels during trial 2 and trial 3 in the B+C– condition, and 2 of 4 capuchin monkeys showed this pattern in a previous test (De Lillo & Visalberghi, 1994). Therefore, the current performance of these capuchin monkeys stands in contrast to previously published studies.

Overall, these data support the idea that capuchin monkeys are learning in a more associative manner rather than on the basis of task rule structure (e.g., win-stay, lose-shift). It is possible that the monkeys were employing multiple response strategies, including some bias toward novel stimuli (which may, in itself, be evidence of rule use) and the differential weighting of more recent outcomes of responses in terms of associative strength. Previous reports have also concluded that capuchins learned more associatively (e.g., De Lillo & Visalberghi, 1994). Rhesus monkeys that have shown more rule-based response patterns had other testing experiences, including oddity learning and discrimination reversal (e.g., Rumbaugh, 1971). Therefore, we will need to reexamine the performance of these capuchins after they have acquired additional experience in a variety of tasks that might promote rule-based responding.

The present data match a recent report by Goulart, Mendonca, Barros, Galvao, and McIlvane (2005) that indicated that capuchin monkeys tested in another reversal learning task also seemed to be responding on the basis of negative stimulus control, or what those authors called reject-control relations. In that task, capuchins performed two-choice discriminations and then had the reward contingencies of the stimuli reversed repeatedly until they rapidly learned to respond to the reversal. Then, one of the two stimuli was replaced with a white square on probe trials, allowing an assessment of whether stimulus control occurred through select-control or reject-control processes (i.e., through differential selection of the white square depending on the alternate choice that was available). Although the two capuchins that were tested showed some variability, Goulart et al. reported reject-controlling relations (especially for probe trials presented during a reversal phase). This finding indicated that reject-controlling relations could emerge without training, although training provided stronger evidence of such relations. Goulart et al. noted that although reject-control relations sometimes are reported for human beings (e.g., Johnson & Sidman, 1993; McIlvane, Kledaras, Munson, King, De Rose, & Stoddard, 1987), there has been less evidence for such control in nonhuman animals because select-control relations (S+ stimulus control) have been more prominent (e.g., Cumming & Berryman, 1965). Therefore, our data from capuchin monkeys are important for further illustrating the role of different types of stimuli in the discrimination performance of nonhuman animals, and we must continue to investigate the relative roles of S+ and S– control in discrimination learning by monkeys to better understand the role of stimuli in associative and relational learning.

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