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Capuchins (*Cebus apella*) Can Solve a Means-End Problem

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KEYWORDS

primates, capuchins, monkeys, tool use, means end

ABSTRACT

Three capuchin monkeys (Cebus apella) were tested on a 2-choice discrimination task designed to examine their knowledge of support, modeled after Hauser, Kralik, and Botto-Mahan's (1999) experiments with tamarins. This task involved a choice between 2 pieces of cloth, including 1 with a food reward placed on its surface, and a second cloth with the food reward next to its surface. After reliably solving the basic problem, the capuchins were tested with various alternations of the original food reward and cloth. The capuchins were able to solve the initial task quickly, and generalize their knowledge to additional functional and nonfunctional variations of the problem. In comparison to the tamarins previously tested on this problem (Hauser et al., 1999), the capuchins were able to reach criterion faster during the training and food size conditions and showed a greater ability to inhibit reaching toward larger food rewards that were unavailable.

Among monkey species, capuchins are perhaps the most skilled tool users observed under captive conditions (Cummins-Sebree & Fragaszy, 2005; Visalberghi, 1990; Westergaard & Fragaszy, 1987; Westergaard, Greene, Babitz, & Suomi, 1995; Westergaard & Suomi, 1995), likely derived from innate behavioral predispositions to manipulate objects (e.g., rocks, branches, logs) in their natural environment for extractive foraging (Chevalier-Skolnikoff, 1990; de A. Moura & Lee, 2004; Fragaszy, Izar, Visalberghi, Ottoni, & Gomes de Oliveira, 2004; Ottoni & Mannu, 2001; Phillips, 1998). Recent studies of capuchin populations have shown that they are quite selective in terms of the stone tools they use to crack nuts and tend to follow an efficient behavioral repertoire in selecting nuts, and also where and how the hammer stones and anvils are used (Schrauf, Huber, & Visalberghi, 2008; Visalberghi et al., 2007; Visalberghi et al., 2008). Such proficient tool use by capuchins appears quite similar to the nut-cracking behaviors observed in wild chimpanzees (e.g., Boesch & Boesch, 1990).

Recently, studies with captive animals have begun investigating whether they understand the necessary functional features of objects used as tools. That is, do animals spontaneously grasp how or why a tool works, or is their success derived from using other approaches, such as trial-and-error? Building on

earlier studies of tool discrimination in nonhuman primates by Spinozzi and Poti (1989, 1993), Hauser, Kralik, and Botto-Mahan (1999) investigated whether cotton-top tamarin monkeys understood the functional properties of tools (Hauser, 1997; Hauser et al., 1999; Santos, Miller, & Hauser, 2003). Markedly different in size, behavior, and social structure from chimpanzees and capuchins, tamarins have not been observed to use tools in the wild, although they learn to use them under captive conditions to reliably retrieve food rewards that are out of reach (Hauser, 1997; Hauser et al., 1999). Following a series of tool studies with tamarins, Hauser and his colleagues (Hauser, 1997; Hauser et al., 1999; Santos et al., 2003) concluded that their subjects understood tools as functional objects, as they were able to tolerate modifications to the color and other nonfunctional properties of the tools without a decrement in performance.

An important methodological component of Hauser's tamarin tool studies was the opportunity for the monkeys to have a choice of tools to use (Hauser, 1997; Hauser et al., 1999; Santos et al., 2003). That is, they could choose between two tools, a functional or a nonfunctional tool, by simply pulling it, rather than being asked to modify an ineffective tool or use one in the most appropriate manner. Other investigators have used these same methodological constraints to investigate the means-end problem-solving behavior of a wide range of animals, such as birds, elephants, various monkeys, and chimpanzees (Cummins-Sebree & Fragaszy, 2005; Irie-Sugimoto, Kobayashi, Sato, & Hasegawa, 2008; Povinelli, 2000; Schmidt & Cook, 2006; Schuck-Paim, Borsari, & Ottoni, 2009; Spaulding & Hauser, 2005). For example, Schmidt and Cook (2006) found that pigeons could learn to discriminate between two ribbon/dish combinations and select the ribbon that was physically attached to the food dish versus the ribbon that was near, but not connected to, the food dish. This discrimination, however, appeared to be based on perceptual features of the task, as performance deteriorated when variables such as the length of the gap between ribbon and the dish, the placement of the ribbon in relationship to the dish, and the color of the ribbon were manipulated (Schmidt & Cook, 2006). In another study, an elephant tested by Irie-Sugimoto and colleagues (2008) learned to discriminate between boards that supported a food reward and those that did not. However, it was unclear whether the discrimination was based only on perceptual features of the task, as no transfer tests were conducted. Captive chimpanzees also have been successful with tool choice tasks and have demonstrated proficiency in distinguishing functional tools, with limited or no previous experience on a novel task (Furlong, Boose, & Boysen, 2008; Herrmann, Wobber, & Call, 2008; Povinelli, 2000).

To understand the development of such tool-discrimination skills, it could be helpful to compare closely related species that face different ecological constraints in the wild, such as tamarins and capuchin monkeys. Indeed, several of the tool results reported for tamarins have recently been replicated with capuchins (Cummins-Sebree & Fragaszy, 2005; Fujita, Kuroshima, & Asai, 2003). For example, several investigators replicated the "cane problem" reported by Hauser (1997) in which the subjects had to select the cane with the food located inside the hook portion of the tool to be successful, rather than a second cane that had the reward placed outside of the hook (Cummins-Sebree & Fragaszy, 2005; Fujita et al., 2003). Two different replications found that capuchin monkeys could take into account the relationship between the placement of the cane with respect to the food and successfully pull the correct cane (Cummins-Sebree & Fragaszy, 2005; Fujita et al., 2003). Notably, Cummins-Sebree and Fragaszy (2005) concluded that capuchins exhibited more flexibility in their behaviors than tamarins by repositioning the canes for accessing the food more often.

Evans and Westergaard (2004) also found that capuchins could discriminate between the functional and nonfunctional properties of throwing tools. In their task, capuchins had to choose the correct combination of a rope with an attached projectile (referred to as a "throwing tool") that could be used to hook a reward container and pull it within reach. In most instances, the monkeys chose the functional materials over the

nonfunctional ones (e.g., those with no rope, short ropes, those with no projectile, projectile too large, etc.) on the first trial, even with novel choices (Evans & Westergaard, 2004). Overall, capuchins tested in tool choice experiments appear to have little difficulty understanding the functional features of tools, compared to what may be more difficult experiments that require tool modification or the use of a tool to push food away to retrieve it, as in the “trap tube” task (Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995; Visalberghi & Limongelli, 1994; Visalberghi & Tomasello, 1998; Visalberghi & Trinca, 1989).

To investigate further what features might guide capuchin tool use in captivity, we tested capuchins with the “On” condition of the support problem that was originally tested with tamarins (Hauser et al., 1999). In this study, Hauser and colleagues (1999) presented cotton-top tamarin monkeys with cloths as a means for accessing food. In the On condition, the animals had to choose between pulling a cloth with a piece of food directly on its surface, or a cloth with food placed next to it. Different functional and nonfunctional aspects of the problem were varied, including properties that would alter the solution to the problem (e.g., food position), compared with properties that had no effect on task solution (e.g., cloth color or food size). The authors concluded that the tamarins’ choices were not affected by alterations of the nonfunctional features of the problem (Hauser et al., 1999). Furthermore, they asserted that the tamarins had learned to discriminate between the functional and nonfunctional aspects of the tool task.

In the current experiment, capuchins were provided with a choice between pulling a length of cloth with a piece of food on its surface or pulling a length of cloth with food directly next to, but not on, the cloth surface. The goals of the experiment were twofold: (1) to determine if the capuchins could solve the cloth support problem and (2) to explore whether the subjects could generalize their problem-solving strategies to novel variations of the task. Specifically, we were interested in determining if the monkeys would attend to the relevant support features of the problem, that is, food placement in relation to the cloth. Alternatively, the problem could be solved by relying on the perceptual features of the task, rather than utilizing the concept of support. If the monkeys approached the problem perceptually on some conditions, they would be likely to attend to irrelevant features such as color or shape. To best compare the performance of Hauser et al.’s (1999) tamarins and the capuchins, our methods followed those described for the On condition (Hauser et al., 1999) as closely as possible.

Method

Subjects

The subjects were three capuchin monkeys (*Cebus apella*). The group was composed of two adult females, Rainy and Jane (6 years and 26 years, respectively), and an adult male, Ulysses (20 years; see Table 1 for the animals’ backgrounds).

All subjects had limited experience with tool tasks, including a task that required them to pull cloths (less than 50 trials per subject). All stimuli used in the present experiment, however, were novel. Since their arrival, the capuchins were housed together in a series of interconnected, environmentally enriched, indoor/outdoor enclosures. All subjects were fed a wide variety of fruit and vegetables twice a day, and provided with monkey chow and water ad libitum.

Apparatus

All trials were presented to the subjects on a wooden tray (42.5 × 40.6 cm) with a handle located 23 cm behind the end of the tray. The tray was divided into two equal halves by a 6.5-cm high cardboard partition and was placed at a height of 0.6 m from the bottom of the indoor enclosure. The cloths used in the task were made of black felt, ranging in size from 6.5 to 21.5 cm long by 11.5 cm wide. The bottom edges of the cloths were placed 17.8 cm from the front edge of the tray, so the subjects could reach the

edge of the material but not the food reward. Cloths were rectangular or square, with the exception of the experimental condition when shape was varied. Food rewards consisted of honey-flavored graham crackers for all conditions, except for the condition that varied food color, during which chocolate-flavored graham crackers were used. The crackers were broken into small squares (approximately 3.2-cm square) for most trials, except the condition in which food size was manipulated (larger rewards were approximately 6.4-cm square).

Table 1. Rearing History of Subjects

Name	Sex	Age (years)	Time at facility (years)	Origin
Rainy	Female	6	5	Laboratory born, home reared
Ulysses	Male	20	8	Laboratory born and reared
Jane	Female	26	13	Laboratory born and reared

Procedure

All subjects were tested individually, with the tray positioned in front of their indoor home cage. A test session began when the experimenter placed a length of cloth on each half of the tray, and then positioned the food rewards in two randomly predetermined positions for each cloth. Placement of the cloths and rewards was always done in the same order, left to right. Next, the experimenter allowed the subject to view the cloths for 3 s, and then pushed the tray forward. As soon as the tray was presented, the experimenter averted her gaze toward the center partition on the tray. This gaze position minimized any possible visual bias toward the stimuli, and was maintained until the subject responded. Once the tray was accessible, the animals had 20 s to select one of the cloths. A choice was considered to have been made if the subject touched or pulled one of the cloths. After each choice, the tray was immediately retracted, and the remaining stimulus materials (cloths and any remaining food) were removed. The stimuli were then repositioned and the next trial was initiated. If an animal was successful and retrieved the reward, he or she was able to consume the food while the stimuli were being repositioned for the next trial.

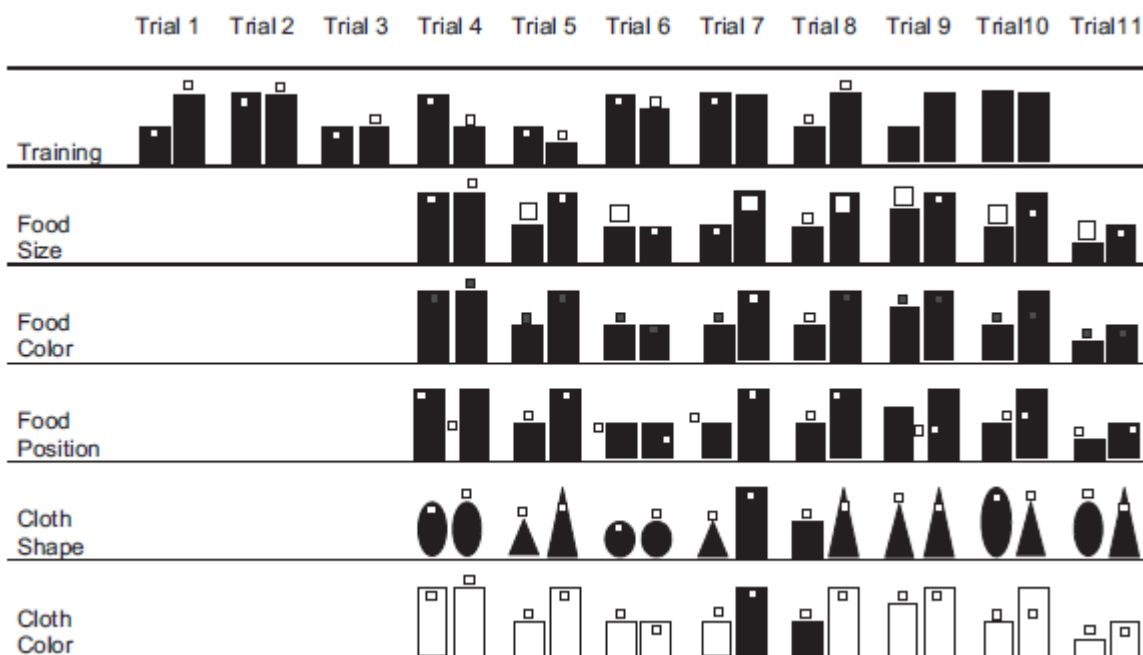
During testing, a second experimenter operated the video camera to record the animals' responses. All trials were recorded using a Logitech (Fremont, CA) PC color video camera. A student assistant coded all recordings off-line for interrater reliability. This measure was high, with strong agreement between the experimenter and the naïve rater ($\kappa = .97$). A trial was considered a success if the subject pulled the cloth with the food on it and therefore, was able to retrieve the reward. A subject failed on a given trial if she touched or pulled the incorrect cloth. The order of trials was quasi-randomized for each session using a random number generator, with the constraint that no more than two trials in a row were presented with the correct cloth on the same side of the tray. The subjects completed one session a day (20 to 22 trials), with no more than 4 days separating any two sessions.

Stimulus configurations for all conditions are depicted in Figure 1 and the rationale for the testing conditions is presented in Table 2. For the training phase, Trial Types 1 to 7 included a choice between two varying lengths of the cloths, with food on one cloth, and food placed directly above the other cloth (or absent, as in the case of Training Trial Type 7). Training Trial Types 8 to 10 were inhibition trials presented to see if the animals would pull a cloth even when food was inaccessible from either cloth, but visible on the tray (Training Trial Type 8), or no food was available on the tray or on either cloth (Training Trial Types 9 and 10). The 10 training trial types were counterbalanced for position, for a total of 20 trials per session. Because it was only possible to reach the food on 14 trials (Training Trial Types 1 to 7), accuracy was determined for these 14 trials only. For each training session, 13 correct responses out of

14 (92% success rate) were required for a subject to reach criterion. This success rate then had to be maintained for five consecutive sessions for a subject to move on to the next condition. In addition, during the training phase, if the subject did not respond within the allotted time, the trial was considered incorrect.

After completion of the training phase, subjects were tested on a series of experimental probe conditions to determine if they were able to attend to the relevant feature of the problem (whether the food had been placed on or off the cloth). Probe trials consisted of altering various irrelevant or relevant features of the task, as described in Table 2. The explicit purpose of the experimental probes was to determine if the subjects understood that the cloth was the functional means for obtaining the reward, or if they were using other more problem-specific perceptual rules. Performance on the first novel trial of each probe condition was used as a measure of the subjects' ability to generalize their understanding from the preliminary training condition.

Figure 1. Cloth/food configurations for training and experimental probe conditions.



During testing with probe conditions, the first three trial types from the training phase were always randomly presented within each session, in addition to eight novel probe trial types. Each trial type was counterbalanced for position, yielding a total of 22 trials per session. Inclusion of training trial types within each probe session provided baseline performance for each experimental condition. For experimental trials where food size was manipulated (food size probe), a 92% criterion was again employed, and had to be maintained over five sessions (100 trials). This strict criterion was maintained for the food size probe because this probe was hypothesized to be especially difficult for the monkeys (Boysen, Berntson, & Mukobi, 2001). In this way, the food size probe served as another check to ensure that the monkeys were performing successfully before they moved on to further probes. During the remaining conditions, which included varying food color, food location, cloth shape, and cloth color, a criterion of 75% correct was required over two sessions (44 total trials). All criteria were based on those used with tamarins by Hauser and colleagues (1999) for the same task.

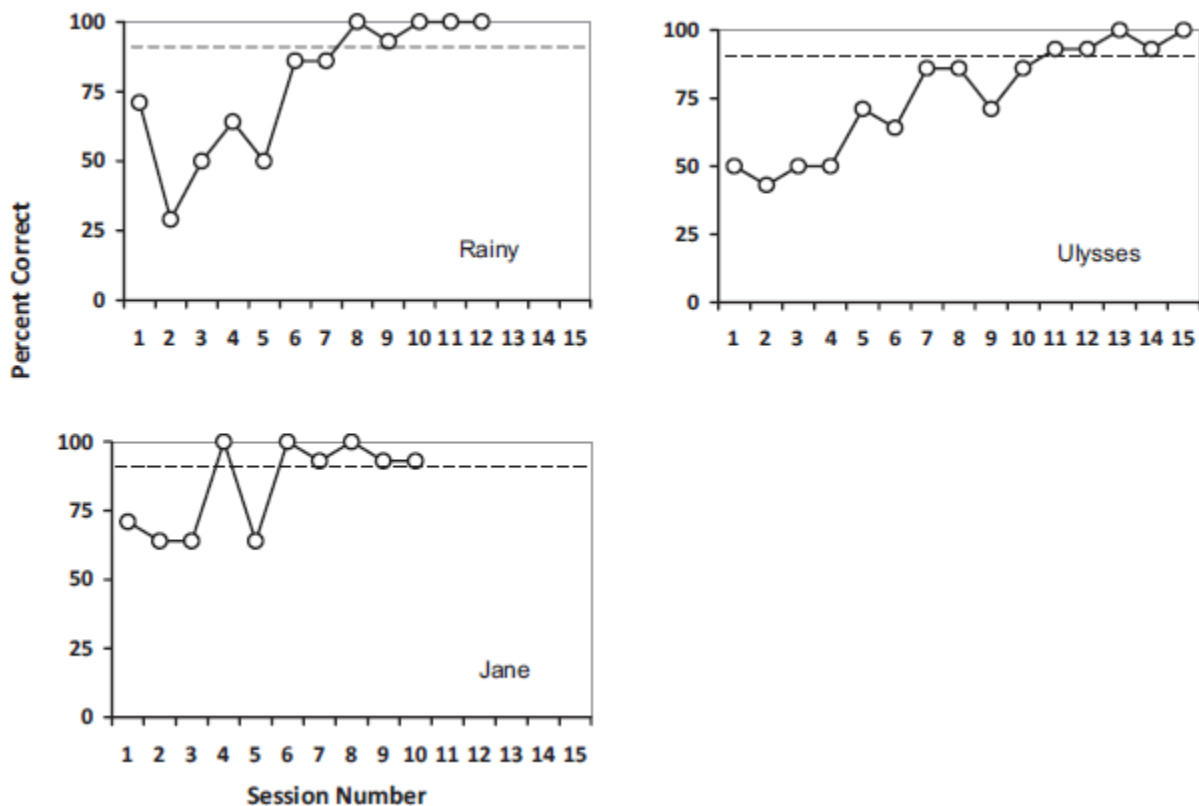
At the end of each probe session, the animals were given an opportunity to redo trials during which they had not responded within the response time (such trials were completed for 18% of the total probe trials, and were equally distributed across experimental conditions). If the subject did not respond again during this second presentation, the trial was recorded as a failure (< 1% of all trials). However, if subjects did respond, the responses were recorded as correct or incorrect, and previous “no response” results were excluded from data analyses. This procedure was not used by Hauser et al. (1999), but was implemented so that subjects were not discredited for inattentiveness or other distractions that might have occurred during testing (e.g., unexpected noise elsewhere in the laboratory, etc.).

Table 2. Description of Experimental Conditions

Condition	Variation from training	Specific changes from training condition
Training	None	None ^a
Food size probe	Nonfunctional	Graham cracker four times larger
Food color probe	Nonfunctional	Graham cracker color changed from tan to black
Food position probe	Functional	Food positions relative to cloth altered
Cloth shape probe	Nonfunctional	Three different size oval cloths and three different size triangular cloths used
Cloth color probe	Nonfunctional	White cloths used instead of black cloths

^a Cloth sizes: 6.5 × 11.5 cm, 11.5 × 11.5 cm, 16.5 × 11.5 cm, 21.5 × 11.5 cm

Figure 2. Training phase by subject: Percentage of correct responses per session. Dashed lines indicate the criterion level of 13/14 correct responses.



Results

All subjects met criteria for each condition, and moved on to subsequent probe conditions. However, each animal required the most sessions to reach criterion during the training phase, with a range of 10 to 15 sessions (see Figure 2). A chi-square test was used to compare the capuchins' performance among the Training Trial Types 1 to 6 and no significant differences were found ($p = .066$).

The time to criterion among the subjects varied only during training (range: 10 to 15 sessions) and the food size probe (range: five to nine sessions). Throughout the remaining probe conditions, subjects met criteria within the first two sessions, and were all above 85% correct for each condition during the first session. During the first novel trial of each probe condition, the monkeys were correct for all experimental conditions, with one exception. One subject (Rainy) failed the first novel probe when cloth color was varied, although this was the only trial she missed in the session. A Mann–Whitney U was performed to examine differences in the number of incorrect trials during the first and second half of each session (Siegel & Castellan, 1988). There were no significant differences between the subjects' performance for the first half of the trials (10.2% incorrect responses) compared to the last half (10.3% incorrect responses) of the sessions ($p > .05$). All subjects also maintained strong performance (245/258, 95% correct response overall) on the baseline training trials that were integrated into each probe condition.

The capuchins' performance on the food size probe is presented in Table 3. With respect to initial performance during Session 1 of the food size probe, the animals' performance was statistically different from chance (51/60, 85% correct, $p < .001$, two-tailed binomial), and was higher than the results reported for Hauser's (1999) tamarins (approximately 45% correct). However, the capuchins' overall performance in the food size condition showed some differences from their 95% performance during the last training session. For example, during food size Trial Type 7, the capuchins were given a choice between a large cracker and a small one. Surprisingly, they selected randomly ($p > .05$, one-tailed binomial probability), indicating no preference for the larger reward. In contrast, on food size Trial Type 8, when they could only attain the larger cracker, they had little difficulty selecting the functionally correct cloth ($p < .05$, one-tailed binomial probability), indicating they had not formed an optimal strategy for obtaining the larger reward, as seen during food size Trial Type 7.

Additional analyses examined the inhibition trials in the training phase. These results revealed that the monkeys were readily able to inhibit a choice when no food was present (Training Trial Types 9 and 10). In fact, on these trials, they selected a cloth with no reward only 15% of the time, which is significantly below chance ($p < .05$, one-tailed binomial probability). However, when the rewards were placed behind the cloths, thus rendering the food items inaccessible (Training Trial Type 8), subjects selected a cloth on 84% of these trials, and these choices were significantly above chance ($p < .05$, one-tailed binomial probability). Therefore, when neither reward was available, yet remained visible, the monkeys had great difficulty inhibiting a tendency to reach for one of the cloth stimuli.

Discussion

The capuchins' performance on the support problem provides empirical evidence for two important conclusions. First, capuchins can solve a simple means-end discrimination problem. Although the tamarins tested by Hauser and colleagues (1999) also solved the task by the end of the training phase, they required a relatively large number of training sessions on average (approximately 25 training sessions) compared to the capuchins (13 sessions). These findings are consistent with the results of other capuchin studies that replicated Hauser's cane study originally conducted with tamarins (1997; Cummins-Sebree & Fragaszy, 2005; Fujita et al., 2003). Both replications provided evidence that the capuchins were equally (or more) successful than tamarins. Second, the present results demonstrated

that our capuchins based their responses on the functionality of the cloth as a means for accessing the food reward. Notably, their performance was not significantly affected by varying the nonfunctional aspects of the task, including food size and color or cloth shape and color. The capuchins also were able to generalize variations in the food location immediately, with no decline in performance, indicating an understanding of the functional aspect of the task.

These results may reflect some level of understanding of the causal or functional features of the task beyond basic perceptual knowledge. For example, the monkeys did not appear to be using a simpler response strategy such as, “always pull the black cloth” or similar rule that guided their choices based on the obvious perceptual features of the various conditions. In addition, because there were no differences in the number of correct responses between the first and second half of the sessions, no additional learning likely occurred within sessions. Instead, these data support the hypothesis that the capuchins acquired a more general knowledge about the cloth and the necessary functional support it provided as a base for a food reward during the training phase. This is also consistent with the conclusion drawn by Hauser and colleagues (1999) for his tamarins.

Table 3. Percentage of Correct Responses When Food Size Varied

Subjects	Session 1 (%)	Total sessions	Trial Type 7 ^a (%)	Trial Type 8 ^b (%)
Rainy	90*	5	20	80
Ulysses	100*	5	30	100*
Jane	65	9	50	88.9*
Group <i>M</i>	85*	---	36.8	89.5*

^a Indicates percentage of responses when larger cracker chosen between both choices (both large and small crackers were accessible).

^b Only the larger cracker was accessible.

* $p < .05$, one-tailed binomial.

It is still possible, however, that the capuchins may have learned a very specific perceptual rule that guided their decisions and also allowed them to be successful in the probe conditions. Indeed, Povinelli, Reaux, Theall, and Giambone (2000) hypothesized that their chimpanzees were solving the basic support problem based on visual “contact” rather than physical connection or support. To investigate this, they tested captive chimpanzees with choices that would be increasingly more challenging if they were relying on visual contact alone to solve the problems. They found that the chimpanzees performed at chance levels when the incorrect cloth/reward choices represented perceptual containment of the reward by the cloth (Experiment 22, Povinelli et al., 2000) as well as current or imminent perceptual contact of the cloth and reward (Experiment 23, Povinelli et al., 2000). Based on these results, Povinelli et al. concluded that their chimpanzees were using very specific perceptual features based on the spatial configuration of the cloth and reward to solve the simpler versions (e.g., “contact/no contact” condition in Experiment 21, Povinelli et al., 2000) of the task and not the concept of support. Although the cloth/reward configurations used by Povinelli et al. were not tested with our capuchins and no direct comparisons are possible, there is no reason to believe that the visual factors measured by Povinelli et al. would be any more influential than those of color, size, and so forth that were tested in our probe conditions.

The capuchins’ performance during the food size condition was examined more closely, because the Hauser et al. (1999) tamarins seemed to have an especially difficult time inhibiting their response for the larger cracker, despite it being unattainable in most trials. Specifically, Hauser and colleagues (1999)

found that none of their subjects were more than 60% correct during their first session with the food size condition, compared with their 92% correct performance by the end of training. The investigators attributed the tamarins' diminished performance to difficulties in inhibiting a natural desire for the larger reward. Indeed, there is previous evidence with chimpanzees demonstrating a powerful response bias, based on food element size (Boysen et al., 2001), as well as earlier results comparing quantities that revealed a powerful behavioral predisposition to choose a larger quantity, regardless of whether it was an edible array or simply a collection of rocks (Boysen interference effect; Boysen & Berntson, 1995). Boysen and colleagues (2001) found that chimpanzees failed to inhibit a choice between two arrays where item size included a larger version of the same candy (gumdrops). Notably, it required a candy array composed of six smaller gumdrops to override the animals' preference for a single, larger gumdrop, despite the fact that three smaller gumdrops were the equivalent mass of one large gumdrop. Thus, element size represented a stronger response bias than the absolute number of smaller items in a competing array, up to a point (Boysen et al., 2001). Why might the capuchins have not shown such a food size bias? One possibility is that they may not have had as strong a preference for the graham crackers when compared to the highly valued candy used by Boysen et al. (2001), and thus, the larger food reward was not necessarily more desirable. Recall that during the food size trials that presented a choice between a large or small cracker, the capuchins chose randomly between the two. Hence, the subjects were able to inhibit the natural predisposition to reach for the larger cracker shown by the tamarins. Yet the capuchins lacked the ability to inhibit making a choice when small food pieces were present and unavailable, which was the case in Training Trial Type 8. In addition, it is clear that the monkeys were not simply avoiding the large cracker, because when they were forced to choose between a large available cracker and a small unavailable cracker, they reliably chose the larger food item (food size Trial Type 8). Overall, these responses suggest that the animals may not have been as motivated to obtain the larger food, compared to the tamarins (Hauser et al., 1999). It may be the case that inhibition did not play a central role. In contrast to the capuchins, the tamarins were maintained at 10% below what their normal body weight would have been under *ad libitum* feeding conditions in captivity. This difference in methodology may account for the animals' increased preference for obtaining a larger reward, despite its inaccessibility (Hauser et al., 1999).

Further studies would be helpful in examining the mechanisms supporting the capuchins' performance. Hauser, Pearson, and Seelig (2002) found that even infant tamarins with no previous access to tools or opportunities to manipulate objects were able to discriminate functionally relevant features and solve the cane problem, in a pattern similar to adult tamarins (Hauser, 1997). They interpreted these findings to mean that such discrimination abilities when using tools are likely "innate" for this species (Hauser et al., 2002). Further testing of their hypothesis, however, indicated that the initial task-specific training condition was necessary for both tamarins and marmosets to successfully solve the cane problem. Consequently, when tamarins and marmosets are first presented with variations of the original task (i.e., changes in tool color, shape, size, orientation), with no prior experience, they cannot successfully discriminate between the two tool choices presented (Spaulding & Hauser, 2005). However, after a limited amount of task-relevant experience, both species discriminated between a wide-range of functional and nonfunctional canes, with marmosets requiring less experience to reach proficiency (Spaulding & Hauser, 2005).

Experience has been cited to play a role in the tool use behavior of wild capuchin populations as well (Visalberghi et al., 2009). Recent field work by Visalberghi and colleagues (2009) demonstrated that capuchins were able to select a functional over nonfunctional stone tool, even in the absence of reliable visual cues. These authors concluded that the impressive and immediate tool discriminations made by wild capuchins are likely based on a lifetime of experience with tools in their natural environment, a setting that cannot be equated to captive environments. Nonetheless, it appears that the initial experience gained by our capuchins during the training phase of the current set of experiments provided enough

information for them to generalize across numerous modifications to the tool and food. Further tests are necessary to clarify if captive capuchins can be successful with more extensive manipulations of the nonfunctional aspects of a tool or food rewards, and precisely what amount of experience is necessary for them to solve similar tool use problems.

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