Journal of Comparative Psychology
2010, Vol. 124, No. 1, 29–37

0735-7036/10/$12.00 DOI: 10.1037/a0018005

Conditional Copying Fidelity in Capuchin Monkeys (*Cebus apella*)

Marietta Dindo
University of St Andrews

Bernard Thierry
Centre National Pour la Recherche Scientifique, Strasbourg, France

Frans B. M. de Waal
Emory University

Andrew Whiten
University of St Andrews

In the last two decades, it became largely accepted that monkeys show little, if any, copying fidelity. However, some recent studies have begun to challenge this notion. To explore reasons for such contrary findings, we designed a foraging apparatus so that in each of two experiments with capuchin monkeys (*Cebus apella*), a model would demonstrate one of two alternative methods to obtain food. The apparatus had a V-shaped track on which a panel could be slid up left or right from the center to reveal food. In Experiment 1, food was located in a cup directly behind the center panel. In Experiment 2, sliding the panel left or right revealed food either in left or right ends of the V-track. Since this sliding movement led directly to one food location exclusive of the other, we predicted capuchins would show greater copying fidelity in this second Experiment. Instead, subjects were significantly more faithful to the model's method in Experiment 1, which provided strong evidence of capuchins copying what they had observed. We suggest that the contrasting results of Experiment 1 may have occurred because capuchins prioritize exploratory behavior when alternative foraging locations are accessible.

Keywords: social learning, social learning strategies, copying fidelity, traditions, capuchin, *Cebus apella*

Local, group-specific traditions have been reported in an increasing variety of animal species, including fish (Warner, 1988), rats (Aisner & Terkel, 1992; Terkel, 1996), birds (Hinde & Fisher, 1951; Lefebvre, 1986; Lefebvre & Giraldeau, 1994), and primates (Leca, Gunst, & Huffman, 2007; Perry et al., 2003; van Schaik et al., 2003; Whiten et al., 1999). Such reports have become particularly numerous in recent years, as long-term field studies have matured (see Laland & Galef, 2009; Whiten & van Schaik, 2007 for reviews). Capuchin monkeys (*Cebus apella*), the subjects of the present paper, have provided particularly intriguing recent evidence, with Perry et al. (2003) describing the rise, diffusion, and loss of social conventions that vary between groups, and Fragaszy et al. (2004); Ottoni and Mannu (2001), and Moura (2007) describing localized patterns of nut-hammering and other forms of tool use that bear a striking resemblance to some of the cultural variations documented for chimpanzees (Whiten et al., 1999).

However, it is difficult to demonstrate convincingly in the wild that such variations are truly socially learned in the rigorous fashion that is possible in controlled experiments with captive animals. In monkeys, such experiments have produced a surprising plethora of negative results that appear in conflict with the conclusions of the field primatologists: reviewing numerous experimental findings, Visalberghi and Munkenbeck-Fragaszy (1990, Visalberghi and Fragaszy, 2002) concluded that the answer to their question "Do monkeys ape?" was an essentially negative one for monkeys in general and for the capuchin monkeys they study in particular.

In recent years, however, some more positive evidence for capuchins' social learning has emerged in 'two-action' experimental designs, in which observers are exposed to either of two different techniques, typically used to gain access to a food reward. In this approach, the extent to which observers preferentially employ the technique of whichever model they see can be sensitively detected and rigorously measured. Dawson and Foss (1965) first used this approach to test the copying abilities of budgerigars (*Melopsittacus undulatus*). Two-action experiments have provided

---

Marietta Dindo, Centre for Social Learning and Cognitive Evolution, School of Psychology, University of St Andrews; Bernard Thierry, Centre d'Ecologie, Physiologie & Ethologie, Centre National pour la Recherche Scientifique, Strasbourg, France; Frans B. M. de Waal, Living Links Center, Yerkes National Primate Research Center, Emory University; and Andrew Whiten, Centre for Social Learning and Cognitive Evolution, School of Psychology, University of St Andrews.

M. D. was supported by an International Primatological Society research grant and a grant from the Russell Trust, B. T. by the Centre National pour la Recherche Scientifique, F. d. W. by National Science Foundation, and A. W. by a Biotechnology and Biological Sciences Research Council grant, the Royal Society, and a Leverhulme Major Research Fellowship. The Centre de Primatologie in Strasbourg, France, complies with all French regulations for primate research. The Yerkes National Primate Research Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care. We are grateful to Andy Burnley for constructing the testing apparatus, to the Yerkes Capuchin Lab manager, Kristi Leimgruber for her assistance, and to the CdP technician, Pierre H. Ulrich. We thank Valerie Dufour and Odile Petit for help with the planning of the project in Strasbourg, Josep Call, and two anonymous reviewers for their helpful comments on the manuscript.

Correspondence concerning this article should be addressed to Marietta Dindo, Mind Brain and Evolution Center, Department of Philosophy, George Washington University, Phillips 525, Washington, DC 20052; or Smithsonian National Zoo, 3001 Connecticut Avenue NW, Washington, DC 20008. E-mail: mdindo@gmail.com

evidence of capuchin monkeys matching the model they see in the case of opening an “artificial fruit” (Custance, Whiten, & Fredman, 1999; Dindo, Thierry, & Whiten, 2008), obtaining juice from a dispenser (Fragaszy & Visalberghi, 2004) and using a tool to extract food from a container (Fredman & Whiten, 2008). The two-action approach has similarly provided some evidence for copying in other monkey species (Voelkl & Huber, 2000). These various studies differ in the kinds of tasks that are presented, but one thing they have in common is that the two distinguishable techniques were always available to the subject. Therefore, when subjects consistently matched the demonstrator’s technique above what we would expect to see at chance levels, we know that the acquisition of the technique was most likely socially influenced. Nevertheless, several researchers have scrutinized these kinds of tests for their limitations in separating or distinguishing the specific learning mechanisms involved (Byrne, 2002; Tomasello & Call, 1997). For example, monkeys may be copying the model’s bodily action (bodily imitation) or the movements of the object (emulation). Indeed, one reason for the more recent positive evidence for copying in monkeys could be that several such learning processes may be at work at the same time. The copying abilities of monkeys may be supported by other learning mechanisms too, such as social facilitation and localized stimulus enhancement (Dindo, de Waal, & Whiten, 2009, but see Fragaszy & Visalberghi, 2004, for review). Given such different learning options, we might expect to see variation in when monkeys do and do not copy.

We suggest that the more recent studies shift our understanding forward, from asking simply “*Can* species *x* copy?” to investigating “*When* does species *x* copy?” In other words, the puzzling mixture of negative and positive findings on social learning in the literature may reflect not mysterious methodological variations among experimenters, but a learning system that is inherently conditional. Laland (2004) has recently distinguished a variety of ways in which animals may employ different ‘social learning strategies,’ or opt for individual learning, in ways adaptive to local circumstances. This might result in either positive or negative evidence of social learning according to the context.

Accordingly we have investigated social learning in capuchin monkeys using two different versions of an artificial foraging task (“artificial fruit”), one of which we predicted would provide more evidence of social learning because the *two-action* alternatives were more exclusive of each other in this case. We used a form of the two-action task called the bidirectional control procedure, in which the two alternatives are stripped down to opposing directions of movement in the apparatus. This was developed by Heyes and Dawson (1990) to study whether rats would copy the direction in which a conspecific pushed a pendulum lever to obtain food (see also Heyes, Jaldow, & Dawson, 1994). This particular experiment was later shown to be unexpectedly influenced by odor cues from the rat models (Mitchell, Heyes, Gardner, & Dawson, 1999), but it paved the way for later two-action experiments that demonstrated matching to a model in species including starlings, *Sturnus vulgaris* (Campbell, Hayes, & Goldsmith, 1999; Fawcett, Skinner, & Goldsmith, 2002), Japanese quail, *Coturnix japonica* (Akins & Zentall, 1996; Akins, Klein, & Zentall, 2002), pigeons, *Columba livia* (Klein & Zentall, 2003; Nguyen, Klein, & Zentall, 2005), budgerigars, *Melopsittacus undulates* (Heyes & Saggerson, 2002), gorillas, *Gorilla gorilla* (Stoinski, Wrate, Ure, & Whiten, 2001), and common marmosets, *Callithrix jacchus* (Bugnyar & Huber, 1997).

In our experiments, a small door panel could be moved up either the left or right arm of a V-shaped track. In Experiment 1, moving the panel up to either the left or right revealed a piece of food in a recess in the bottom of the V (see Figure 1a). This task bears some similarity to that used by Klein and Zentall (2003) with pigeons and Hopper, Lambeth, Schapiro, and Whiten (2008) with chimpanzees and children, where a panel could simply be slid either left or right to reveal food. Anticipating that the busy manipulations of capuchins might easily lead them to accidentally push both ways in such a task, we designed the V-shaped track, where sliding left or right also required upward movement, thus adding another element of effort to the task.

In Experiment 2, moving the same panel up further to the left revealed food in a recess at the top of that arm of the V, whereas moving it in the other direction revealed food at the top of the right arm. There was no food in the center. Whereas in Experiment 1, a small movement in the opposite direction to that an observer had

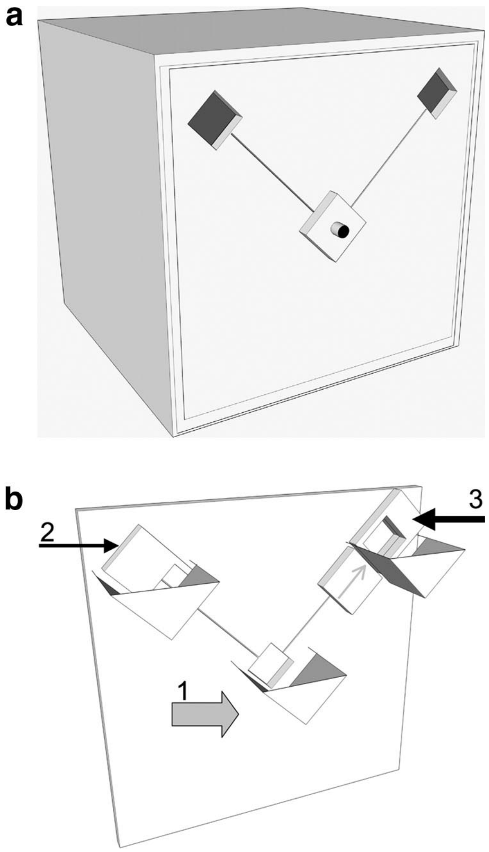

Figure 1. The foraging apparatus is shown here with the door resting in the center of the V-shaped track (1a). The door is covering the center recess, and the dark shaded squares are covered by panels, which obscure the top left and top right recesses (1b). In Experiment 1, only the center cup is baited (arrow 1), and pins prevent the door from pushing the panels (arrows 2 and 3). In Experiment 2, the pins are removed, allowing the door to push either panel upward and reveal food. Arrow 2 shows the panel in the closed position, and arrow 3 shows the panel being pushed open by the door.

witnessed could reveal the food, in Experiment 2, moving the panel further up the same arm as the model had done, toward the food goal location, made it increasingly less likely that the alternative action would be employed. We predicted that this degree of mutual exclusivity of actions in Experiment 2 would be associated with stronger evidence of social learning than the more fragile difference embodied in Experiment 1.

Experiment 1

Method

Subjects and housing. To assemble a substantial sample size, this experiment was conducted at two study sites, the Centre de Primatologie (CdP) in Strasbourg, France, and the Yerkes National Primate Research Center (Yerkes) in Atlanta, Georgia.

Subjects from the CdP were six male and six female brown capuchin monkeys (*Cebus apella*) ranging in age from 3 to 14 years (*Mdn* 5; mean 6.2). Subjects were selected from a colony of 20 individuals (six males, 11 females, and three infants) and were housed in a home enclosure measuring 33 m^2 indoors and 45 m^2 outdoors. The outdoor enclosure was divisible into three sections, and all tests were conducted in one 15 m^2 division outside with subjects having full access to that entire area. A visual barrier prevented nontest subjects from viewing test conditions.

Subjects at Yerkes were one male and three female brown capuchin monkeys from colony A, and one male and three female brown capuchin monkeys from colony B. Yerkes subjects ranged in age from 3 to 35 years (*Mdn* 22; mean 17.5). Colony A consisted of 15 monkeys (six males, nine females, 0 infants), and colony B consisted of 16 monkeys (four males, 10 females, two infants). Both groups were housed in the same building, and were visually but not acoustically separated from each other. The combined indoor/outdoor home areas measured 25 m^2 (A) and 31 m^2 (B) respectively. Tests were conducted in a mobile chamber (144 × 60 × 60 cm), which was located directly in front of the monkeys' indoor home area. This allowed for visual separation from future subjects. The separation procedure has been routinely used for several years and is documented in detail in de Waal (2000). The test chamber was divided with a mesh partition into two sections measuring 72 × 60 × 60 cm, allowing one model from each colony (A & B) to serve as a demonstrator to all subjects within his or her respective group without being displaced from the apparatus. Unlike the Yerkes colonies, the CdP subjects were not separated by a mesh partition, which meant that all test pairs had to be socially tolerant to allow observations in close proximity to the model. The limited number of subjects in the CdP colony and issues of social compatibility between certain models and observers meant that, in addition to two trained monkey models, one pilot-test subject and two observer subjects subsequently served as models to future observers. Therefore, the total number of subjects in this experiment was 22, with seven models, 12 observers, and five pilot-test subjects.

At both study sites, all tests were performed in less than 30 minutes; therefore a subject's separation from the colony was minimal. No subject was ever food or water deprived.

Apparatus (a)

The foraging apparatus was constructed from Lexan and measured 28 × 28 × 28 cm. The front panel of this apparatus had a V-shaped sliding track, with a small handle on a square panel at the bottom center of the V. The square panel at the bottom of the V obscured the view of a food cup. The square's round handle allowed subjects to move the panel by sliding it up-left or up-right to retrieve food from the center cup (see Figures 1 & 2). If the subject let go of the handle, the square panel fell back into the neutral, center position, and the hole became obscured again. For each trial, one piece of Coco-puffs cereal was placed in the cup behind the panel by the experimenter. Using one piece of cereal prevented scrounging by the observer or food sharing. The experimenter sat or stood behind the apparatus, with the subject viewing the front of the panel and the experimenter viewing the back of the panel. Each trial was defined by one food retrieval followed by the return of the door to the original (center) location.

CdP subjects accessed the apparatus through the 6.35 cm holes of the chain-link fence that surrounded their home enclosure. Yerkes subjects accessed the apparatus through 6.35 cm round holes in the Lexan test chamber. In both cases, subjects were able to extend their entire arm or arms through the respective barrier holes.

Procedure

Pilot tests. In order to establish if the apparatus was suitable for capuchin monkeys, five subjects were presented with the apparatus for pilot tests without any prior exposure to the apparatus nor any human or conspecific model to demonstrate the left or right slide technique. Pilot test subjects had 15 minutes, or 20 trials, in which to retrieve food from the center location only. We were interested to discover if they showed interest in the task, would approach it, if any would open it and if so, whether they

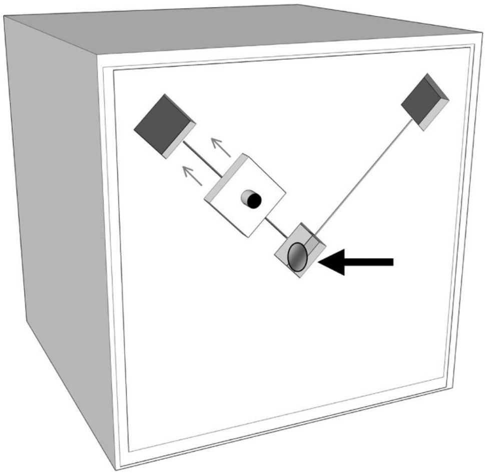

Figure 2. In Experiment 1, a square door, which moves along a V-shaped track, can be pushed either left or right to reveal food behind the door. This figure shows the Left Center (LC) method for moving the square left and revealing food in the center recess (noted by a black arrow). The shaded squares at the top left and top right of the V- track are inaccessible recesses and do not contain food in Experiment 1.

would confirm that both left and right pushing responses are feasible for these monkeys, and the artificial task thus clearly suitable for the experiment proper.

Model Training and Selection

CdP models. Two high-ranking males were selected as models for the left (LC) and right (RC) methods for uncovering food. High-ranking models were selected in order to avoid displacement at the apparatus by observer subjects.

Training consisted of three sessions of 20 trials each on three separate days. The experimenter demonstrated for the model twice, and then held the door open for the model. Once the model reached for the cereal piece, the door was released, requiring the model to hold it open while extracting the food from the hole.

Models were considered proficient for demonstration sessions after three sessions in which the model exclusively used the trained method. Due to rank and social compatibility issues, these two models were only compatible with subjects close in rank. Therefore, after their first session as a model, they had to be replaced by slightly lower-ranking models. Dindo et al. (2008) address the issue of model-observer compatibility in greater detail. The first observer subject in the RC group became the model for the second observer, and that second observer, in turn, became the model for the third observer subject in that group. In the LC group, a pilot-test subject was trained in the same manner as the original models on the "left" method. This model served as the model for the second and third observers.

Yerkes models. One monkey from each Yerkes group was trained as a model for the LC and RC methods. The LC model was the alpha-female of Group A, and the RC model was the beta-male of Group B. The lack of tolerance between one of the originally selected male CdP models and other observer subjects negatively affected viewing opportunities; therefore, when we selected models at Yerkes, we aimed to find models that were high-ranking and tolerant of others, regardless of their sex, which is why the alpha female was selected as the LC model. Both models were trained in the same way as the CdP models, with three days of 20 trials each. Because a mesh partition could be placed between models and observers, these two models were able to act as demonstrators to all three observers in their respective groups.

To avoid any site biases in results, the sample of monkeys at each site was split such that approximately half were allocated to each of the two 'two-action' experimental conditions.

Demonstration Sessions and Observer Tests

Each test consisted of two parts: (1) demonstration session and (2) observer test. At both study sites, the model demonstrated his or her method (LC or RC) to a naïve observer monkey for 40 trials. Each demonstration trial consisted of the model opening the door by sliding up left or up right and collecting one piece of cereal from the cup located behind the sliding door. Once the model let the door fall back into the center location of the V, the experimenter rebaited the cup with one piece of cereal.

At the CdP the subject had the opportunity to watch all 40 trials while standing next to the model. Subjects were free to move around the enclosure and to choose which side of the demonstrator to watch from. The subject also had the opportunity to explore the 15 m^2 enclosure instead of watching the demonstrations; therefore 40 trials were presented to ensure that at least 20 trials would be observed. At Yerkes, subjects were presented with the first 20 trials from behind the mesh divider ($<$60 cm from the model). This was done to ensure that they would have at least 20 trials to watch without displacement of (or by) the model. Although the observer had full view of the front of the apparatus, they were observing the first 20 trials from the left side of the model. Therefore, after 20 trials, the observer was given access to the other side of the mesh partition (alongside the demonstrator) in order to provide the same opportunity to view from both sides of the demonstrator, and also have the same level of proximity to the model as the CdP subjects had.

After the demonstration sessions (40 trials total), the apparatus was taken away from the model and presented to the observer subject. At the CdP, this involved moving the demonstrator to the adjacent home enclosure area. At Yerkes, the model and observer were once again separated by the mesh partition.

For the observer tests, subjects exchanged places with the model so that they were presented with the apparatus in the same location as where they witnessed the demonstration sessions. Subjects were given 20 trials in which to collect food, and both methods were always possible. The experimenter showed the subject a Coco-puff reward before placing the food in the collection cup. The cup was rebaited if a subject slid the door, collected the food, and then returned the door to the neutral position. If a subject were unable to open the device, the test ended after 15 minutes.

Data Collection and Analysis

All tests were recorded using a digital video camera. The first author dictated the method used, and whether or not the observer watched the demonstration. A subject was considered to be *watching* when he or she was facing the apparatus and model. This occurred either directly in front of the apparatus, or off to the side of the model and apparatus. In the more common case where the observer was with the model in front of the apparatus, the experimenter could assess watching by seeing the top of the capuchin's head. Although eye-gaze was not always visible to the experimenter, this also meant that the experimenter's gaze was not visible to the observer unless he or she was off to the side of the apparatus. When the observer was not in front of the apparatus, eye-gaze and body-orientation were visible to the experimenter. The experimenter looked directly ahead at the back of the apparatus, in order to rebait the cup for each trial, looking up at the observer when the model pushed the door. In these cases, the head orientation of the experimenter was toward the observer, and this orientation was toward the side the observer was located, rather than reflecting the side toward which the model had pushed. Furthermore, observations could be viewed and scored from the videotapes.

Tapes were coded (1) for the number of trials out of 40 in which the subject was considered watching and (2) for the number of left slides or right slides used to successfully gain food during the total 20 test trials (see Table 1). The latter has the advantage that coding was unambiguous for all cases where food was obtained. Kappa for the agreement of trials watched or not watched was 0.945, indicating strong agreement.

Table 1
Individual Results by Subject for Each Group in Experiments 1 and 2

Experiment 1

Left group

Subject	Percent trials observed (%)	Left-bias score (0–1)	Percent trials matched' (%)	Trial number of 1st match [1st mismatch]
Lulu	94	1.00	100	1 [x]
Winnie	72	1.00	100	1 [x]
Winter	77.5	0.75	75	1 [5]
Raven	100	0.90	90	2 [1]
Alila	76.7	0.95	95	1 [5]
Kinika	100	0.70	70	2 [1]

Right group

Subject	Percent trials observed (%)	Left-bias score (0–1)	Percent trials matched' (%)	Trial number of 1st match
Georgia	77.5	0.25	75	4 [1]
Snarf	95	0.00	100	1 [x]
Mango	100	0.10	90	1 [4]
Popeye	83	0.30	70	1 [12]
Paola	100	0.05	95	1 [4]
Olive	80	0.00	100	1 [x]

Experiment 2

Left group

Subject	Percent trials observed (%)	Left-bias score (0–1)	Percent trials matched' (%)	Trial number of 1st match
Lancey	50	0.00	0	x [1]
Nicole	85	0.40	40	2 [1]
Wilma	94.5	0.45	45	4 [1]
Wookie	75	0.90	90	2 [1]
Lucas	100	1.00	100	1 [x]
Ike	57	0.95	95	1 [6]

Right group

Subject	Percent trials observed (%)	Left-bias score (0–1)	Percent trials matched' (%)	Trial number of 1st match
Bias	60	0.65	35	3 [1]
Bravo	70	0.30	70	2 [1]
Goya	80	1.00	0	x [1]
Bailey	90	0.55	45	1 [2]
Star	100	0.25	75	1 [9]
Gretal	100	0.65	35	1 [4]

Note. The rate of observation is shown as a percentage of the total 40 demonstrations each subject observed. The left-bias score represents the amount of left actions performed during the subject's 20 trials, with a 0.00 representing no left actions and 1.00 representing all left actions. The 'percent trials matched' column shows the degree of fidelity to the model's method, and the last column specifies at which trial the subject first matched the behavior of the model and at which trial the subject used the opposite method than the model [shown in brackets]. An 'x' is put in the place of a trial number when subjects never matched or mismatched the group method.

Results

(a) Pilot Tests

All five pilot-test subjects interacted with the foraging apparatus by touching the front, top, and sides of the apparatus and by touching the handle to the door behind which food was obscured. Two subjects, an adult male and an adult female, never discovered the upward-slide movements necessary for retrieving food, despite handling the door of the apparatus. One adult female collected food using the LC method for 17 out of 20 total trials (85% left).

Another adult female and a juvenile male used the RC method for 20 and 15 trials out of 20, respectively (100% and 75% right). The discovery and use of both methods during pilot testing confirmed that the left and right pushing actions were both physically possible for capuchin monkeys, and therefore suitable for testing. In addition, however, the failure of two subjects suggested the task is not oversimple for capuchins.

(b) Demonstration Sessions

Each test subject was presented with one demonstration session consisting of 40 trials in which the model demonstrated either the LC or RC method for obtaining food from the foraging apparatus. Models exclusively demonstrated either the LC or the RC for all 40 trials, and subjects in both conditions and test sites were given the opportunity to watch from either side of the model in close proximity. Subjects in the LC group observed between 72% and 100% of the 40 trials (*Mdn* 86%, $n = 6$). Subjects in the RC group spent between 77% and 100% of the 40 (*Mdn* 89%, $n = 6$) trials observing the demonstrations (see Table 1). There was no significant difference between the LC and RC subjects in the time spent observing the model (Mann–Whitney Test, two-tailed, $U = 13{,}5$, $n_1 = 6$, $n_2 = 6$, $p = .462$).

(b) Test Sessions

After observing the demonstration session, each subject was presented with the foraging apparatus and was allowed to manipulate the device using either method for a total of 20 trials. Each subject's performance was coded L or R for the method used in each trial. A "left-bias" score was calculated for the number of left actions out of 20 that each subject performed using the equation, $N = L/(L + R)$. A score of 0 represented 0 out of 20 left slides (20 out of 20 right slides), and a score of 1 represented 20 out of 20 left slides (0 out of 20 right slides). A low score thus represented a right-bias, a high score represented a left-bias, and a score of 0.5 represented no bias (10 right and 10 left). The median score for the six LC subjects was 0.9 (range 0.7 – 1), whereas the six RC group subjects had a median left-bias score of 0.1 (range 0 – 0.3; see Table 1). A two-tailed Mann–Whitney Test showed a significant difference between the method scores of subjects in the LC versus RC groups ($U = 36$, $n_1 = 6$, $n_2 = 6$, $p = .005$). Further analysis determined that Experiment 1 subjects showed significant differences within the first five trials (Mann–Whitney Test, two-tailed, $U = 3$, $n_1 = 6$, $n_2 = 6$, $p = .015$), but not for the first trial alone (Binomial test: $p = .146$). There was no significant difference in performance scores between CdP and Yerkes subjects (Mann–Whitney Test, two-tailed, $U = 15.5$, $n_1 = 6$, $n_2 = 6$, $p = 0.75$).

In order to asses the overall copying trends in both LC and RC conditions, each trial was also coded as matching or nonmatching to reflect the number of trials out of 20 in which a subject's method corresponded with the method of the model. The median percent of matched behaviors for the 12 subjects (i.e., both groups) was broken down into five trial increments (1 to 5, 6 to 10, 11 to 15, and 16 to 20). This breakdown shows that a high copying fidelity was consistent throughout the 20 trials, with very little range in interquartile values by increment (see Figure 3). Only 3 of the 12 subjects did not use the modeled method in the first trial (see Table 1); however, these subjects continued to show a strong bias for the method they had observed and did not continue with the alternative method they had discovered, suggesting that the bias was not due to trial-and-error learning.

Experiment 2

Method

Subjects and housing. Experiment 2 was conducted entirely at the Yerkes National Primate Research Center. Subjects were

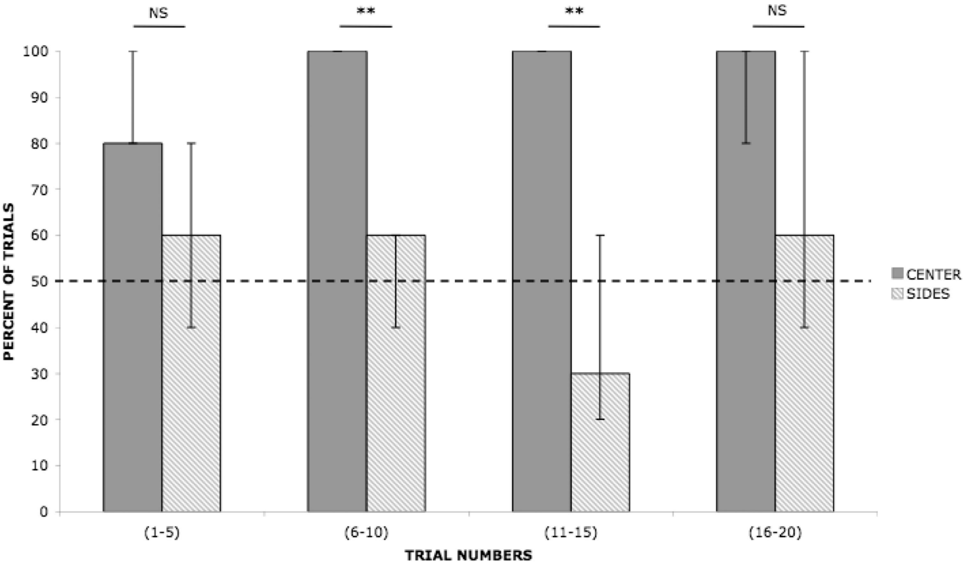

Figure 3. Median and interquartile ranges for "matched" behaviors in Experiment 1 (Center condition) and Experiement 2 (Sides condition) for Trials 1–5, 6–10, 11–15, and 16–20. Significant differences of $p < .005$ are marked with two stars.

three male and four female brown capuchin monkeys from colony A (Nuts group) and two male and five female monkeys from colony B (Bolts group). The subjects ranged between 3 and 35 years in age (*Mdn* 8; mean 12.9).

Tests were conducted in the same mobile test chamber as in Experiment 1 and the same separation procedure was employed.

Apparatus (b). The same foraging apparatus (see *apparatus* [*a*]) had two alternative locations for obtaining food: top-left end (TL) and top-right end (TR) of the V-track (see Figure 4).

In Experiment 2, the center square panel at the bottom of the V could be pushed up-left or up-right to retrieve food from cups in the top ends of the V. One piece of cereal was placed in each TL and TR cup prior to every trial, but only one food retrieval was permitted per trial. Each trial was defined by one food retrieval followed by the return of the door to the neutral (center) location. No food was placed in the center hole, and all subjects in Experiment 2 were naïve to the conditions of Experiment 1.

Model training and selection. The LC and RC models from Experiment 1 became the left-side (LS) and right-side (RS) models for Experiment 2.

Demonstration sessions and observer tests. The conditions for demonstration sessions and observer tests were the same as in Experiment 1, as were the data collection and coding processes.

Results

(a) Demonstration sessions. Each test subject was presented with one demonstration session consisting of 40 trials in which the model demonstrated either the LS or RS method for obtaining food from the foraging apparatus. Subjects in the LS group observed between 50% and 100% of the 40 trials (*Mdn* 80%, $n = 6$). Subjects in the RS group observed between 60% and 100% of the 40 trials (*Mdn* 85%, $n = 6$) observing the demonstrations (see Table 1). There was no significant difference between the LS and RS subjects in the time spent observing the model (Mann–Whitney Test, two-tailed, $U = 14{,}5$, $n_1 = 6$, $n_2 = 6$, $p = .519$). No significant difference was found between observation rates of Experiment 1 and 2 subjects (Mann–Whitney, two-tailed, $U = 54.5$, $n_1 = 12$, $n_2 = 12$, $p = .327$).

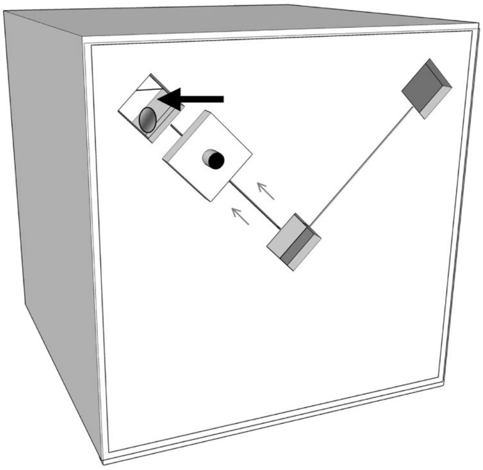

Figure 4. In Experiment 2, the top Left Side (LS) and top Right Side (RS) recesses contain food and the center recess is empty. The apparatus is shown here when the square door is pushed from the center position to the left, thus pushing the panel that covers the top left recess (as noted by a black arrow).

(b) Test sessions. As in Experiment 1, each subject's performance was coded L or R for the method used and a left-bias score was calculated for the number of left actions out of 20 that each subject performed using the equation $N = L/(L + R)$. The median score for the six LS subjects was 0.7 (range 0–1) and the six RS group subjects had a median left-bias score of 0.6 (range 0.25–1; see Table 1). Unlike Experiment 1, subjects in Experiment 2 did not show a significant bias during the 20 total trials toward the method they observed ($U = 16.5$, $n_1 = 6$, $n_2 = 6$, $p = .818$). Experiment 2 subjects did not show significant differences in the first 5 trials (Mann–Whitney Test, two-tailed, $U = 12.0$, $n_1 = 6$, $n_2 = 6$, $p = .485$) or in the first trial (Binomial test: $p = .774$).

In order to assess the overall copying trends in both LS and RS conditions, subject trials in both LS and RS groups were scored as matching or nonmatching by trial for all 20 trials of their respective test. The percent of trials that matched the behavior of the model were again broken down by Trials 1 to 5, 6 to 10, 11 to 15, and 16 to 20 in order to distinguish when fidelity to the modeled method was strongest. The median and interquartile ranges for all 12 subjects were calculated for these intervals and reported alongside Experiment 1 results (see Figure 3). Subjects showed no significant difference in copying behavior in the first trial of Experiment 1 (Mann–Whitney Test, two-tailed, $U = 48.0$, $n_1 = 12$, $n_2 = 12$, $p = .105$), nor was there a significant difference in the number of matched behaviors in the first five trials between Experiments 1 and 2 (Mann–Whitney Test, two-tailed, $U = 46.0$, $n_1 = 12$, $n_2 = 12$, $p = .121$). Significant differences in the level of copying (i.e., median matched behaviors) become apparent when comparing Trials 6–10, and 11–15, but not for the last Trials 16–20 (Mann–Whitney, two-tailed (6–10), $U = 17.5$, $n_1 = 12$, $n_2 = 12$, $p = .001$; Mann–Whitney, two-tailed (11–15), $U = 18.5$, $n_1 = 12$, $n_2 = 12$, $p = .001$; Mann–Whitney, two-tailed (16–20), $U = 46.0$, $n_1 = 12$, $n_2 = 12$, $p = .101$).

Figure 3 shows the clear trend for copying in Experiment 1 relative to Experiment 2, contrary to our original prediction. This difference in copying might be explicable in part by variations in copying fidelity early in the first few trials, that is, at which trial the first matching, and nonmatching responses occurred (see Table 1). However, there is no significant difference between Experiment 1 and Experiment 2 in the first trial number in which matching or nonmatching occurred (1st matched trial: Mann–Whitney, two-tailed, $U = 45$, $n_1 = 12$, $n_2 = 12$, $p = .08$; 1st unmatched trial: Mann–Whitney, two-tailed, $U = 41.5$, $n_1 = 12$, $n_2 = 12$, $p = .07$; Table 1 x-values were given the value 20).

Discussion

Following the rationale explained in our introduction, we had predicted that fidelity of social learning would be greater in Experiment 2 than Experiment 1. However, we found the reverse. Only in Experiment 1 was there evidence of copying the direction for pushing. Indeed, the fidelity in Experiment 1 was strong, extending through the whole sequence of 20 trials in both the Left Center (LC) and Right Center (RC) conditions. More generally, the results of Experiment 1 are important in that they extend the growing evidence that monkeys may, at least in certain contexts, copy with more fidelity than previously thought (Bonnie & de Waal, 2007; Dindo et al., 2008; Fredman & Whiten, 2008; Price & Caldwell, 2007; Rigamonti, Custance, Previde, & Spiezio, 2005; Voelkl & Huber, 2007). Whether this copying involves bodily imitation is another matter, and beyond the scope of our study. Mere stimulus enhancement appears inadequate to explain the results, because both actions were focused on the same object, the panel, and because if stimulus enhancement were influential, a stronger effect might have been expected in Experiment 2, which did not occur. The copying we documented might have involved copying the bodily actions of the model (bodily imitation) or the movements of the panel (emulation or object movement reenactment) or some mixture of these; further experiments such as "ghost" manipulations, in which the panel moves without a model pushing it (Hopper et al., 2008), will be needed to differentiate such mechanisms.

By contrast with Experiment 1, Experiment 2 revealed only a weak and nonsignificant initial trend consistent with copying; the monkeys in Experiment 2 explored both food locations through the 20 trials. One possible explanation to be considered could be a lack of attention to the demonstrator in Experimenter 2 compared with Experiment 1. It was therefore important that we document attention in our two experiments. However, we found that the median percentage observation time was similar in both experiments (86% and 89% in Experiment 1, 80% and 85% in Experiment 2). These high levels of attention cannot explain the lack of matching behavior in Experiment 2. Instead, what appeared to happen in Experiment 2 was that once monkeys explored both directions of movement, and once they discovered that food might be available in either location at the ends of the V, they maintained a steady tendency to examine both, across the 20 trials.

Was it, then, the case that the monkeys anticipated that the second location might hold food, in Experiment 2? Evidence for that possibility would be that they switched between the matching response and a nonmatching one earlier in Experiment 2 than in Experiment 1. However, that was not the case (see Table 1): in Experiment 2, seven monkeys already tried the nonmatching response in the first five trials, but as many as seven also did so in Experiment 1. In Experiment 2, 11/12 monkeys explored the nonmatching option, but so did 8/12 in Experiment 1. Thus it appears that despite capuchin monkeys' capacity and motivation for social learning revealed in Experiment 1, this species also maintains a motivation to take the risk of occasionally exploring alternatives, a strategy that may well be adaptive under natural conditions. This "exhaustive search" style (Janson, 2000) has been attributed to capuchins both in the wild (DeLillo, Visalberghi, & Aversano, 1997), as well as in captive experiments that require searching for food (Basile, Hampton, Suomi, & Murray, 2009; Paukner Anderson, & Fujita, 2006). Given that in Experiment 2, this led to discovery of the two possible food locations, we suggest that these monkeys were possibly pursuing an adaptive strategy, in continuing to check both locations rather than stick to the direction of push used by the model.

However, this leads us back to Experiment 1, to question why the monkeys did not also push in both directions, given that here, too, they had discovered doing this provided equivalent rewards. We conclude that capuchins' copy conditionally, and our study suggests the rules "when alternative options do not gain more, or a different, reward, copy what others are doing" (Experiment 1), whereas "when alternative options yield rewards at different locations, keep checking both, irrespective of whichever others prefer" (Experiment 2). Given that the results went against our original hypothesis, it is important to acknowledge that this attempt to explain them is post hoc and in the nature of a further hypothesis to drive future research. However we think it plausible that such social learning rules, could be adaptive strategies, of the kind that Laland (2004) urged researchers to search for.

It is also possible that this study may help explain some past controversies over whether primates do or do not imitate, as our two experiments show us that capuchin monkeys may use different strategies under different contexts. Our results bring the monkey findings into a closer conjunction with recent studies with apes, human children, and dogs that have demonstrated marked context sensitivity in the occurrence of imitation (Buttelmann, Carpenter, Call, & Tomasello, 2007; Gergely, Egyed, & Kiraly, 2007; Horner & Whiten, 2005; Range, Viranyi, & Huber, 2007; Schweir, van Maanan, Carpenter, & Tomasello, 2006). However, it does not follow that the rules employed by the capuchins here embody the kind of "rational copying" claimed by these other studies. Rather, what our results show most importantly is that monkeys' social learning can be similarly context dependent. It seems that our principal research question should no longer be, "*Do* monkeys copy the actions of others?" but instead "*When* do monkeys copy, or not, and *why*?"

References

Aisner, R., & Terkel, J. (1992). Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus. Animal Behaviour, 44,* 327–336.

Akins, C. K., Klein, E. D., & Zentall, T. R. (2002). Imitative learning in Japanese quail (*Coturnix japonica*) using the bidirectional control procedure. *Animal Learning and Behavior, 30,* 275–281.

Akins, C. K., & Zentall, T. R. (1996). Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *Journal of Comparative Psychology, 110,* 316–320.

Basile, B. M., Hampton, R. R., Suomi, S. J., & Murray, E. A. (2009). An assessment of memory awareness in tufted capuchin monkeys (*Cebus apella*). *Animal Cognition, 12,* 169–180.

Bonnie, K. E., & de Waal, F. B. (2007). Copying without rewards: Socially influenced foraging decisions among brown capuchin monkeys. *Animal Cognition, 10,* 283–292.

Bugnyar, T., & Huber, L. (1997). Push or pull: An experimental study on imitation in marmosets. *Animal Behaviour, 54,* 817–831.

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science, 10,* F31–F38.

Byrne, R. W. (2002). Imitation of novel complex actions: What does the evidence from animals mean? *Advances in the Study of Behavior, 31,* 77–105.

Campbell, F. M., Heyes, C. M., & Goldsmith, A. R. (1999). Stimulus learning and response learning by observation in the European starling, in a two-object/two-action test. *Animal Behaviour, 58,* 151–158.

Custance, D., Whiten, A., & Fredman, T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus* apella). *Journal of Comparative Psychology, 113,* 13–23.

Dawson, B. V., & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour, 13,* 470–474.

DeLillo, C., Visalberghi, E., & Aversano, M. (1997). The organization of exhaustive searches in a patchy space by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 111,* 82–90.

de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour, 60,* 253–261.

Dindo, M., de Waal, F. B. M., & Whiten, A. (2009). Social facilitation of exploratory foraging behavior in capuchin monkeys (*Cebus apella*). *American Journal of Primatology, 71,* 419–426.

Dindo, M., Thierry, B., & Whiten, A. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings in Biological Sciences, 275,* 187–193.

Fawcett, T. W., Skinner, A. M. J., & Goldsmith, A. R. (2002). A test of imitative learning in starlings using a two-action method with an enhanced ghost control. *Animal Behaviour, 64,* 547–556.

Fragaszy, D., & Visalberghi, E. (2004). Socially biased learning in monkeys. *Learning & Behavior, 32,* 24–35.

Fredman, T., & Whiten, A. (2008). Observational learning from tool using models by human-reared and mother-reared capuchin monkeys (*Cebus apella*). *Animal Cognition, 11,* 295–309.

Gergely, G., Egyed, K., & Kiraly, I. (2007). On pedagogy. *Developmental Science, 10,* 139–146.

Heyes, C. M., & Dawson, G. R. (1990). A demonstration of observational-learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology Section B-Comparative and Physiological Psychology, 42,* 59–71.

Heyes, C. M., Jaldow, E., & Dawson, G. R. (1994). Imitation in rats: Conditions of occurrence in a bidirectional control paradigm. *Learning and Motivation, 25,* 276–287.

Heyes, C. M., & Saggerson, A. (2002). Testing for imitative and non-imitative social learning in the budgerigar using a two-object/two-action test. *Animal Behaviour, 64,* 851–859.

Hinde, R. A., & Fisher, J. (1951). Further observations on the opening of milk bottles by birds. *British Birds, 44,* 393–396.

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through "ghost" conditions. *Proceedings of the Royal Society B: Biological Sciences, 275,* 835–840.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition, 8,* 164–181.

Janson, C. (2000). Spatial movement strategies: Theory, evidence, and challenges. In S. Boinski & P. A. Garber (Eds.), *On the move. How and why animals travel in groups* (pp. 165–203). Chicago: The University of Chicago Press.

Klein, E. D., & Zentall, T. R. (2003). Imitation and affordance learning by pigeons (*Columba livia*). *Journal of Comparative Psychology, 117,* 414–419.

Laland, K. N. (2004). Social learning strategies. *Learning & Behavior, 32,* 4–14.

Laland, K. N., & Galef, B. G. (Eds.). (2009). *The question of animal culture.* Cambridge, MA: Harvard University Press.

Leca, J. B., Gunst, N., & Huffman, M. A. (2007). Japanese macaque cultures: Inter- and intra-troop behavioural variability of stone handling patterns across 10 troops. *Behaviour, 144,* 251–281.

Lefebvre, L. (1986). Cultural-diffusion of a novel food-finding behavior in urban pigeons—an experimental field-test. *Ethology, 71,* 295–304.

Lefebvre, L., & Giraldeau, L.-A. (1994). Cultural transmission in pigeons is affected by the number of tutors and bystanders present. *Animal Behaviour, 47,* 331–337.

Mitchell, C. J., Heyes, C. M., Gardner, M. R., & Dawson, G. R. (1999). Limitations of a bidirectional control procedure for the investigation of imitation in rats: Odour cues on the manipulandum. *Quarterly Journal of Experimental Psychology: Section B, 52,* 193–202.

Moura, A. C. A. (2007). Stone banging by wild capuchin monkeys: An unusual auditory display. *Folia Primatologica, 78,* 36–45.

Nguyen, N. H., Klein, E. D., & Zentall, T. R. (2005). Imitation of a two-action sequence by pigeons. *Psychonomic Bulletin & Review, 12,* 514–518.

Ottoni, E. B., & Mannu, M. (2001). Semi-free ranging tufted capuchin monkeys (*Cebus* apella) spontaneously use tools to crack open nuts. *International Journal of Primatology, 22,* 347.

Paukner, A., Anderson, J., & Fujita, K. (2006). Redundant food searches by capuchin monkeys (*Cebus apella*): a failure of metacognition. *Animal Cognition, 9,* 110–117.

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., et al. (2003). Social conventions in wild white-faced capuchin monkeys—Evidence for traditions in a neotropical primate. *Current Anthropology, 44,* 241–268.

Price, E., & Caldwell, C. A. (2007). Artificially generated cultural variation between two groups of captive monkeys, *Colobus guereza kikuyuensis*. *Behavioural Processes, 74,* 13–20.

Range, F., Viranyi, Z., & Huber, L. (2007). Selective imitation in domestic dogs. *Current Biology, 17,* 868–872.

Rigamonti, M. M., Custance, D. M., Previde, E. P., & Spiezio, C. (2005). Testing for localized stimulus enhancement and object movement reenactment in pig-tailed macaques (*Macaca* nemestrina) and young children (*Homo sapiens*). *Journal of Comparative Psychology, 119,* 257–272.

Schweir, C., van Maanan, C., Carpenter, C., & Tomasello, M. (2006). Rational imitation in 12-month-old infants. *Infancy, 10,* 303–311.

Stoinski, T. S., Wrate, J. L., Ure, N., & Whiten, A. (2001). Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *Journal of Comparative Psychology, 115,* 272–281.

Terkel, J. (1996). Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In C. M. Heyes & B. G. Galef Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 17–48). London: Academic Press.

Tomasello, M., & Call, J. (1997). *Primate cognition.* New York: Oxford University Press.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., et al. (2003). Orangutan cultures and the evolution of material culture. *Science, 299,* 102–105.

Visalberghi, E., & Fragaszy, D. M. (2002). Do monkeys ape? Ten years after. In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 471–500). Cambridge, MA: MIT Press.

Visalberghi, E., & Munkenbeck-Fragaszy, D. (1990). Do monkeys ape? In T. S. Parker & K. R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 247–273). Cambridge, U.K.: Cambridge University Press.

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour, 60,* 195–202.

Voelkl, B., & Huber, L. (2007). Imitation as faithful copying of a novel technique in marmoset monkeys. *PLOS One, 2*(7), e611 (online 1–5).

Warner, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish. *Nature, 335,* 719–721.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (1999). Cultures in chimpanzees. *Nature, 399,* 682–685.

Whiten, A., & van Schaik, C. P. (2007). The evolution of animal "cultures" and social intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362,* 603–620.

Received May 29, 2008
Revision received September 28, 2009
Accepted October 6, 2009 ■