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RESEARCH ARTICLE

When and How Well Can Human-Socialized Capuchins Match Actions Demonstrated by a Familiar Human?

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Capuchin monkeys have provided uneven evidence of matching actions they observe others perform. In accord with theories emphasizing the attentional salience of object movement and spatial relationships, we predicted that human-reared monkeys would better match events in which a human demonstrator moved an object into a new relation with another object or surface than other kinds of actions. Three human-reared capuchins were invited repeatedly by a familiar human to perform a fixed set of actions upon objects or upon their bodies, using the ‘‘Do as I do’’ procedure. Actions directed at the body were matched less reliably than actions involving objects, and actions were matched best when the monkey looked at the demonstration for at least 2 sec and performed its action within a few seconds after the demonstration. The most commonly matched actions were those that one monkey performed relatively often when the experiment began. One monkey partially reproduced three novel actions (out of 48 demonstrations), all three involving moving or placing objects, and two of which it also performed following other demonstrations. These findings contribute convergent evidence that capuchin monkeys display social facilitation of activity, enhanced interest in particular objects and emulation of spatial outcomes. This pattern can support the development of shared manipulative skills, as evident in traditions of foraging and tool use in natural settings. The findings do not suggest that human rearing substantively altered capuchins’ ability or interest in matching the actions of a familiar human, although visual attention to the human demonstrator may have been greater in these monkeys than in normally reared monkeys. Am. J. Primatol. 73:643–654, 2011.

Key words: visual attention; movement; imitation; spatial cognition; human rearing

INTRODUCTION

The possibility that monkeys and apes imitate actions, and acquire new skills in this way, has received a great deal of interest from comparative behavioral scientists, not least because learning from observation is thought to be a significant component of culture [e.g. Hurley & Chater, 2005]. Skeptical statements that empirically sound evidence for imitative capacities was not available for monkeys or apes [Visalberghi & Fragaszy, 1990] prompted studies that have now provided experimental evidence that all the great apes can, under certain conditions, reproduce novel actions demonstrated to them by a familiar human [Buttelmann et al., 2007; Call, 2001; Custance et al., 1995; Horner & Whiten, 2005; Miles et al., 1996; Myowa-Yamakoshi & Matsuzawa, 2000; Stoinski et al., 2001; Tomasello et al., 1993; Whiten et al., 1996]. In all studies reporting positive results, the subjects developed a strong emotional attachment to humans and saw a familiar human demonstrator performing the actions they subsequently reproduced. Rearing in a human environment or by human caretakers has been posited to have long-lasting effects on the nonhuman individual’s attention toward familiar humans, and possibly affecting other aspects of its evaluation of human behavior [Call & Tomasello, 1996; Furlong et al., 2008; Gomez, 1996; Russon, 1996]. Human-rearing may also facilitate imitation through repeated exposure to objects and the ways that humans handle them [Buttelmann et al., 2007; Custance et al., 1999; Whiten et al., 1996]; see Bering, 2004 for an alternative hypothesis]. Studies with other species provide support for the idea that human rearing promotes matching actions

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demonstrated by humans [see Józef et al., 2006; Moore, 1992 for dogs and an African Grey parrot, respectively].

Attention toward humans by nonhuman primates may also be directly affected by training. Kumashiro et al. [2003] showed that Japanese monkeys trained to achieve joint attention with humans exhibited ''natural imitation'' of a variety of actions, including tongue protrusion, touching various objects and performing actions on an object (separating a piece of cotton into two pieces, for example). Unfortunately, these authors did not report how the monkeys in their experiment were reared or their ages at the time of testing.

Aside from Kumashiro et al.'s [2003] study, attempts to demonstrate imitation of novel actions in normally reared monkeys employing monkey observer/human demonstrator paradigms similar to those employed with apes have generally failed [e.g. Mitchell & Anderson, 1993; for review see Visalberghi & Fragaszy, 1990, 2002; Whiten & Ham, 1992]. Interpretation of these studies has always been muddied by the possibility that rearing differences, rather than phylogenetic differences, were responsible for the monkeys' failure to imitate a human demonstrator [see Call & Tomasello, 1996 for a similar view]. Custance et al. [1999] and Fredman and Whiten [2008] focused on a more promising comparison group, human-reared capuchin monkeys. In Custance et al.'s paradigm, capuchin monkeys watched a human opening a box containing food. While there were varying degrees of reproduction by the subjects, the authors state that the monkeys were, at the very least, re-enacting the movement of the object. Fredman and Whiten [2008] reported that human-reared capuchins were more likely to use a specific technique with a tool (to poke or to lever) demonstrated to them by a human to open a box than were mother-reared monkeys that observed a conspecific demonstrator using one of the two techniques. This latter group was, however, more likely to open the box than a control group that saw no demonstrator, indicating a positive role for conspecific demonstrators, although they had a less specific effect on action than a human demonstrator.

Factors other than social circumstance of early experience also impact the probability that apes will reproduce an action event. Although chimpanzees and orangutans have sometimes matched gestures directed at the body [Call, 2001; Custance et al., 1995; Miles et al., 1996; Russon & Galdikas, 1993], chimpanzees at least are thought to be more likely to reproduce events in which an object moves directionally toward a new location, or into a new relation with another object or surface than actions that lack this structure [Myowa-Yamakoshi & Matsuzawa, 1999, 2000].

Overall, it seems that apes and monkeys are more likely to match actions with objects than actions without objects. We think this is an important clue about how matching can arise, particularly in circumstances where the action itself produces no obvious beneficial outcome [as in the ''Do as I do'' paradigm; see also Guillaume, 1971]. We propose that the particular spatiotemporal structure of the events that an observer sees performed, and that it subsequently may perform itself, directly impacts the probability of matching [see also Topál et al., 2006; for an opposing view, Subiaul, 2007]. Actions with objects may produce a long-lasting change in the spatial relation between an object and a surface or another object, as when an actor places an object into a container and leaves it there. These kinds of actions are more likely to be matched than actions that do not produce an outcome persisting after the action is completed (for example, a gesture toward one's own body). Moreover, naïve individuals' attention may intrinsically be more drawn to movements of objects than of actors, as suggested by Csibra and Gergely [2006] and by Guillaume [1971] for human infants.

To the extent that faithfully matching an action performed by another depends upon observation of the entire action sequence, sustained visual attention is a critical precondition. Studies with wolf pups [Virányi et al., 2007] and chimpanzees [Buttelmann et al., 2007] support the view that human rearing impacts the organization of visual attention in nonhuman animals. To the extent that human rearing increases sustained visual attention to a human actor, hand-reared nonhuman primates should be better than their normally reared counterparts at behaviorally matching actions demonstrated by a human observer. In any case, direct measurements of visual attention could help to interpret performance in studies of behavioral matching.

We report here a study with three human-reared tufted capuchins (*Cebus apella*) exposed to a familiar human demonstrator modeling familiar and novel actions. The monkeys were hand-reared as part of a program seeking to determine the value of tufted capuchins as trained aides to quadriplegic humans (Programme d'Aide Simienne aux Tetraplégiques; hereafter, PAST and Centre National de la Recherche Scientifique, CNRS, France). Our study largely replicates the design and methods of Custance et al.'s [1995] study with nursery-reared chimpanzees. In Custance et al.'s study, two young chimpanzees were first taught to match 15 familiar actions involving a gesture or action with a body part when these were demonstrated by the human experimenter. When they were reasonably proficient at this task, 48 novel actions were added into the stream of familiar actions the subjects were asked to match. The novel actions included such items as lip smacking, clapping their hands and placing one hand on the knee. The two young chimpanzees were able to reproduce 17 and 18, or 37.5%, of the modeled novel actions with moderate accuracy or better.

Capuchins manipulate objects frequently in foraging and in captive situations, and routinely combine objects with substrates or other objects [Fragaszy & Adams-Curtis, 1991; Fragaszy & Boinski, 1995; Fragaszy et al., 2004a]. They appear to have particular interest in producing certain kinds of spatial relations between objects and surfaces [Fragaszy & Cummins-Sebree, 2005]. We included actions combining objects or acting on a substrate in the demonstrated repertoire for our capuchin subjects on the expectation that these actions would be intrinsically interesting to the monkeys and that actions that occur with no reference to an external object (gestures) should hold less interest for them. Accordingly, we used actions performed on the body, as did Custance et al. [1995], but we specified additional classes of actions based upon the involvement of a substrate, an external object, or an object/substrate combination in the demonstrated action.

We also evaluated the quality of the monkeys' response to the demonstrated action in relation to their degree of visual attentiveness to the demonstrator and their latency to respond. We expected that longer durations between demonstration and commencement of response would be associated with a poorer quality of matching by the capuchins.

METHODS

Design

In the first phase (Training), subjects were asked to ''do this'' after the experimenter demonstrated a familiar action to the subject. Sixteen actions were included in the training demonstration set (Table I). Actions were distributed among four categories: actions to own body, to a substrate, to an object or combining an object and substrate. A familiar human demonstrated the actions to the subject 5 days per week, once each day, in two or more sessions lasting 6–7 min each.

The most cooperative subject advanced to the Experimental phase, in which every fourth action was novel. Novel actions were selected randomly and without replacement from among the list of 16 actions shown in Table I. Familiar actions were selected equally from all four categories of action. Each novel action was demonstrated three times (i.e. we completed three replications of the full series of novel actions, together with a much large number of familiar actions).

The research protocol was conducted under the auspice of PAST. All aspects of management and experimental protocol were approved by the authorizing governmental entities in France concerning the ethical treatment of nonhuman primates. The study was conducted at the Centre Mutaliste de Rééducation et Réadaptations Foncionnelles, Kerpape-L'Orient, France, in 1995–1996. The rearing and training program for monkeys participating in PAST is more fully described in Deputte and Busnel [1997]. This work was conducted in accord with institutional and national regulations concerning the humane treatment of animals in research and was approved by the research review board of the Station Biologique de Paimpont, CNRS, and was in compliance with the

TABLE I. Actions Demonstrated During the Training Phase and the Experimental Phase

A. Training Phase
Category 1.1—Combination of two objects
  1.1.1—Pushes a stick through a hole in the vertical wooden pole
  1.1.2—Puts a ring around a vertical wooden pole
  1.1.3—Puts a ring into a plastic box
  1.1.4—Puts a book on top of a plastic box
Category 1.2—Actions on one object involving manipulations on that object or its use on a surface
  1.2.1—Rubs the table with a stick
  1.2.2—Hits a surface with a ring
  1.2.3—Unzips a zipper
  1.2.4—Opens a book
Category 1.3—Actions on the subject's own body
  1.3.1—Rubs own chest
  1.3.2—Puts own wrist on mouth
  1.3.3—Scratches the head with one hand
  1.3.4—Rubs own eyes with one hand
Category 1.4—Actions performed with a body part on a surface or an object
  1.4.1—Rubs a surface with one hand
  1.4.2—Slaps a surface with one hand
  1.4.3—Puts a finger within the hole of the vertical wooden pole
  1.4.4—Puts a ring on the mouth, with or without actual bite
B. Novel actions demonstrated during the Experimental Phase
Category 2.1—Combination of 2 objects
  2.1.1—Fits a notched block onto another notched block
  2.1.2—Twists a screw with a screwdriver
  2.1.3—Hits a particular note of a xylophone with a wooden stick (the particular note has a unique color)
  2.1.4—Pushes a stick through a tube opened at both ends
Category 2.2—Actions on one object involving manipulations on that object or its use on a surface
  2.2.1—Turns a crank
  2.2.2—Folds a sheet of paper
  2.2.3—Makes a loop with a string
  2.2.4—Turns a wooden screw with one hand
Category 2.3—Actions on the subject's own body
  2.3.1—Puts both hands on top of the head
  2.3.2—Crosses arms
  2.3.3—Puts both hands behind the back
  2.3.4—Claps hands
Category 2.4—Actions performed with a body part on a surface or an object
  2.4.1—Puts the forearms on the table and crosses hands
  2.4.2—Hits the table with one fist
  2.4.3—Puts head on the table
  2.4.4—Puts an elbow on the table and supports the head with the corresponding hand

American Society of Primatologists' Principles for the Ethical Treatment of Primates.

Subjects

Three young adult (4.5 years) female tufted capuchins (*Cebus apella*), Bara, Corsen and Cosig, participated in the experiment. These monkeys were raised in human families from 12 to 16 weeks of age until their arrival at the laboratory at 4 years of age. The monkeys had been housed individually in a group colony room in the laboratory for one month prior to the start of testing, but spent at least 4 hr of each day interacting with humans outside the cage in a home-like setting. During most of this period they were being trained to follow voice and other forms of commands for their future function as aides for quadriplegic humans. They continued this training during their participation in this experiment.

Apparatus

We used two identical sets of objects in the Training phase, one set for the experimenter to use in giving demonstrations of actions to be replicated, and one set for the monkeys' use. Four objects, novel to the subject at the start of testing, were mounted on a board (50 cm × 25 cm) including (a) a wooden pole (11 cm × 4 cm), mounted vertically, with a hole (1.2 cm diameter) in the top; (b) a plastic box (11 cm × 8.5 cm × 7.5 cm); (c) a zipper (15 cm long) sewn into cloth attached to the board; and (d) two wooden planks colored distinctively with paint, one white square (16 cm × 16 cm × 2 cm) and one red circle (12 cm diameter × 2 cm). Several loose objects were also presented on the board: a metal ring (5 cm diameter), a wooden stick (17.5 cm × 1 cm) and a "book" (two boards, each 17.5 cm × 13.5 cm, connected by hinges). The objects were available to the monkey only during testing periods. The monkeys had encountered sticks, rings and sturdy books previously, but these particular exemplars were novel. All objects were presented to subjects in each test session on a rolling table, at the same height as the table surface on which the monkey was asked to remain during testing.

During the Experimental phase, we fixed new objects on the table along with the familiar ones. The new objects included (a) a wooden tube, 8 cm × 4 cm, mounted vertically, and with a 1.2 cm hole drilled horizontally through the middle; (b) a toy xylophone with three sounding bars (16 cm × 11 cm × 6 cm); (c) a vertically mounted wooden panel (16.5 cm × 8.5 cm) with a screw (2.5 cm diameter shaft) loosely threaded through the center; (d) a wooden block (15 cm × 5 cm × 3.5 cm) with a center notch 5.5 cm wide; and (e) a crank attached to a base. The handle of the crank extended in an *L* shape 11.5 cm and 6.5 cm from the base, and turned easily in both directions. A screwdriver (10 cm long) and a second wooden block, identical to the one mounted on the table and notched to fit into it, appeared loose on the table, along with the familiar stick, ring, book and string. The monkeys had not seen or touched the objects prior to the start of testing.

Procedure

Testing occurred while the monkey moved freely within a large room furnished with chairs, TV set and so forth, which was used for training the monkeys to perform actions to help their human companions. The experimental testing table was positioned in an open space in this room. To begin a session, the monkey was called to the testing area. When it was seated and calmly facing the demonstrator (seated across the table 1 m away), the demonstrator said, "(Name), watch," and demonstrated the action on the objects in front of her, or on her body. Then the demonstrator said, "(Name), do it," while pushing the subject's object set toward the subject. The subject was given 30 sec to perform any action (see Fig. 1). Verbal praise was given for each action judged to be an attempt to follow the demonstrator's instruction. After an attempted match, or at the end of 30 sec, if no relevant action had been observed, the experimenter started again by repositioning the monkey and proceeding with the next action from a predetermined randomized order of all actions. A different randomized order for actions was used each test day. From time to time, between demonstrations, the subject was given a raisin to maintain its cooperative attitude. The subject was expressly not rewarded with food for any particular action following demonstrations, but

Fig. 1. A monkey acts on the zipper after watching a human unzip the zipper.

for a general attitude of participation, as consistent with the training procedures the subjects experienced during their training to become helpful to human companions. The demonstrator was the trainer who worked with the subject intensively on a daily basis outside the testing context.

We began by demonstrating actions with an object or combining an object with a substrate. After 20 sessions for Cosig and 64 for Bara, actions on the body or involving the body and a substrate were added to the training set. We added these actions later because we wanted subjects to be experienced in the testing format before we asked them to do something that we expected would be difficult for them. Corsen received only demonstrations of the actions with objects and combining objects and substrates. Due to disinterest in the task, she did not participate in further testing. After these ''training'' sessions, Cosig and Bara completed 20 sessions with eight body and substrate actions intermixed with eight actions involving objects and objects combined with the substrate. Cosig subsequently completed three replications of each of the 16 novel actions (48 trials total), together with an additional 184 familiar actions (all 16 of those demonstrated previously, 11 or 12 times each).

A video camera placed behind the demonstrator recorded the demonstrator's voice (but did not include a view of her actions) and the subject. In a first pass through the video records, the person who conducted the testing (C.H.) scored which object the monkey contacted, latency to act (in seconds), visual attentiveness to the demonstrator (on a four-point scale; see Table II) and degree of match to the demonstrated behavior (also on a four-point scale; see Table III). Latency was scored as the duration from the voice signal, ''(Name), do it,'' until the subject began an action (disregarding leaving the test area). Latency data were read from video time codes. Visual attention was rated according to the duration of the subject's visual orientation to the demonstrator during the demonstration, also read from video time codes.

TABLE II. Attentiveness Rating Scale

0	Subject's attentiveness constituted no clear fixation on the demonstrated action
1	Subject's attentiveness constituted a quick glance at the demonstrated action
2	Subject's attentiveness constituted a fixation of 1–2 sec on the demonstrated action
3	Subject's attentiveness constituted fixation equal to or more than 3 sec on the demonstrated action

TABLE III. Matching Rating Scale

0	No attempt and no match
1	Attempt, but the scorer cannot tell what
2	Attempted action is an incomplete version of what was demonstrated
3	Complete reproduction of demonstrated action

Partial matches included using two hands rather than one, adding additional elements, or omitting an element. Inter-observer reliability between C.H. and an independent observer (B.D.) for matching was determined according to the κ coefficient, using the data over six test sessions (122 trials) for Cosig where both familiar and novel actions were presented. κ for this variable exceeded $+0.80$.

Subsequently, two other individuals naïve to the experiment coded actions and degree of matching for Cosig using a blind coding procedure. The coders first reviewed the trials and agreed on descriptions for frequent actions performed by the subject. Then, they independently coded 357 trials, using their descriptions. Later, they matched their descriptions to the list of demonstrated actions, trial by trial, and through this comparison, determined degree of match to the demonstrated action. These coders judged that Cosig partially or fully matched 24% of familiar actions demonstrated in the Experimental phase, slightly more than the 20% matches coded by the first scorer for the same phase. They also noted the same matches of novel actions as the original coder. We concluded that the first coder accurately captured the monkeys' behaviors of interest in this study, and we report analyses of the data from her coding.

Analysis

We employed nonparametric statistics for a within-subjects design. For the Training phase, we averaged ratings of degree of match, duration of looking and latency to respond for the multiple trials per action per day for the final 40 replications using the full set of 16 actions to arrive at a score per demonstrated action per replication. We considered the relation among these variables using Spearman correlations. We examined the distribution of actions with ratings of Attention (pooled into two categories, low and high) and ratings of Match (unrelated action and partial or full match) using Kruskal–Wallis tests within subject, and using trial as the unit of analysis, with h approximating χ^2 due to large n. For the Experimental phase we compared ratings of degree of match and duration of visual attention to familiar and novel actions using Mann–Whitney tests, with action as the unit of analysis. We calculated the relations among these variables within Familiar and Novel actions using Spearman correlations with action as the unit of analysis. For all analyses, a two-tailed α of 0.05 was used for determinations of statistical significance.

We examined Cosig's actions following demonstrations in the first seven sessions of the Training phase to determine the frequency with which she performed any of the demonstrated behaviors (partially or fully as in the demonstration). We assume these data represent the monkey's intrinsic rate of performing these behaviors in our test circumstances when somewhat familiar with the objects and with the testing arrangement. As the monkeys were given access to the experimental objects only during experimental sessions, in accord with the constraints on their experiences as part of the PAST program, we could not collect standard baseline data. This analytical procedure provides a substitute.

RESULTS

The monkeys participated with interest during the testing procedure, which was similar to their training experiences for their later careers as aides for handicapped humans. For example, the monkeys were accustomed to attending to a human's verbal cues, moving to and staying in one place for a short time, as well as acting after a verbal cue. They responded with apparent pleasure (marked by a rapid approach and/or contented vocalizations) to the experimenter's verbal praise and caresses. They typically attended overtly to the demonstrations for one to several seconds, and they typically moved from where they sat to the objects and performed an action within 6 sec of demonstration (Training phase). The monkeys watched the demonstration for 3 sec or more in 18–35% (mean = 27%) of demonstrations. They did not, however, immediately perform any of the demonstrated ''training'' actions. They were free to leave the test area between demonstrations, which they did often. The short duration of the testing sessions (5–7 min) was geared to the monkey's voluntary participation.

Table IV presents percentages of actions ranked according to the degree of conformity and degree of match to the demonstrated act for the last 40 replications of the Training phase. Bara, Cosig, and Corsen clearly matched only a small percentage (20, 11 and 4%, respectively) of all actions demonstrated to them. Degree of matching averaged 1.3, Bara, 1.1, Cosig, and 0.9, Corsen on a scale of 0–3, where 3 is the strongest. That is to say, the monkeys usually performed an unrelated action after the demonstration (a score of 1). The average level of attention was judged to be 1.6–1.9, where 1 is a brief glance and 2 is a look of 1–2 sec (see Table III). For both Bara and Cosig, a significant positive relation existed between attention and accuracy of matching the demonstrated action, with attention pooled into two categories, good (2–3) or poor (0–1), and degree of match similarly pooled into two categories, good (2–3) or poor (0–1), Kruskal–Wallis: $df = 1$, $N = 517$ and 951, Cosig and Bara, respectively, $\chi^2 = 22.9$ and 52.7, $P < 0.001$. This relationship was not found for Corsen. Out of the 229 scored trials, Corsen responded with a match of 2 or better only 24 times, and these were equally divided between episodes with good attention and poor attention.

TABLE IV. Matching (see Table III) and Attentiveness (see Table II) Per Monkey in Phase 1

	% behaviors matched at Level 3	Mean degree of match	Mean degree of attentiveness
Cosig	20%	1.3	1.6
Bara	11%	1.1	1.9
Corsen	4.3%	0.9	1.8

We further examined the relations between degree of match and attention, and latency to respond for Cosig. She made better matches when she responded more quickly (Spearman's rho: $r_s = -0.72$, $P < 0.01$, $N = 40$; see Fig. 2) and was more attentive ($r_s = +0.95$, $P < 0.01$).

Comparison of Action Categories

Cosig and Bara attended to some demonstrated actions more closely than others, and they matched some actions better than others. As we expected from the monkeys' spontaneous manipulation, they were better at matching actions in Categories 1 and 2 (manipulation of an object) than those in Categories 3 and 4 (action directly on the body or the body directly on a substrate). For example, Cosig earned an average match score of 1.45 for actions in Categories 1 and 2 compared to 0.77 for actions in Categories 3 and 4 (Mann–Whitney: $U = 9$, $N1 = N2 = 8$, $P < 0.05$). For the latter categories, she earned scores above 1 only for the action: ''Puts a ring on the mouth, with or without actual bite.'' This action she did moderately well (score of 2) 18 of 40 times. Degree of attention to the demonstration was also greater for actions in Category 1 and 2 vs. Category 3 and 4. Cosig averaged an attention score of just over 2 (2.04) for the first two categories, and 1.46 for the latter two ($U = 6$, $N1 = N2 = 8$, $P < 0.05$).

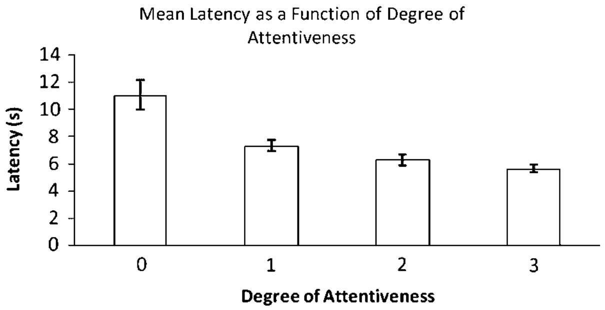

Fig. 2. Cosig's latency to respond plotted against degree of attention in Training phase. Trials in which actions were coded as 0 for degree of match are not included. Bars indicate Standard error of the mean.

Bara's data were similar as she never matched any action in Categories 3 or 4. Further, there was only one instance where she performed any action following a Category 3 or 4 demonstration (''Puts a finger within the hole of the vertical wooden pole'').

For Cosig and Bara, two training actions (both in Category 2) stood out as more often well-matched: ''Opens a book'' and ''Unzips a zipper.'' Cosig and Bara earned matching scores of 2.5 or better for these two actions, vs. averages of 1.0 (Cosig) and 0.8 (Bara) for the other six actions. The third subject, Corsen, also earned her highest matching scores for these two actions, although the magnitude of the difference with the other six actions was minimal (0.2 or 0.3 scale units higher than the next action, vs. 1.5 units for the other two subjects).

Selection of Objects Following Demonstration

Although performance was poor for matching most demonstrated actions, the subjects frequently selected the appropriate objects in their responses. Corsen was the least apt at this, selecting the correct object in 27% of her demonstrations. The other two subjects each selected the correct object following 65% (Bara) and 69% (Cosig) of demonstrations of Categories 1 and 2 actions. As there was a 17% chance of correct selection of objects by chance, given that there were six objects, all three subjects demonstrated a significant deviation from chance in this evaluation (Corsen, $\chi^2 = 22.5$, df = 1, $N = 288$; Bara, $\chi^2 = 389.1$, df = 1, $N = 240$; Cosig, $\chi^2 = 630.7$, df = 1, $N = 320$; all $P\text{s} < 0.001$). This is strong evidence for social enhancement in object selection.

Cosig's Initial Rates of Performing the Demonstrated Actions

We examined Cosig's actions in the first seven sessions (constituting 184 demonstrations) to evaluate her initial rates of performing the demonstrated actions with objects. In these sessions, she performed no action following 25 demonstrations (14%), and in 14 cases, she performed two actions in quick succession (both were tallied), producing 173 actions following 159 demonstrations. Following the 159 demonstrations, she performed one action far more often than any other: ''Puts a ring around a vertical wooden pole'' (76 times; 44% of all actions). Seven times this action followed a demonstration of the same action. She opened the book 24 times, 13 times following a demonstration of that action and 15 times she pulled the zipper, 11 times following a demonstration of that action. ''Pushes a stick into a hole in the vertical wooden pole,'' ''Puts a ring into a plastic box'' and ''Puts the ring to the mouth, with or without actual bite'' were other popular actions (10, 15 and 18 times each, respectively; 6–10% of all actions). Each of these actions followed a demonstration of the action in less than half the cases. As we shall see next, these same actions remained the most likely to follow a demonstration of either a familiar or a novel action in the next phase.

Comparison of Behavior Following Demonstrations of Familiar and Novel Actions in Experimental Sessions

Cosig's performance in the Experimental phase is detailed in Table V. Cosig attended to the demonstrations of novel actions to the same degree that she attended demonstrations of familiar actions presented in the same sessions ($U = 98.5$, $N1 = N2 = 16$, NS). She also responded with similar latencies following the demonstration of novel actions and familiar actions ($U = 93.5$, $N1 = N2 = 16$, NS). She responded most quickly (in less than 4 sec, on average) following demonstrations of unzipping the zipper and opening the book, the two actions that she matched most accurately in the Training phase and the Experimental phase. Cosig performed some action following demonstration of novel and familiar actions for the same percentage of trials (88%). She matched partly or fully seven familiar actions (most effectively, ''Opens a book,'' ''Unzips a zipper,'' ''Puts a ring around a vertical wooden pole,'' and ''Puts a ring on the mouth, with or without actual bite'').

Cosig never perfectly matched a novel action and her degree of matching novel actions was lower (mean = 1.0, meaning on average she performed some action unrelated to the demonstration) than her degree of matching familiar actions (mean = 1.3); these degrees of matching differed significantly ($U = 3$, $N1 = N2 = 8$, $P < 0.05$). Nine percent of familiar demonstrations were matched at Category 2 (incomplete version), and 13% at Category 3 (complete reproduction), for 22% partial or full matches, similar to the 20% matching observed in the Training phase. Cosig performed partial matches (degree of match = 2) of three different novel actions (2.1.1, 2.2.1 and 2.2.4 in Table I) in six trials, out of 48 demonstrations (12.5%) of novel actions. The matched actions included ''Twists a screw with a screwdriver,'' ''Fits a notched block onto another notched block'' in an *X* pattern, and ''Turns a crank.'' The deviations from perfect matching included not perfectly setting the notched block into the mounted notched block and not turning the screwdriver or the crank the same full rotations as the demonstrator. Cosig turned the crank 12 times and the screw 11 times following the 232 demonstrations in the Experimental phase, just five of these times following a demonstration of these actions. She fixed the notched block onto the mounted block just once.

Cosig's actions following all 230 demonstrations in the Experimental phase (that were not matches of the demonstrated action) included, prominently, three familiar actions demonstrated in Phase 1: Putting

TABLE V. Cosig's Performance in Experimental Phase: Average Values Per Trial for the Level of Visual Attentiveness and Degree of Match (Ranked From 0 to 3), and Latency to Act (in Seconds) Following Demonstrations of Familiar and Novel Actions

Familiar				Novel			
ACT	Atten[a]	Match	Latency	ACT	Atten[a]	Match	Latency
111	2.00	0.82	8.10	211	2.00	2.00	14.25
112	2.29	1.67	4.13	212	2.67	1.00	14.73
113	2.67	1.27	5.24	213	2.00	1.00	7.10
114	1.78	0.82	4.69	214	1.50	0.67	4.35
121	2.22	0.83	9.75	221	1.50	1.67	4.77
122	2.25	0.67	11.23	222	1.00	1.00	5.47
123	2.90	3.00	3.20	223	3.00	1.00	10.27
124	2.80	2.83	3.73	224	2.67	1.33	8.53
131	0.83	0.73	12.00	231	0.00	1.00	5.87
132	0.71	0.92	10.70	232	1.33	0.67	5.95
133	0.82	0.83	7.84	233	0.50	0.67	5.10
134	1.38	0.91	9.35	234	2.00	0.67	14.95
141	1.60	1.00	8.51	241	1.00	1.00	10.40
142	1.60	0.82	12.59	242	2.50	1.00	16.20
143	2.25	1.00	6.63	243	1.33	1.00	12.23
144	2.44	1.67	6.60	244	0.67	0.67	14.65
Sum	30.54	19.78	124.27		25.67	16.33	154.82
Mean	1.91	1.24	7.77		1.60	1.02	9.68
St Dev	16.38	10.58	67.60		14.17	8.94	82.40

[a] Atten, attention.

the ring around the pole (11% of total), putting the ring to her mouth (12%), and unzipping the zipper (10%). Cumulatively, these three familiar actions accounted for one-third of her actions in this phase. She also frequently contacted the screw, crank, and book (collectively, 22% of actions)—all objects that move or have a moving part. Forty-six times (20% of actions) she moved an object into relation with another object (excluding the body) following a demonstration in this phase (actions 1.11, 1.12, 1.13 and 2.11 from Table 1). Overall, she displayed a wide variety of behaviors (65 unique actions) following demonstrations in the Experimental phase. Following the 48 demonstrations of novel actions, 12 times she contacted a familiar object (ring, zipper, or vertical pole) and 11 times she contacted one of the novel objects (notched block, crank or screw).

In Experimental sessions, Cosig's latency to respond varied systematically with the degree of match following demonstration of familiar actions ($r_s = -0.755$, $N = 16$, $P < 0.01$) as in the Training phase, but this association did not appear following demonstration of novel actions ($r_s = +0.04$, $N = 16$, NS). Cosig's degree of attention to familiar actions was significantly positively associated with degree of match ($r_s = +0.624$, $N = 16$, $P < 0.05$) and significantly negatively associated with latency ($r_s = -0.697$, $P < 0.01$). Her scores for the degree of attention to novel actions were also positively associated with scores for the degree of match for these actions, although less strongly ($r_s = +0.379$, $N = 16$, NS). However, for novel actions, attention was positively associated with latency ($r_s = +0.41$, NS) rather than negatively correlated, as for familiar actions.

DISCUSSION

This study lends support to Fredman and Whiten's [2008] suggestion that hand-reared capuchins can match some familiar actions with objects and substrates demonstrated to them by a human. It may be more accurate to state that the monkeys can reproduce some familiar events. Our findings suggest that capuchins' ability to reproduce events using matching actions depends strongly, if not entirely, on the spatial and temporal structure of the events they witness. Monkeys were modestly able to reproduce familiar events in which actions moved objects in some specific relation to a stationary object or a substrate, and that they had a relatively strong propensity to perform anyway. They did not reproduce familiar gestures or other familiar actions not involving an object. The one action directed at the body that they did reproduce, putting a ring in the mouth, involved an object. Moreover, it could be argued that this is a feeding action and thus likely to be socially facilitated. That is, the demonstrator's action increased the probability that the monkey would perform the same familiar action.

Our results mark a distinct and important difference from the findings with chimpanzees older than four years. Chimpanzees can sometimes reproduce gestural actions with no object referent modeled by familiar humans [Custance et al., 1995;

Myowa-Yamakoshi & Matsuzawa, 2000]. Similarly, rehabilitant orangutans reproduce actions on their bodies, such as shampooing themselves [Russon & Galdikas, 1993], and one orangutan has reproduced hand and arm postures and gestures, as well as other kinds of actions [Miles et al., 1996]. It seems that capuchins are more dependent on allocentric spatial referents to organize their actions than are apes. The difference between capuchins and apes in their reliance on allocentric spatial referents is likely to be one of the degree. Myowa-Yamakoshi and Matsuzawa [2000] showed that some adult chimpanzees, like capuchin monkeys, are better at reproducing a demonstration that involves moving an object than they are at reproducing gestural actions of the sort used by Custance et al. [1995].

The single capuchin to observe novel action events was slower to respond when she had paid longer attention to the demonstrator performing novel actions, a reversal of the pattern with familiar actions. These findings suggest, at the least, that she recognized that the demonstrated action was novel. She partially reproduced 3 of 16 novel actions in 6 trials out of 48 demonstrations (12.5% of demonstrations of novel actions). All the novel action events the monkey reproduced involved producing a novel spatial relation between two objects (i.e. fitting two notched blocks together, turning a screw with the screwdriver, and moving a crank handle around a pivot). However, two of the three novel actions that she matched moderately well (turning the screw and turning the crank) she also performed several times when these actions were not demonstrated (10 and 11 times each, in addition to when they followed a demonstration). She placed one notched block into the matching mounted notched block only once, after a demonstration of that action. Thus, this action stands out as the most different from a baseline rate of performance, and therefore the strongest evidence for purposeful matching of the demonstrator's action. But it was a single event.

We provide weaker evidence for matching than that provided by Fredman and Whiten [2008] for capuchin monkeys. It may be important that Fredman and Whiten presented a box containing food, and the subject monkey saw the demonstrator expose the food, thus providing a strong motivation for the monkey to open the box. Following Custance et al. [1995], our experimental paradigm relied solely on the monkeys' interest in cooperating with a familiar human companion. It appears that, although capuchin monkeys respond affiliatively to humans who match their actions [Paukner et al., 2009], they are not strongly inclined (or not able) to match the gesture or manipulative actions of humans with whom they are affiliated.

The bias to attend to, and therefore to reproduce, events that involve moving objects may be widely shared across species, including humans. Gergely and Csibra [2007] go so far as to argue that young humans (through 14 months old) do not necessarily interpret others' actions with respect to intentions, but rather develop ''object-centered representations'' (p. 141) in the absence of ostensive cues from the other person. For example, 14-month-old infants copy an adult's novel means of achieving a goal only when the adult provides appropriate ostensive cues [Gergely & Csibra, 2005]. According to Csibra and Gergely [2006], the shift toward interpreting others' actions in terms of goals or intentions is enabled by a particularly human bias for teleological reasoning, coupled with a particular human propensity to provide referential cues. In our view, Csibra and Gergely's [2006] theory of pedagogy is a more comfortable fit for comparative data than theories that posit that matching actions depends from the start upon interpreting the goals or intentions of another [e.g. Tomasello et al., 2005]. We interpret our findings to be supportive of Csibra and Gergely's [2006] theory that individuals of diverse species will attend to actions with objects and the movements of objects, even when they do not attribute intentionality to the actor [see also Guillaume, 1971]. Kumashiro et al. [2003] make a similar suggestion, phrased in terms of the form of attention that Japanese macaques achieved with a human demonstrator (joint attention to another object, or attention directly to the demonstrator).

All three monkeys in this study watched 18% or more of the demonstrations in Phase I for more than 3 sec. We do not have the necessary data to determine whether this duration of focused attention on a familiar human's action is greater than normally reared capuchins exhibit. Some data suggest that capuchins typically look at one another more briefly than we observed in this study toward the human demonstrator. In an experiment where capuchin monkeys could view an adjacent space through a one-way window, capuchins looked at familiar group mates for about one second on average [Johnson, 1995]. This style of visual attention does not lend itself to tracking actions of another through time. For this reason, if human rearing influences the organization of visual attention in capuchin monkeys toward longer periods of focused attention on human actions, these individuals will be more likely to match a human demonstrator's actions than are normally reared monkeys in the same situation. However, this ''advantage,'' if the capuchins in this study had it, did not result in effective matching behavior. On the other hand, Pitman and Shumaker [2009] argue that rearing situations (e.g. by the mother, or in a nursery) for the first six months of life did not affect patterns of visual attention in great apes older than three years.

For two of the capuchin monkeys, degree of attentiveness to the demonstrator was strongly associated with how quickly they acted following the demonstration and how well they reproduced familiar events. For this analysis, we pooled Attentiveness scores of 2 and 3 (looks lasting for 1 sec or more). In our study, looks of at least one second were sufficient to support quick action by the monkey following the demonstration, and to support attention to the objects used in demonstrated action. Custance et al. [2006] provide similar findings from a study in which pig tailed macaques (*M. nemestrina*) watched a demonstrator moving bolts that held a box closed. On average, the demonstration in their study lasted 31 sec, but the monkeys looked at the demonstration in bouts of just over 1 sec, and then looked away for more than 3 sec before looking again at the demonstration. Even with this intermittent style of attention, which is similar to that which we found for the capuchin monkeys, Custance et al. found a positive relation between the amount of time that the monkeys watched the bolts being manipulated and the amount of time they touched the bolts.

Human-reared capuchins manifest social facilitation of activity [*sensu* Clayton, 1978], including manipulation of objects in the company of their human caretakers, and local enhancement of interest in specific objects [*sensu* Galef, 1988; see Zentall, 2006 for review]. Hervé and Deputte [1993] reported that an infant capuchin (8 months old) reared in a human home contacted and manipulated objects more frequently after its human caretaker had pointed them out than if she had not. In a longitudinal study of one human-reared capuchin, Deputte et al. [1995] found that both the form of the caretaker's interest (touching vs. manipulating) and the subject's pre-existing interest in manipulating the object influenced the subject's behavior following the caretaker's actions with objects. Capuchin monkeys reared in species-normal circumstances also show increased manipulation of objects handled previously by their groupmates [reviewed in Fragaszy & Visalberghi, 2004], and wild capuchin monkeys show enhancement of interest in places where their groupmates have been foraging [Gunst et al., 2008]. We think that social facilitation, enhancement and an intrinsic interest in objects moving in relation to surfaces, supporting emulation of the end products of an action by the human demonstrator, are sufficient to explain the modest degree of matching that the capuchin monkeys demonstrated in this study.

Studies with young children suggest that this is the case for humans as well. Horne et al. [2009] show that enhancement and demonstration of the affordance of objects support the production of object-directed actions by very young humans (six months old in their study) as well as did full demonstrations of a target action. They showed infants a puppet wearing a mitten. Separate groups of infants observed an adult take the mitten off the puppet, an adult point to the mitten or the mitten simply falling off the puppet. When they were given the puppet immediately afterward, with the mitten replaced, all three groups of infants removed the mitten from the puppet more often than a control group. Overall, demonstration of affordance seemed the most effective event to elicit the desired target action by the infants [see Huang et al., 2002 for similar findings with older children]. The role of affordance demonstration in behavioral matching by nonhuman primates deserves similar attention.

Subiaul [2007], in an interesting theoretical review of the imitation literature in monkeys and apes, suggests imitation is a modular cognitive faculty that can be subdivided into "familiar imitation" and "novel imitation." Subiaul suggests that monkeys are capable of "familiar imitation" of actions and rules (such as "select objects in this sequence"), and capable of "novel imitation" of rules, but not actions. However, our findings suggest that for capuchin monkeys, this conclusion applies only to actions (or perhaps more accurately, events) with a particular spatial and temporal structure. Specifically, capuchin monkeys are not able to reproduce all kinds of familiar events equally well. They are most likely to move an object into a new position as they have seen another individual do. Perhaps also to some small degree they can reproduce novel events, so long as these also have the structure of an object moving in relation to another spatial element. These abilities, even if modest, mean that observing others acting with objects, particularly if the others produce the same events repeatedly, can in principle support "doing like others."

Acting with objects in relation to substrates is a species-typical behavior for capuchin monkeys, and in natural habitats is a distinctive feature of their extractive foraging [Fragaszy et al., 2004a]. Some foraging activities involve specific positioning of objects on a substrate. For example, cracking nuts with a hammer stone, a typical foraging behavior in certain populations of wild and park-living capuchins [Fragaszy et al., 2004b; Ottoni & Izar, 2008], requires placing a nut on an anvil surface, then striking the nut with a stone. Young monkeys avidly watch proficient nut-crackers placing nuts and cracking them [Ottoni et al., 2005]. Resende et al. [2008] note that positioning the nut on the anvil is the last component of nut-cracking to appear when young monkeys learn to crack nuts. Our findings suggest how observation of others can support practice at positioning nuts (by increasing the likelihood that the young monkey will place the nut on the anvil) as well as support interest in nuts, stones and anvils separately. Whether one labels this kind of social influence on activity "familiar imitation" [per Subiaul, 2007] or something else, it can in principle contribute to learning. As our understanding of the web of social contributions to specific manipulative activities in capuchins becomes richer, the convergent evidence that these monkeys have foraging traditions and traditions of tool use becomes stronger [see also Perry et al., 2003].

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