18 "Do Monkeys Ape?"—Ten Years After

Elisabetta Visalberghi and Dorothy Fragaszy

18.1 Introduction

In 1990 we published a chapter entitled "Do Monkeys Ape?" included in a volume edited by Sue Parker and Kathleen Gibson (Visalberghi and Fragaszy 1990a). In our chapter, we noted that the view that monkeys are able to learn by imitation was widespread among laymen belonging to different cultures as well as among scientists (e.g., Romanes 1884/1977). However, in our review of the scanty empirical evidence supporting that view, we noted that it came from anecdotal observations that were anthropomorphically interpreted, or from studies lacking the necessary control procedures to rule out alternative, equally plausible, explanations. For example, the spread of the food-washing behavior in Japanese macaques can be accounted for by learning processes other than imitation (Galef 1990, 1992; see also Visalberghi and Fragaszy 1990a,b). Finally, we presented evidence from several studies carried out in our own laboratories with tufted capuchin monkeys (*Cebus apella*) to argue that monkeys did not learn novel behaviors by imitation.

During these past ten years, social learning processes in animals, and in nonhuman primates in particular, have been the subject of much additional research and discussion (e.g., Heyes and Galef 1996; Tomasello and Call 1997). The definition of imitative learning, whether it exists in nonhumans, and if so, in what animals and under what circumstances, all remain points of controversy; for example, we have seen titles such as "Do apes ape?" (Tomasello 1996) and "Do rats ape?" (Byrne and Tomasello 1995), and many other detailed treatments focused on imitation (e.g., Whiten and Ham 1992; Byrne and Russon 1998). We have also continued our investigations of social learning in capuchin monkeys in the controlled (but socially and physically enriched) settings of our laboratories and we have tested capuchins and other species (common chimpanzees and young children) in the same tasks (e.g., Bard, Fragaszy, and Visalberghi 1996; Perucchini et al. 1997; Modena and Visalberghi 1998). Overall, our data highlight the

Figure 18.1 Tufted capuchin monkeys (*Cebus apella*) are usually very interested in what conspecifics are doing.

definition does capture the essence of what *learning by imitation* is about.

Capuchin monkeys (from South and Central America) possess several characteristics that make them particularly suited for studying how they might use information provided by others to learn a novel behavior. Capuchin monkeys are generally tolerant to other members of their groups, especially to immature individuals, and young animals in particular are persistently interested in others' activities (Fragaszy, Feuerstein, and Mitra 1997) (figure 18.1). Capuchin monkeys of all ages devote considerable time and energy to manipulating objects, and they spontaneously display many innovations in their manipulative activity, including the use of tools (Fragaszy and Adams-Curtis 1991; Visalberghi 1987; Fragaszy and Visalberghi 1989). Indeed, capuchins are the most versatile tool users among monkeys (Visalberghi 1990; Anderson 2000; Tomasello and Call 1997). Occasionally, capuchin monkeys living in the wild and in seminatural conditions have been seen to use tools as

well (e.g., Fernandes 1991; Boinski 1988; Boinski, Quatrone, and Swarts, submitted), indicating that their prowess with tools in the laboratory is not solely an artifact of captivity. If prevalence of social learning is related to potential opportunities for, and benefits of, learning socially, if manipulative propensity is indicative of an underlying cognitive sophistication, and/or if learning abilities are modular in some sense, one could reasonably predict that capuchins should possess stronger social learning propensities than other primate species that do not display equivalent tolerance, interest in each others' activities, and innovations in manual activity. Perhaps for these reasons, capuchins have been regarded as strong (and perhaps the best) candidates for elaborated social learning abilities among monkeys.

In contrast to their noteworthy status in social and instrumental domains, capuchins are comparable to other species of monkeys in their achievements in tasks commonly used to assess memorial, attentional, and conceptual abilities (e.g., Piagetian sensorimotor tasks, various discrimination, matching, and conceptual learning tasks, and social cognition tasks; D'Amato and Salmon 1984; Adams-Curtis 1990; Antinucci 1989; Anderson 1996; De Lillo; see Tomasello and Call 1997 for comparative review). If one adopts a domain-general model of cognitive organization (e.g., Case 1994) that posits core attentional, memorial, and relational characteristics constrain individual performance, one would predict that capuchins should present monkey-typical social learning abilities. That is, what they learn socially ought to be consistent with what they learn in individual contexts. In this chapter, we discuss the results of many recent studies carried out with capuchin monkeys by us and by others that support the domain-general view of their social learning abilities, and that argue against a capacity to imitate in a strong sense. Capuchins are unusual among monkeys in some ways, but not in their abilities to match actions. Taxa from other orders in addition to primates, including many mammals, birds, and fishes, also exhibit extensive social learning, and some exhibit sophisticated imitative abilities (i.e., dolphins, *Tursiops truncatus*, Mercado et al. 1998; and Herman, chapter 3 of this volume; and parrots, *Psittacus erithacus*, Moore 1992, 1996; see Box and Gibson 1999 for general review). The argument for modular social learning abilities may be better supported in these other groups; this is an open question in our minds. However, these matters are beyond

the scope of our chapter. Here we restrict our discussion to capuchin monkeys for the purposes of highlighting one (rather unusual) taxon's social learning propensities.

For capuchin monkeys, learning to use an object as a tool is possible when the task is fairly simple (as in pushing something with a stick), but it is unlikely in any given short period of time. In the past, we have experimentally investigated the capacities of capuchin monkeys to learn to use different tools (and to perform other innovative behaviors) with and without conspecific models as proficient demonstrators (Visalberghi and Fragaszy 1990a; Fragaszy and Visalberghi 1989, 1990). In our tasks, both model and learner worked with apparatus that contained or delivered a highly desired food item, and the task involved simple actions well within the capabilities of the subjects. We concluded that although social influences on behavior were clearly evident and supporting of learning to solve the tasks, there was no evidence for imitative learning per se. For example, Visalberghi (1993) reported lack of imitation in a task requiring the use of a stick tool to push a reward out of a horizontal transparent tube (figure 18.2). In this experiment, unsuccessful adult and juvenile capuchins were exposed to proficient conspecifics (models) repeatedly solving the tube task. The results showed that although the capuchin observers had ample opportunity to watch the model(s) solving the task, none of them acquired tool use by imitation, nor did they improve the orientation of the tool toward the tube after exposure to the models. Furthermore, data also showed that the visual attention of capuchin observers was not selectively focused on the events relevant for learning (e.g., insertion of the stick in the tube, pushing the reward vs. holding the stick, eating the reward). In short, the potential learners did not behave as if they regarded the model's actions as relevant to their own activities.

Modena and Visalberghi (1998) conducted a cross-sectional study with children using the same tube task as was presented to the monkeys. Sixty-five children of 12, 15, 18, 21, and 24 months of age were tested (figure 18.3). Children were first presented with a three-minute pretrial of the tube task and the 44 children who were not successful were randomly assigned to the control group (no model) or to the model group and received two trials with the tube task. The children in the model group witnessed the model solving the task twice; after each solution they were invited to get the reward themselves. In the control group children were invited
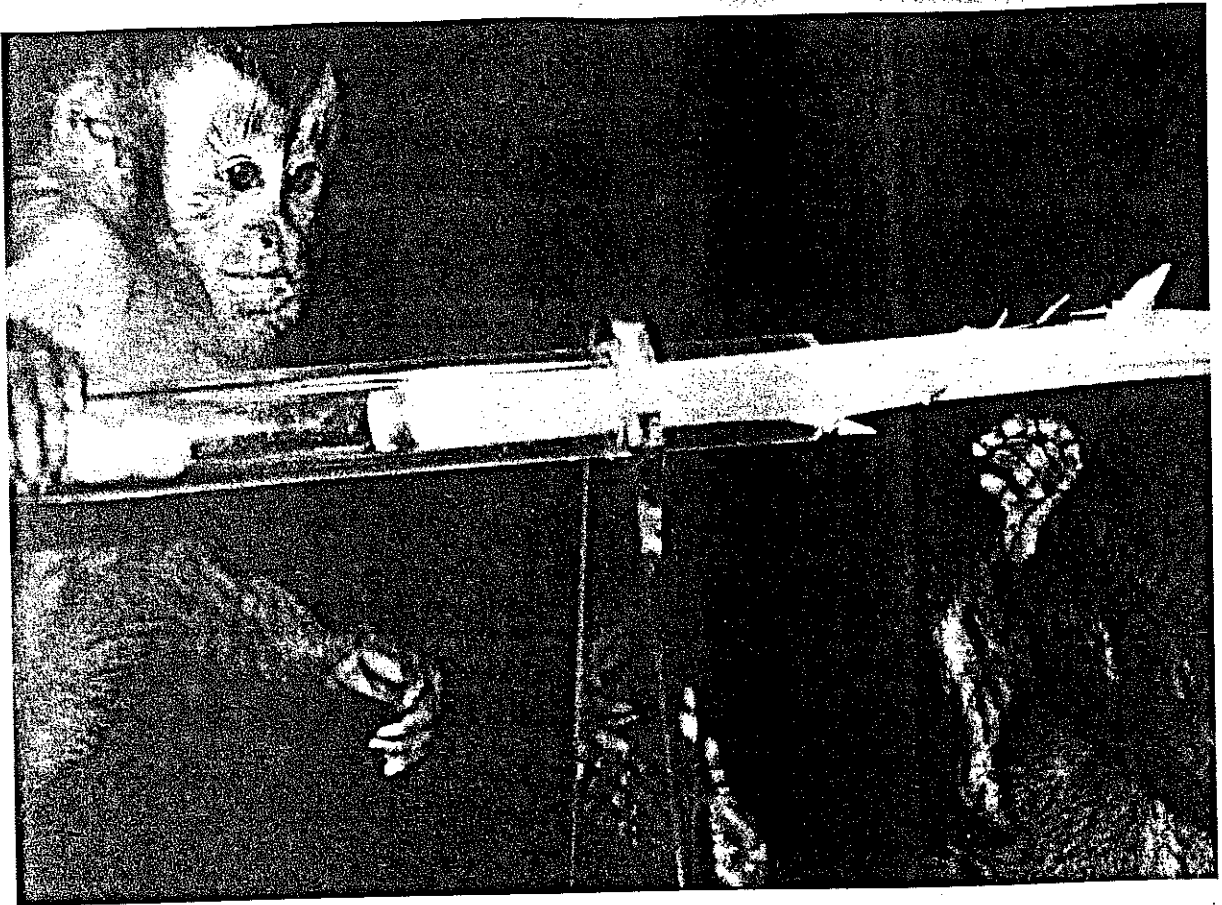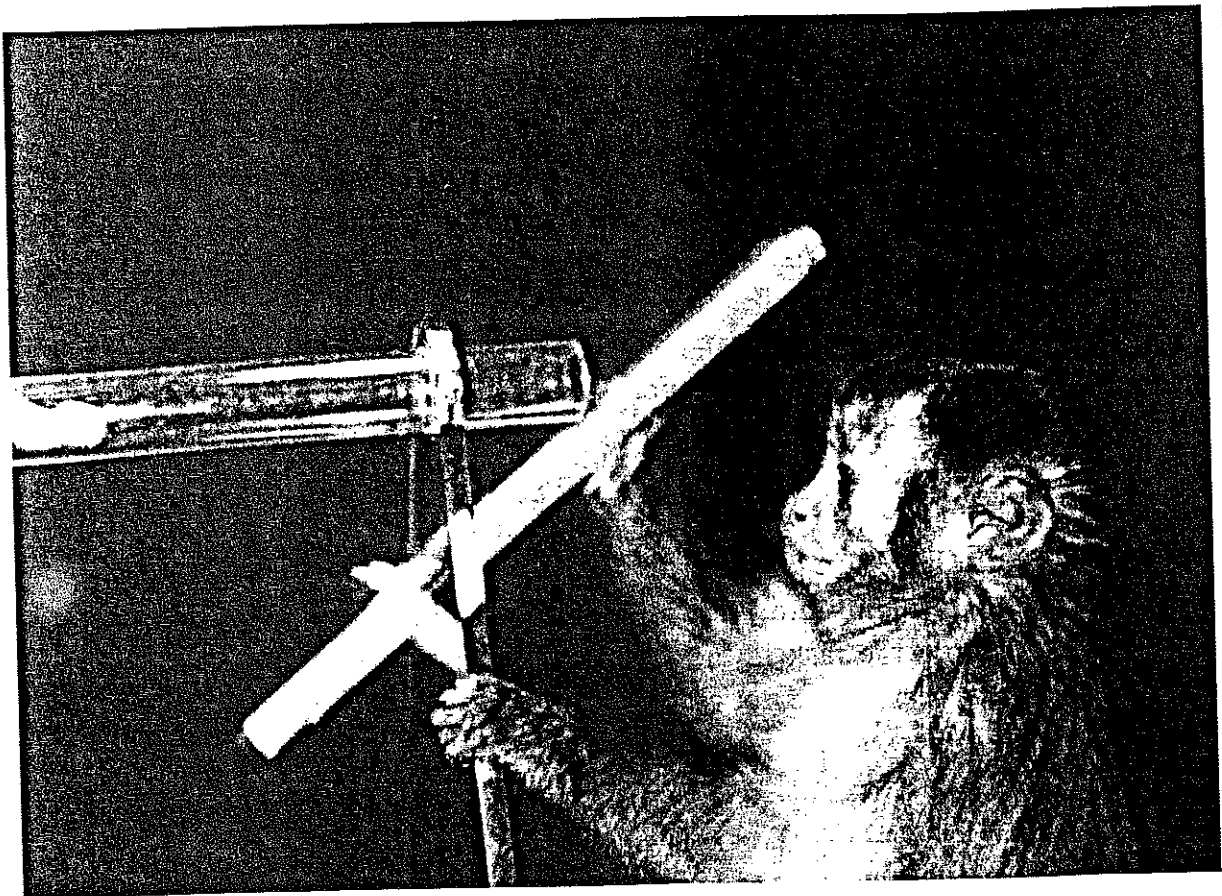
Figure 18.2 (a) The capuchin monkey on the left, who does not know how to use a stick to push the peanut out of the tube, attentively observes a group member solve the task. (b) Despite having observed many solutions, the observer makes awkward attempts to obtain the peanut and does not succeed.
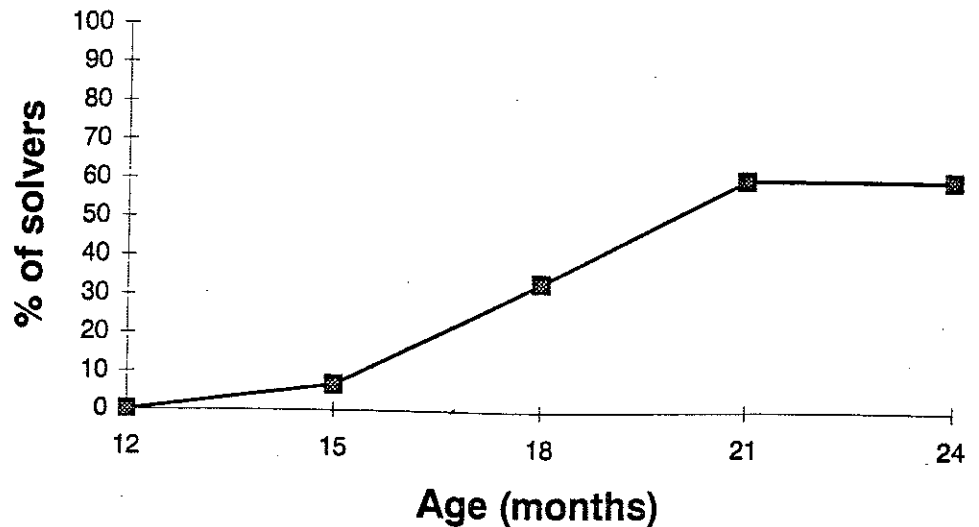
3-MIN PRE-TRIAL

Figure 18.3 Percentages of infants who spontaneously solved the tube task during the first 3-min trial. The infants tested were $N = 10$ at 12 and 24 months of age and $N = 15$ at 15, 18 and 21 months of age.

by the experimenter to try to get the reward out of the tube by themselves. Watching the model solve the task twice did not improve the performance of 12-month-old children compared to that of children in the control group (in fact, there were no solvers in both cases). Watching the model significantly improved the performance of 15-, 18- and 21-month-old children, compared to that of the children in the control groups (figure 18.4). All the 24-month-old children became successful regardless of whether they were in the model or in the control condition; at this age, exposure to the task without a model improved performance as effectively as watching a model solving the task. In short, whereas capuchin monkeys did not learn how to solve the tube task by watching a model, 15- to 21-month-old children did; however, very young children, for whom the task is not within their grasp through other modes of experience, are not able to benefit from watching the model.

18.2 New Data from Capuchin Monkeys about Repeating Familiar Actions and Matching Novel Actions

Given the generally unpromising results concerning capuchins' abilities to learn how to use a tool from observing conspecifics, we decided to change the focus of our efforts to assess their social
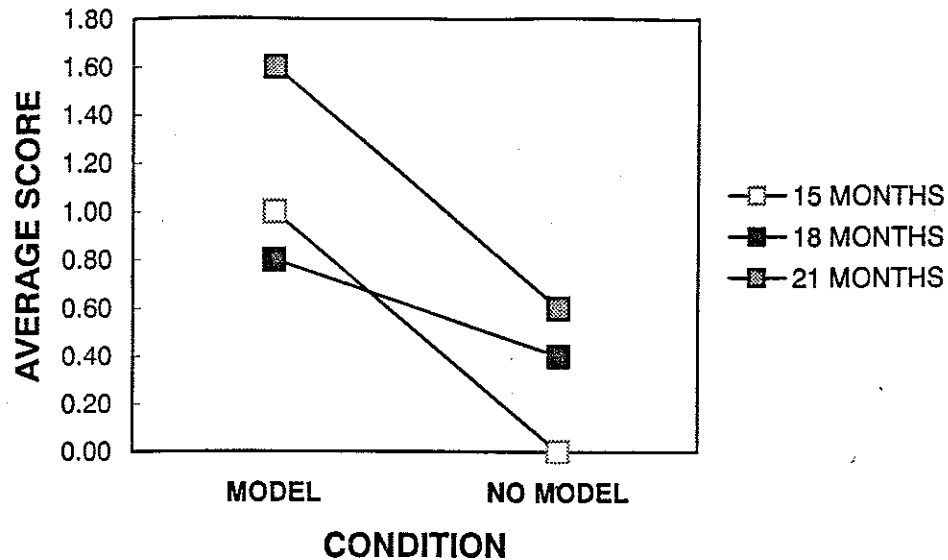
Figure 18.4 Average score obtained in the tube task by 15-, 18-, and 21-month-old infants in the Model and Control conditions (No Model). An infant who solves the tube task in the first trial (in the Model condition this means in the trial after 1 demonstration) gets a score of 2; an infant who solves the tube task in the second trial (in the Model condition this means after 2 demonstrations) gets a score of 1; an infant who does not solve the tube task gets a score of 0.

learning abilities. We chose something that we expected they would be more likely to achieve: replicating a behavior that is already in their repertoire when they observe a model (a conspecific or a human model) performing it (imitation, in the sense of Meltzoff).

Imitation, in the sense of Meltzoff consists of:

1. something C (the copy of the behavior) is produced by an organism
2. where C is similar to something else M (the model behavior)
3. observation of M is *not* necessary for the production of C, but it makes C more frequent than in the baseline activity
4. C is designed to be similar to M [since there is no obvious goal, it cannot be assessed]
5. the behavior C is *not novel*

In essence, all that is required is that the organism produce C where C is like M.

Early Imitation

This paradigm has been used very successfully by Meltzoff and others to examine imitative learning in human infants. Meltzoff and Moore (1977, 1983) reported that human newborns are able to

perform some facial movements they have just witnessed a person doing in front of them. From birth and for the next several weeks, a full-term infant sometimes protrudes its tongue when it sees the model doing so, opens its mouth when the model does so, and so on. According to these authors, infants reliably imitated the behavior they witnessed (rather than making some other facial movement not witnessed). However, in these experiments no learning is evident because the infant is already able to perform those different actions. The infant just performs the same behavior it saw the model performing; the infant matches the model's behavior. Although in an extensive review and reanalysis of neonatal imitation data Anisfeld (1996) argues that of the several behaviors listed by Meltzoff and Moore (1977), only mouth opening is reliably imitated across experimental studies—in any case, the phenomenon of imitation in children at later ages is more than robust (Meltzoff 1996).

An experiment similar to that of Meltzoff and Moore (1977) has been carried out by Myowa (1996), with one nursery-reared infant chimpanzee from week 5 to week 15. In Myowa's study, the experimenter made three different facial movements (mouth protrusion, lips protrusion, and mouth opening) or presented a still face to the neonate. Her results show that the chimpanzee was able to imitate tongue protrusion between the fifth and the tenth week of age and mouth opening between the fifth and the eleventh week of age (but see Bard and Russell 1999, for an extensive review of imitation of facial expressions and movements in infant chimpanzees). Matching by neonatal chimpanzees is fragile and to some extent context dependent, but it is present. The same is true for humans.

On a few occasions, we have tried to elicit matching of these kinds of facial movements in neonatal infant capuchin monkeys; however, we have not been successful. Given the difference in the scale and morphology of the human face and the capuchin face, this is perhaps not surprising. However, neonatal capuchins, like neonatal chimpanzees and neonatal humans, do turn their heads toward the human voice and do visually track the human face (Fragaszy and Bard 1997).

Repetition of Familiar Actions and Matching of Novel Actions

CONSPECIFICS AS MODELS

Let us see what older capuchin monkeys spontaneously do when they are allowed to perform the same action(s) they see a monkey

model perform. Some years ago Perucchini and colleagues (1997) replicated with capuchin monkeys an experiment previously carried out by Camaioni, Baumgartner, and Pascucci (1988) with 12–24-month-old children. Children were tested in pairs in a room in which two sets of identical toys and opportunities for play were available to them. The authors scored the frequency of various types of spontaneous imitative actions in the children (facial imitation, vocal imitation, linguistic imitation, and imitation of exploratory, manipulative activities with objects). Imitation was scored when all three of the following conditions were met: (1) the observer watched the model before performing the behavior; (2) the observer performed the behavior right after having watched it; (3) the behavior was not probable in that context. Imitation might occur on the same object or the other one like it.

Perucchini and colleagues (1997) followed as much as possible the same procedure and presented one pair of juvenile capuchins and one pair of adult capuchins with sets of identical objects for six sessions of 5 min each. They scored the occurrence of interactions with objects for both subjects. They focused on (1) the frequencies of imitation (the requirements for imitation were the same as for children, see above); (2) the frequencies of replication of routine actions (social facilitation); and (3) the frequencies of activity by one monkey toward an object followed by the partner contacting the same (or the corresponding) object (social enhancement). Note that these latter two categories were not scored for children because these behaviors were too frequent.

By comparing the results of these two experiments, striking differences emerge. The frequencies of imitation of actions with objects in 12-month-old children and 24-month-old children were 0.44 and 0.40 per min, respectively, whereas no imitation of this kind was ever observed in the capuchin pairs. Juvenile and adult capuchins performed replications of common actions (social facilitation) 0.16 times per min and 0.12 times per min, respectively; and stimulus enhancement was scored 0.51 times per minute for juveniles and 0.17 for adults. Like children, monkeys were interested in the objects and played and explored with them. But in contrast to children, monkeys did not watch each other very much and did not spontaneously match each other's activities, including nonroutine actions. Capuchins do attend to each other intently and perform mutual gaze for extended periods of time in other circumstances, however, such as during social play and most especially during courtship.

A rather different paradigm for studying imitation was developed by Heyes and Dawson (1990). In this paradigm, one rat observed a "demonstrator" rat from a face-on position while the demonstrator moved a lever to one side. Then the observer was placed in the demonstrator's place, and the direction the observer pushed the lever was noted. Recently, Gardner, Visalberghi, and Heyes (submitted; see also Gardner 1997) have tested capuchins in a task designed to be similar to that used by Heyes and Dawson (1990) with rats. Two subjects (members of two different groups) were trained to slide to the right or to the left a transparent Plexiglas panel in order to get access to a food reward. A hole, the rim of which was painted black, in the panel afforded the monkey a grasp of the panel and facilitated the sliding action. The training of the "demonstrators" required only a few minutes of behavioral shaping. These monkeys served as "demonstrators" for 10 "observer" capuchins (five in each group). The apparatus was positioned in a connecting opening between two adjacent concrete cages.

In phase 1, the demonstrator and the observers were in the two adjacent cages. Five "observer" monkeys observed through the transparent panel their "demonstrator" sliding the ring to the left and getting the reward; five other observer monkeys saw their demonstrator sliding the ring to the right and getting the reward. Immediately after having observed the demonstrator, each subject spent 10 min in the cage where their demonstrator had been, so that they now had access to the panel. For the observers, success was possible by sliding the panel in either direction. In phase 1, each observer subject had two such sessions. The experimenters scored whether the subject had acquired the technique for getting the reward (which consisted of grasping the panel ring and sliding it) and whether it moved the panel in accord with its own egocentric axis (i.e., the demonstrator moved the panel on its own left; therefore, since it faced the demonstrator, the subject saw the panel moving to its own right; then, when the subject moved to the adjacent cage, it subsequently moved the panel to its own right), or alternatively, whether it moved the panel in accord with the allocentric axis of the space in which the object moved (i.e., the subject saw the panel moving toward the left corner of the test cage, and subsequently moved the panel toward the same corner of the cage). Only two of the ten observer monkeys succeeded in phase 1; these solvers saw the demonstrator moving the panel to its own

right (i.e., to the observer's left) and, when given access to the panel, both observers tended to move the ring to their egocentric left direction.

The other eight subjects entered phase 2. In this phase the observers were in the same cage with their demonstrator for 10 min and then the demonstrator was removed. It should be noted that in phase 2 the demonstrator and the observers were in the same cage and the observers had continuous visual and manual access to the panel while the demonstrator slid the ring and got the reward, and that allocentric and egocentric axes matched. In this phase, when the demonstrator was removed, seven of eight subjects slid the panel toward the left and obtained the reward. Only one of these eight subjects slid the panel in the opposite direction of its demonstrator. Overall, across both phases, eight of nine solvers moved the panel in accord with their own egocentric observation of the most recently observed solutions. These results do not provide evidence of imitation; instead they provide some evidence of object movement reenactment (i.e., that the capuchins reproduced the direction in which they saw an object moved; see Custance, Whiten, and Fredman 1999 and below for further details). This form of matching is the only aspect of matching detected in the human-reared monkeys studied by Custance, Whiten, and Fredman (1999) and Fragaszy and colleagues (unpublished) using two other testing paradigms (see below).

HUMANS AS MODELS

Recent studies have investigated whether monkeys will match actions they see a human "demonstrator" perform. For example, Deputte and colleagues have conducted studies with capuchin monkeys participating in the "programme d'aide simienne aux tétraplégiques" of Kerpape-Lorient (France); this program was aimed at evaluating the feasibility of using monkeys as helpers for quadriplegic human beings. Given this goal, scientists were interested in finding the most effective and efficient way to teach the subject to perform specific behaviors and sequences of behaviors relevant to assisting the handicapped person. Social learning is an obvious possibility in this effort. In a first study, Hervé and Deputte (1993) report how the manipulative behavior of an 8-month-old infant capuchin monkey was affected by the trainer showing simple actions on objects. They found that the monkey contacted more objects and manipulated them more after the trainer had

designated them; however, the monkey never matched the action the trainer performed on objects.

In a second study (Hemery, Fragaszy, and Deputte 1998; Fragaszy et al., unpublished), three young ($4\frac{1}{2}$-year-old) capuchins raised in human homes were tested in a version of the Hayes and Hayes (1952) "Do as I do" paradigm, in a partial replication and extension of Custance, Whiten, and Bard's (1995) study with chimpanzees. The capuchins were trained to match the demonstrator's actions by rewarding them for performing familiar actions upon objects or species-typical actions upon their bodies following their demonstration by a familiar human. For the actions including an object, the human demonstrator handled one object from a set of eight on a tray in a distinctive way (for example, unzipping a zipper, or opening a hinged wooden "book"), or combining one object with another (for example, placing a stick into a hollow cylinder). The sessions were videotaped. Several forms of data were collected by an observer familiar with the testing protocol from the videotapes. The extent of visual attention to the demonstrator and the degree to which the performed action matched the demonstrated action were rated using a 4-point scale. For actions, a score of 0 indicated that the subject did not act after the demonstration, or did an action completely different from the one demonstrated, and on a different object; a score of 3 indicated that the subject unambiguously performed the full action on the correct object. For visual attention, a score of 0 indicated that the subject did not watch the demonstration at all; a score of 3 indicated the subject maintained visual attention during the demonstration for 3 or more seconds. We also noted what object(s) the monkey contacted. Two capuchins contacted the same object(s) contacted by the human following 60% of demonstrations; and the third monkey in 30% of demonstrations. However, they unambiguously matched the *action* in only a small percentage (20%, 11%, and 4.3%, respectively) of all the actions. For the two better subjects, level of matching was better when they were more attentive to the demonstration, and was better for those actions that involved contacting an object (e.g., open a book) and combining an object with another object or surface (e.g., put a stick into a cylinder) than for an action on the body (e.g., touch the arm).

Only the best performer entered the second phase of the experiment in which novel actions were interspersed with familiar ones in a one-to-four ratio. The familiar observer again coded the data

for degree of match and visual attentiveness. In this phase, scores for visual attention and performance of the familiar actions were maintained at the rates evident at the end of the training sessions. The rate of contacting the objects that the demonstrator had contacted was also similar as in the previous phase. However, although the subject responded as quickly to demonstrations of novel actions as of familiar actions, and performed some action on nearly all trials (88%), 3/4 of the demonstrations (36 out of 48) of novel actions were followed by an action that was judged to be unrelated to the one demonstrated. In the remaining 12 trials, the monkey contacted the same object, but only partially performed the demonstrated action.

Videotapes from this phase were also scored using a double-blind procedure. First, naive scorers independently noted what actions the monkey performed at each trial, using agreed-upon descriptors of the common actions and the experimental objects. They produced identical descriptions on 68% of trials, descriptions that varied by the addition of one other action by one observer on 19% of trials, and on 13% of trials they produced different descriptions, or one scored no action while the other scored an action. These data indicate that naive observers could identify the monkey's actions and the objects it contacted with acceptable reliability. Next, the scorers were given a list of the demonstrated actions. They then reviewed the tapes a second time to judge whether the subject's action on a given trial matched any item in the demonstrated repertoire. The observers agreed 100% on which trials the subject produced a demonstrated behavior, and agreed on which action it was on 90% of these trials. Finally, the two scorers were given the ordered list of demonstrated actions. Of the 96 familiar actions demonstrated in the experimental phase, the scorers judged that the subject matched the demonstrated action on 24% of the trials, replicating the results of the first scoring. Of the 24 novel actions demonstrated, the subject was judged to have matched the action on three trials (12.5%). The matched actions included turning a screw with a screwdriver, putting one notched block across another matching notched block in an X pattern, and turning a crank handle. These actions the first scorer had considered imperfect matches, because the objects were not fully aligned (blocks), or the subject did not move the crank or the screw the same distance or number of rotations as the demonstrator. The rate of matching the novel actions (that all involved repositioning an

object) is half that of familiar actions, which was already a modest rate, but it is above zero.

To establish that this rate differed from chance, we would need to provide the same objects to monkeys without a demonstrator, to determine a baseline rate of these particular forms of repositioning. Although they are not a fully adequate comparison, we do have some relevant data on this point. In a previous study with a different aim (Fragaszy et al., unpublished), a series of objects like the crank and the screw were provided to untrained group-housed monkeys for several half-hour sessions. We saw some exploratory contacts with these objects, including some that produced motion in the crank (1/4 turn or less) very like that seen in the study under discussion here. Thus, capuchin monkeys have some low probability of repositioning an object in the same ways the human demonstrated through independent exploratory activity. However, in this study, the subject had only a short time to act, many other objects to contact, and many other things it could have done with the object used by the demonstrator. Thus, it seems unlikely that the subject produced even three partial matches fully by chance. Fragaszy and colleagues conclude that capuchin monkeys predictably contact objects that have been acted upon by the demonstrator, as found also by Hervé and Deputte (1993), and (with a much lower probability) they will move an object to achieve (or toward) a demonstrated movement or new position of the object. However, except in this circumstance, capuchins do not match the *actions* performed by others.

These findings are similar in substance to those reported by Custance, Whiten, and Fredman (1999) with a larger number of capuchin monkeys similarly in training to become helpers for quadriplegic humans in Israel. These investigators used a two-action design, in which two distinctive actions on an object are shown and each group of subjects is exposed to one of the two actions. They examined whether the monkeys would perform more frequently the actions they had seen performed by a human demonstrator than the actions they had not seen. The task consisted of opening a transparent box containing a food reward; the box was closed by a "barrel latch," or by a "bolt latch." Each latch could be opened with two techniques. Each technique consisted of two related actions. Eleven subjects saw their familiar caretaker acting on the latches to open the box. In the "barrel-latch" task, half the subjects saw a pin at the front of the box being *turned* sev-

eral times and then a handle *turned*; the other half saw the pin being *spun* and then the handle *pulled*. In the "bolt-latch" task, half the subjects saw two rods at the top of the box being *poked* and *pushed*; the other half saw the rods being *twisted* and *pulled*. Custance, Whiten, and Fredman (1999) assessed for each type of latch whether the monkeys used the particular opening actions they witnessed more than the alternative ones. Two scorers, who knew what actions were demonstrated but were naive as to which actions each monkey had observed, viewed videotapes of the experimental sessions. They were asked to: (1) make a decision about which of the two demonstrations each subject had seen and then rate the confidence about that decision, and (2) count the number of each of the two actions (e.g., poking vs. twisting, pushing vs. pulling, etc., and other related subcategories) each subject performed.

Results showed that in the "barrel" latch, the monkey subjects did not reproduce the demonstrated technique at different frequencies than the nondemonstrated one. Nor were the human scorers able to infer reliably which technique the monkeys saw demonstrated. Similarly, in the "bolt" latch, the monkey subjects did not reproduce the demonstrated technique at different frequencies than the nondemonstrated one. However, the human scorers were able to infer reliably which technique the monkeys saw demonstrated. Therefore, for this latch, in addition to the modeled technique (*poke-push* vs. *twist-pull*), Custance, Whiten, and Fredman (1999) paid attention to the location (front vs. back of the box) where the monkeys acted and they analyzed the directions in which the rod was acted upon and from where it was removed (back vs. front, respectively). They found that their experimental groups differed in the frequencies with which they (a) pulled the rod from the front or the back side of the box, (b) pushed the rod from the front side of the box (but not from the back side), and (c) removed the rod from the front or from the back side of the box. It should be noted that pulling or pushing, followed by removing, constitute behavioral sequences in which actions are dependent on one another. For example, if a monkey pushes the rod from the front of the box, it is likely to pull it and remove it from the back of the box. The spatial features of the monkeys' actions (i.e., whether they occurred in the front or the back of the box) appear likely to have been the cues that allowed the naive scorers to discriminate between the experimental groups. For example, the scorers could have discriminated between

groups on the basis of the side of the box from which the rods were removed.

Custance, Whiten, and Fredman (1999) label the phenomenon of reproducing the direction of the rods' movement as "object movement re-enactment." They suggest that either this interpretation or "perhaps simple imitation" (p. 21) of the modeled familiar acts may account for their results and that they cannot be distinguished in their study. However, because the frequencies of the specific modeled techniques were not affected by their demonstrations for either latch, we conclude that imitation (as we define it) is not a possible interpretation of their data. Instead, the notion that the monkeys acted to move an object at the front or at the back of the box (the side where they saw it move) is plausible.

The foraging actions of capuchins incorporate many forms of poking, pushing, or pulling, and attending to the spatial relations of an object in relation to substrate (such as front vs. back) in such situations seems potentially very useful. This form of social influence is like the one seen in the Fragaszy and colleagues (unpublished) study reviewed above (see also Gardner, Visalberghi, and Heyes, submitted), in which capuchins acted to bring together objects that the experimenter had handled and brought together, and (at least a few times) to move an object to reproduce its movement or a new position. Capuchins that are attentive to human demonstrators seem able to capture some of the spatial relations about objects from the human's actions with those objects.

In collaboration with Custance, we have also attempted to test our socially housed capuchins in both of these paradigms ("Do as I do" and with a two-action task, with human demonstrators). Informally, we have also tried several times with different subjects, apparatus, and reinforcement procedures to shape or elicit matching behaviors in capuchins with human demonstrators. All these efforts have come to naught. We thought that attention to the human demonstrator (or rather, lack of it) in group-housed monkeys might have been responsible for the monkeys' poor performance. In retrospect, we can see that intensive and prolonged interaction with humans (during early life, and in the course of extended training to respond to verbal commands issued by humans) does affect capuchins' visual attention to humans, and enhances their interest in objects a human touches, and these perceptual tendencies may enhance the monkeys' probability of matching object

movements. However, such experience does not seem to lead to enhanced ability to match *action*, the signature feature of imitation.

It is interesting to note that the two young chimpanzees in Custance, Whiten, and Bard's (1995) study were able to match to a moderate degree a considerable proportion (38%) of novel actions involving only the body (e.g., touching the nose, or clapping hands) or acting on a substrate (e.g., slap the floor), whereas capuchin monkeys had the most trouble with these actions. Custance and colleagues did not include actions with objects in their list of modeled acts. Recently, however, that has been done by Myowa-Yamakoshi and Matsuzawa (1999), working with chimpanzees, in a study designed to investigate whether chimpanzees were better able to match certain kinds of manipulative actions than others. These authors report that chimpanzees were better able to match a novel action if the action involved orienting an object toward something else (another object, the substrate, or the subject's own body) than if it involved manipulating the single object alone. They concluded that directionality of the object's movement was a more salient cue for their subjects than the demonstrator's bodily movements. Thus, it seems that both capuchin monkeys and chimpanzees share a perceptual bias to notice directional movement of objects, more so than movement of a conspecific's arms or hands. It remains to be seen if this is true of humans as well, although Whiten and Custance's (1996) findings with children suggest that it is not true of 2- to 4-year-old children. In any case, incorporating this bias to notice and remember direction of object movement might be a useful starting point for a digital model of a "novice imitator" that can, with practice, expand its ability to notice action as well. In at least some situations, objects stay in their new positions for a longer duration than the movements that put them there, affording more time to see and remember them in the new location. Perhaps this temporal property supports the capuchins' and chimpanzees' better abilities to match direction of object movement and object positions than movements of an animate actor.

Byrne's (1999) description of a new theory to explain imitation by string-parsing algorithms seems compatible with this idea. According to Byrne's theory, an individual detects, over repeated encounters, the unvarying or highly probable sequence of actions leading to a goal. The learner eventually perceives the regularity of

action, the organization of activity, and can reproduce it in its own action. This view has much in common with Gibsonian theory (Gibson 1966, 1979), which also emphasizes the perceiver's improving detection of environmental regularities as a core element in learning.

To summarize all the laboratory studies to date on capuchins' matching of acts they have observed:

1. They can match familiar actions with objects, but this requires overt training. They have greater difficulty matching a familiar action on the body. (Mitchell and Anderson 1993 report that a long-tailed macaque learned to produce scratching on cue, but it was not easily learned.)
2. They do not match novel actions.
3. They can reproduce positions of objects somewhat.
4. Neonatal capuchins do not match human facial expressions.

In comparison, under similar circumstances, chimpanzees can match objects on the body, can match novel actions, are better at reproducing object position than movement, and exhibit a fragile ability as neonates to match human facial actions (tongue protrusion and mouth opening). Overall, it seems clear, chimpanzees are somewhat better than capuchin monkeys at noticing and reproducing humans' actions and movements of objects. Presumably, these characteristics contribute to behavior in natural circumstances, and it is thus not surprising that stronger evidence of traditions in natural circumstances (but not imitation, in the strict sense of our 1990a definition) is available for chimpanzees than for capuchins (Boesch and Tomasello 1998; Whiten et al. 1999).

The negative findings about capuchins' abilities to match actions do not mean that social influences are unimportant to capuchins' behavior, in the laboratory or in nature. Instead, they suggest we should look for different kinds of social learning processes than imitation in the sense of Visalberghi and Fragaszy (1990a), imitation in the sense of Meltzoff and Moore (1977, 1983), imitation in the sense of Camaioni, Baumgartner, and Pascucci (1988), imitation in the sense of Heyes and Dawson (1990), and the repetition of familiar actions or the matching of novel actions. Therefore, we have looked to feeding behavior for contexts where social influences could be expected to impact behavior.

18.3 Social Influences on Feeding

It has often been argued that social learning might be of great advantage in learning when, how, and what to feed upon (e.g., Giraldeau 1997). Dietary convergence in wild groups is often interpreted as due to social learning and the common view is that most primates, being social animals, learn to identify the foods they eat from watching conspecifics eating (e.g., King 1994; Byrne 1999; for a critical review, see Visalberghi 1994). We know that humans can be socially influenced both to initiate and to continue food consumption and to choose certain foods that are eaten by others (Rozin 1988; Birch and Fisher 1996). For example, De Castro (1990) has shown that the presence of others affects the onset of a meal, and increases the amount of food eaten and duration of time spent eating. Our studies, which are in the same vein as those with humans, investigated whether in capuchin monkeys the initiation, the consumption, and the selection of foods are affected by the feeding activity and by the food choices of a conspecific.

Visalberghi and Fragaszy (1995) found that the presence of group mates (and possibly the fact that they were eating) does not increase consumption of familiar foods but does increase consumption of novel foods when encountered for the first time. Do these results mean that homogeneity of diet within a group of monkeys is aided by social influences on acceptance of novel foods? To explore this, Visalberghi, Valente, and Fragaszy (1998) carried out an experiment that looked at consumption of novel foods when these foods are repeatedly encountered by individuals only when alone, or when encountered *only* in the presence of group mates. The results showed that during the first several encounters, eating is socially facilitated—that is, monkeys eat more of unfamiliar foods when in the presence of their conspecifics. After five to six encounters, the difference in the amount of time spent feeding by the monkeys who encountered the unfamiliar foods in a group versus those who encountered the unfamiliar foods alone disappeared.

At this point it becomes important to understand better the manner in which the presence or activity of conspecifics affect consumption. Galloway (submitted) investigated the effects of a conspecific A eating a particular food on the feeding behavior of an individual B. She tested four pairs of male *Cebus apella*. Each pair was housed together, constituting a long-term and compatible

social unit. Within each pair, one individual was the facilitator and the other was the observer for a given procedure, and then roles were reversed. The question was whether observers choose to eat the same food the facilitator is eating. The food presented was applesauce, a desirable and familiar food to all the monkeys. The appearance of the applesauce was the independent variable. The addition of red or yellow food colors produced two different experimental foods. Capuchins were shown to able to discriminate these colors. For half the subjects, the facilitator had red applesauce; the other half had yellow applesauce when they served as facilitators. All observers had applesauce of the two colors from which to choose. The results show that the observers ate red and yellow applesauce equally often, regardless of the color of the food eaten by the facilitator, and that the experimental subjects' first choices of food were evenly distributed between red and yellow. In short, "what" the facilitator was eating did not affect the food choices of the observer.

Galloway (submitted) also showed that *whether* animals in any pair were feeding did affect the likelihood that animals in any other pair in the same room would eat. In this experiment, the monkeys were observed a few hours after the morning meal had been given. All pairs had a quantity of the primary diet (pellets of commercial monkey chow) remaining in the cage. One experimenter gave one pair (the facilitator pair) additional fruit, and another monitored the feeding behavior of the other pairs. Social facilitation of eating (familiar) foods was evident: the nonsupplemented pairs ate more of their leftover chow in this setting than they did in the control condition, when the experimenter stood in front of the facilitator pair's cage but did not give them supplemental foods.

On the basis of these results, we may look again at the results of our experiments that suggested social facilitation increased consumption of novel or unfamiliar foods. It is possible that consumption of novel food is greater in the presence of familiar conspecifics than when alone because the absence of the familiar companions induces stress, or alternatively, because their presence reduces the neophobic response (Greenberg 1990), or because their presence increases the perceived "value" of the food (as a function of perceived competition). It is also possible that the facilitatory effect in the novel food condition might have been related to a nonspecific facilitation of eating more when others were eating, regardless of the exact type of food the other monkey(s) were feed-

ing upon. The simple facilitation of eating can result in an individual accepting and consuming more of a novel food if that novel food is what the observer has available. The results of a recent experiment by Visalberghi and Addessi (2000) fully supports this last hypothesis; they demonstrated that when group members were present and eating a familiar food, there was a significant increase in the acceptance of novel foods. Therefore, they argued that social facilitation of eating may indeed be a quicker way to overcome neophobia than encountering food alone. However, social facilitation is not necessarily a safe way to learn about a potential new food's palatability unless it works selectively and attention is paid to what the others are eating.

18.4 Conclusions

Social learning in animals can be described as socially biased individual learning (Galef 1995), and as learning about the environment from information provided by others. Experiments with tufted capuchin monkeys afford insight into the strength and specificity of social bias affecting the manipulation of objects, the replication of familiar action, the matching of novel actions, the initiation feeding, and food choice. Capuchins can be taken either as representative of monkeys in general (in line with cognitive abilities), and thus could be expected to illustrate monkey-typical social learning, or they can be taken as probable candidates for elaborated social learning, and more specifically, for imitative ability (on the basis of social and instrumental proclivities) (see section 18.1, Introduction). We have found that social partners do affect many aspects of behavior in capuchins, in line with their social proclivities. However, they do not imitate or learn unlikely behaviors from one another. The domain-specific hypothesis that imitative ability co-varies with manipulative ability is not supported. As capuchins do not imitate, we have no strong grounds at present for expecting that any other species of monkey will be able to do so. In fact, despite the many efforts to find imitative learning in other monkey species, the recent data supporting it are few and, like the earlier studies cited in our original "Do Monkeys Ape?" chapter in 1990, open to alternative interpretations. For example, Tanaka (1995) reported on the basis of extremely detailed field recordings that techniques of allogrooming were shared among members of the same low-ranking matriline. Although fascinating

findings in their own right, these are correlative data that do not permit one to infer any particular basis for the similarity in actions. In another recent report, Bugnyar and Huber (1997) tested marmosets with a dual-action task. In their study, the experimental monkeys observed a trained demonstrator pulling a door open on a test apparatus and then the observers could act on the door themselves either by pulling or by pushing. Control subjects encountered the apparatus without having seen the demonstrator acting on it. Three of five subjects that watched the demonstrator pull the door initially pulled it more than pushed it when they began to interact with the apparatus, and they persisted in the same form of action for somewhat longer bouts than the other two monkeys or the control (naive) monkeys. The other two monkeys in the experimental group did not show these biases. Naive monkeys were equally likely to push or pull when they first encountered the apparatus, and to alternate among these actions rapidly. Although the researchers claim some support for imitative learning from these data, in our view the results are not clear enough to draw any strong conclusions. Moreover, a better explanation for the findings is a weak tendency to match the direction of object movement, as we have argued occurs in capuchins as well. In both taxa, the phenomenon appears to be rather weak, and in the case of marmosets, further study is required to confirm its existence.

Many years ago, the English biologist George Romanes (1884/ 1977, p. 477) wrote that "it is proverbial that monkeys carry the principle of imitation ... they are animals that imitate for the mere sake of imitating." Although his words are eloquent, we think Romanes dramatically overstated the case. On the basis of both older and newer studies, for capuchin monkeys (and other monkey species too), imitation has yet to be demonstrated. Instead, others' actions influence whether or not the capuchin observer eats (but not what it eats), and channels its interest in particular objects, and perhaps where objects are moved (but not the details of what the other does with those objects). Under natural circumstances, these influences are sufficient to support the development of group-homogeneous patterns of food choice and to synchronize feeding activities, and probably many other kinds of behavioral coordination among members of a group. We think this characterization of susceptibility to social influence in action fits other non-human primates well, including the apes, which admittedly have expressed greater likelihood of reproducing object movements,

and even of reproducing actions (as in Myowa's 1996 study with neonatal chimpanzees reproducing facial movements) than have monkeys. Nothing in our findings suggests specialized abilities in social learning that are not evident in other domains; a domain-general view of cognition seems to work better.

Social learning continues to fascinate us, as well as many others in the fields of comparative psychology and evolutionary biology (e.g., Laland, Odling-Smee, and Feldman, 2000). Perhaps it is good to remind ourselves that dichotomous approaches to social learning ("can they or can't they") are misguided *because* the paths through which knowledge is acquired are redundant: an individual, and even more so an individual in a social situation, may learn the same thing by more than one process. This means that the same behavior can be learned through different processes by different individuals and/or that the same individual may learn similar tasks (e.g., different types of tool use) through different processes, and that several processes can contribute to learning the same behavior by one individual. However, in all cases, social learning should lead to faster dissemination of a learned behavior in a group than individual learning, as social learning depends on "public information" from behavior and each new proficient individual provides such information to those around itself when it performs the learned behavior (Giraldeau 1997).

Finally, a new puzzle has recently appeared for primatologists, like us, and neurologists as well, to solve. Neuroscientists have identified neurons in a particular area of premotor cortex of macaques that fire selectively in response to both an *executed* grasping action, and an *observed* grasping action performed by another individual, monkey or human (di Pellegrino et al. 1992; see also Rizzolatti et al. 1996; Arbib, chapter 10 of this volume). The researchers who discovered these neurons designated them as "mirror neurons" and they proposed that these neurons' activity constitutes a system for matching observation and execution of motor actions. Perhaps these neurons provide a neural substrate for segmenting a stream of action into discrete elements matching those in the observer's repertoire, as Byrne (1999) has suggested in connection with his string-parsing theory of imitation. It is tempting to think that these neurons may provide us with insight into how the brain achieves matching of observed movement to produced movement. Many puzzles must be solved to know if they can meet this expectation. The first puzzle is whether neural

"mirror" responsiveness contributes to monkeys' abilities to produce object movements and positions, in addition to detecting them. If they are involved in production, a second puzzle is to identify those additional processes that allow humans to match actions, in addition to object movements and positions, and so afford humans an imitative "edge."

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