

Socially biased learning in monkeys

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We review socially biased learning about food and problem solving in monkeys, relying especially on studies with tufted capuchin monkeys (*Cebus apella*) and callitrichid monkeys. Capuchin monkeys most effectively learn to solve a new problem when they can act jointly with an experienced partner in a socially tolerant setting and when the problem can be solved by direct action on an object or substrate, but they do not learn by imitation. Capuchin monkeys are motivated to eat foods, whether familiar or novel, when they are with others that are eating, regardless of what the others are eating. Thus, social bias in learning about foods is indirect and mediated by facilitation of feeding. In most respects, social biases in learning are similar in capuchins and callitrichids, except that callitrichids provide more specific behavioral cues to others about the availability and palatability of foods. Callitrichids generally are more tolerant toward group members and coordinate their activity in space and time more closely than capuchins do. These characteristics support stronger social biases in learning in callitrichids than in capuchins in some situations. On the other hand, callitrichids' more limited range of manipulative behaviors, greater neophobia, and greater sensitivity to the risk of predation restricts what these monkeys learn in comparison with capuchins. We suggest that socially biased learning is always the collective outcome of interacting physical, social, and individual factors, and that differences across populations and species in social bias in learning reflect variations in all these dimensions. Progress in understanding socially biased learning in nonhuman species will be aided by the development of appropriately detailed models of the richly interconnected processes affecting learning.

Studies of social learning in monkeys began in the laboratory in the 1930s and 1940s (e.g., Warden, Fjeld, & Koch, 1940). In these studies, an observer–demonstrator paradigm was adopted, in which one monkey watched another perform an arbitrary task (usually, choosing one of two objects, one of which covered a well containing a piece of food and the other an empty well). Following opportunities to observe their partners solving these problems, the observer monkeys learned to select the correct object more quickly than monkeys that did not observe a demonstrator. This work supported the notion that monkeys could learn from each other, but it did not lead directly to investigations of the phenomenon in more natural social circumstances or in a broader variety of learning contexts (e.g., problem solving, in which the actor initiates varied behaviors to discover a solution). Wider interest in social learning awaited other developments, some conceptual (e.g., reasons to think about social

learning in wild animals; Klopfer, 1961) and some empirical (e.g., evidence that monkeys learn from each other in nature).

Reports about social learning in wild monkeys date back to the 1950s, when food washing and other unusual feeding behaviors acquired by Japanese monkeys at Koshima garnered great attention (Itani & Nishimura, 1973; Kawai, 1965; Kawamura, 1965). Studies of social relationships and of potentially socially acquired behaviors in free-living Japanese macaques continue to this day and have proven to be a rich source of ideas and information (Hirata, Watanabe, & Kawai, 2001; Huffman, 1996; Huffman & Hirata, 2003; Watanabe, 1994). Eventually, observational and experimental studies of social learning in groups of captive monkeys began to appear (e.g., Cambefort, 1981; Lepoivre & Pallaud, 1985). This line of research gained momentum in the 1980s as social learning received wider interest in comparative psychology and in biology as a whole (Zentall & Galef, 1988), and behavioral variation as a source of innovation and adaptability received increasing attention (Kummer & Goodall, 1985). Meanwhile, laboratory studies with monkeys using the familiar observer–demonstrator paradigm showed that monkeys are highly sensitive to other monkeys' expression of strong negative affect, suggesting an avenue for social learning of fears and avoidance (Mineka & Cook, 1988). Early reports about tool use in wild

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chimpanzees (Goodall, 1964; McGrew, 1974; McGrew & Tutin, 1973), coupled with reports of imitation in a human-reared chimpanzee (Hayes & Hayes, 1952), fueled interest in the possibility that monkeys and apes might learn innovative behaviors, such as the use of tools and other skills, through imitation or a related process.

Looking for Imitation

Unlike all other monkeys, capuchins readily use tools (Fragaszy, Visalberghi, & Fedigan, 2004; Visalberghi, 1990). When we began our collaboration about 20 years ago, we did not know whether capuchins could learn something quite specific from each other about how to use an object as a tool, whether social context might exert some less specific influence on activity that could promote learning and behavioral convergence, or whether social factors were of little importance. At that time, the view that monkeys were able to learn new behaviors or solve problems through imitation was widespread among our colleagues as well as among laymen (Visalberghi & Fragaszy, 1990a). Thus, we embarked on a research program to clarify how social context affected individual capuchins' discovery of how to use an object as a tool.

In our first collaborative study (Fragaszy & Visalberghi, 1989), we presented two different food-providing apparatuses to two groups of monkeys. One apparatus functioned like a vending machine: When a rod chained to the apparatus was inserted far enough into a transparent tube, a small quantity of sunflower seeds fell into a cup below the tube. The other apparatus was a wooden platform with several walnuts glued into holes so that only the tops of the shells were exposed. A hexagonal steel nut (with an open center, threaded to fit a bolt) that the monkeys could hold easily with one hand was tied to the platform. The monkeys could open the walnuts by pounding on them with the steel nut. Several monkeys in each group learned to solve these problems. However, analyzing when each animal interacted with the apparatus, what it did, with what companion(s), and the order in which individuals solved the tasks did not enable us to pinpoint any necessary role of social influence or to identify a common effect of social influence for all individuals. Instead, we found a far more complicated picture. Those monkeys that solved the problems explored the apparatus most often while alone. Some monkeys hung around the apparatus to collect bits of food provided by others, and these monkeys did not learn to solve the problems themselves. Some approached the apparatus only briefly when others who were usually there moved away; a few of these peripheralized individuals still managed to use the tools successfully once or twice. In short, social context exerted a complex and sometimes inhibitory influence on individual activity and a differential influence on each individual. We concluded that capuchins did not learn about specific instrumental relations (i.e., how to use a tool) by observation, but they did quickly learn the relationship between another's actions at the apparatus and the appearance of food (hence,

the value of scrounging). This study made us far more skeptical about the probability that monkeys learned new behaviors, or how to solve problems, by imitation (Visalberghi & Fragaszy, 1990a).

In another attempt to assess imitation in a tool-using task, Visalberghi (1993) presented capuchin monkeys with sticks and a baited tube. Three of the 6 capuchins tested spontaneously solved the task within 2 h of presentation. Despite their interest in the food in the tube and sustained manipulation of the sticks, the other 3 capuchins (1 adult and 2 juveniles) did not use the sticks as tools to push out the food even after many trials. To assess how the model's actions might influence their behavior, these 3 monkeys were presented with the tube task again in what we called "lessons." During the lessons, they had the opportunity to watch capuchin models insert the stick into the tube and push out the reward. The three "pupils" witnessed 57, 75, and 75 solutions, respectively. To make a long story short, these capuchins contacted the tube with the stick significantly more often during and after the lessons than before the lessons. Nevertheless, after watching the models, none of them solved the problem (Figure 1), nor did they improve the orientation of the stick in relation to the opening of the tube. Analysis of the videos taken during the lessons revealed that they did not look selectively at the actions of the model while it solved the problem in comparison with other periods (i.e., during insertion of the stick in the tube and pushing the reward vs. during holding the stick and eating the reward). The monkeys clearly did not imitate the model.

Following these failures to demonstrate imitation in capuchin monkeys, we tried a different paradigm, suggested by Tomasello, Kruger, and Ratner's (1993) hypothesis that human-reared apes are better able to attend to and copy a human model than are apes reared by other apes. Custance, Whiten, and Bard (1995) showed that young nursery-reared chimpanzees could reproduce some actions demonstrated by a familiar human companion, replicating in part the classic report by Hayes and Hayes (1952). Inspired by these ideas, and in a partial replication and extension of Custance et al.'s (1995) study with chimpanzees, Fragaszy and colleagues (Fragaszy, Deputte, Hemery, & Johnson, 1998; Hemery, Fragaszy, & Deputte, 1998) tested 3 young (4.5-year-old) capuchins raised in human homes. The capuchins were first trained to match familiar (i.e., species-typical) actions, on their bodies or with objects, when a familiar human demonstrator performed the actions on her own body or with identical objects. For the actions including an object, the human demonstrator handled in a distinctive way one object of a set of eight on a tray (for example, unzipping a zipper or opening a hinged wooden "book") or combined one object with another (for example, placing a stick into a hollow cylinder). The experimental objects were scaled to an appropriate size so that the monkeys could manipulate them easily. The sessions were videotaped. Several forms of data were col-



Figure 1. The capuchin monkey on the left, which does not know how to use a stick to push the peanut out of the tube, attentively observes another monkey solve the task. Despite having observed many solutions, the observer did not succeed when she acted with the stick herself.

lected from the videotapes by an observer familiar with the test protocol. Two capuchins contacted the same object(s) contacted by the human following 60% of the demonstrations; the third monkey did so following 30% of the demonstrations. However, they unambiguously matched the demonstrator's *action* in only a small percentage of trials (20%, 11%, and 4.3%, respectively). For the two better subjects, level of matching was better when they were more attentive to the demonstration and for those actions that involved contacting an object (e.g., opening a book) and combining an object with another object or surface (e.g., putting a stick into a cylinder) than for actions on the body (e.g., touching the arm).

The best performer proceeded to a new phase of testing, in which novel actions were interspersed with familiar ones in a 1:4 ratio. The monkey's scores for visual attention to the demonstrator's actions, contacting the objects the demonstrator had contacted, and performance of the familiar actions were maintained in this phase at the rates evident at the end of the training sessions. The subject responded as quickly to demonstrations of novel actions as to those of familiar actions and performed some action on nearly all trials (88%). However, two scorers blind to the demonstrated novel actions judged the subject to have matched the action on only 3 of 24 trials (12.5%). The matched actions included turning a screw with a screwdriver, putting one notched block across another, and turning a crank handle. Even in these cases, the blocks were not fully aligned, and the subject did not move the crank or the screw the same distance or the same number of rotations as the demonstrator did. The rate of matching the novel actions (all of which involved repositioning

an object), although above zero, is half that of matching familiar actions, which was modest to begin with (see Visalberghi & Fragaszy, 2002, for further details).

Intensive and prolonged interaction with humans (during early life and in the course of extended training to respond to verbal commands issued by humans) seems to affect capuchins' visual attention to humans and to enhance their interest in the objects that a human touches (Hervé & Deputte, 1993). These perceptual tendencies may increase the monkeys' probability of matching object movements. However, such experience does not seem to lead to enhanced ability to match *action*.

These findings are similar in substance to those reported by Custance, Whiten, and Fredman (1999) with a larger number of hand-reared capuchin monkeys. These investigators used a two-action design in which a demonstrator took two distinctive actions on an object; each group of subjects saw just one of the two actions. Custance et al. (1999) examined whether the monkeys would perform the actions they had seen performed by a human demonstrator more frequently than the actions that 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 consisting of two related actions. Eleven subjects saw their familiar caretaker acting on the latches to open the box. In the barrel latch task, half of the subjects saw a pin at the front of the box being *turned* several times and then a handle being *turned*; the other half saw the pin being *spun* and then the handle being *pulled*. In the bolt latch task, half of 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*.

The monkeys used the demonstrated technique and the nondemonstrated technique with the barrel latch at equivalent frequencies, and the human scorers were unable to infer reliably which technique the monkeys had seen demonstrated. Similarly, the monkeys used the two techniques for the bolt latch at equivalent frequencies. However, for this object, the human scorers were able to infer reliably which technique the monkeys had seen demonstrated. Custance et al. (1999) therefore analyzed the directions in which the rod was acted upon and from which it was removed (back vs. front, respectively) for the bolt latch. They found that their experimental groups differed in the frequencies with which they (1) pulled the rod from the front or the back side of the box, (2) pushed the rod from the front side of the box (but not from the back side), and (3) removed the rod from the front or the back side of the box. These actions are partially dependent on one another: 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 human scorers to discriminate between the two experimental groups of capuchins.

Custance et al. (1999) label the phenomenon of reproducing the direction of the rods' movement "object movement re-enactment." The notion that the monkeys acted to move an object at the front or at the back of the box (the side on which they had seen the rod moved by the human model) is plausible and consistent with the low level of matching object movements that Frigaszy et al. (1998) observed in the hand-reared monkey exposed to novel actions. Recall that the capuchin in Frigaszy et al.'s (1998) study did not match, even partially, novel actions that did not involve moving an object, nor those that involved an action directed to its own body. (Custance et al., 1999, did not include actions with objects in their list of modeled acts.) In sum, both of the studies carried out with hand-reared capuchins suggest that capuchins that are attentive to human demonstrators seem able to capture some of the spatial relations about objects from the humans' actions with those objects.

Whereas capuchin monkeys had the most trouble matching actions involving the body, 2 young chimpanzees in Custance et al.'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 a substrate (e.g., slapping the floor). Adult 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 (Myowa-Yamakoshi & Matsuzawa, 1999). In the latter study, directionality of the object's movement was a more salient cue for the subjects than the demonstrator's bodily movements.

Myowa-Yamakoshi and Matsuzawa (2000) also showed that chimpanzees reproduced the directional movement of the object during solution of a manipulative problem that they had seen a familiar human solve. Thus, it seems that capuchin monkeys and chimpanzees share a perceptual bias to notice directional movement of objects more than movement of another actor's arms or hands. 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 for observers to perceive and remember them in the new location. Perhaps this temporal property supports the capuchins' and chimpanzees' better abilities at matching direction of object movement and object positions than at matching movements of an animate actor.

Note that other perceptual biases may also contribute to behavioral matching and that these biases may be differentially present across species. Voelkl and Huber (2000) showed that marmosets that had viewed another marmoset opening a small container by pulling with hands and mouth were more likely to use the mouth than were marmosets that had seen the other using only its hands to open the same container. Apparently, marmosets are more likely to use the same body part as a demonstrator used during action on a novel object.

This aspect of behavioral convergence has not been examined explicitly in capuchins or in other primate genera, but it seems of general significance to social influence on action and may link studies in this domain with recent discoveries of *mirror neurons* (neurons in premotor cortex that respond to the sight of action with a particular body part performed by the individual as well as by others; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The relation between mirror neurons and socially biased action is likely to receive much attention in the future.

Looking for Social Influences Supporting Learning of Novel Behavior—Food Washing

Like many other primatologists, we were inspired by the long-term studies carried out by Itani, Kawai, and others on Japanese macaques (*Macaca fuscata*) living in Koshima, studies that continue to this day (see above). In the 1960s, these monkeys became famous as an example (in fact, the only example) of "protoculture" among monkeys. About 50 years ago, researchers began to give sweet potatoes on a regular basis to a group of monkeys at a sandy beach on the small islet. At that time, sweet potatoes were a new kind of food for these monkeys. One individual began to take her potato to shallow water and to rub it in the water with her hand(s), a behavior not seen before at Koshima with any food. Other members of her social group slowly began to do roughly the same over a period spanning several years. Over time, a variety of actions combining potatoes and water could be distinguished, and individuals performed them differentially (Hirata et al., 2001). These behaviors are collectively

identified as *potato washing*. Most researchers found the sequence of events (discovery, spread, and elaboration of washing) at Koshima compelling evidence that socially biased learning in some form played a pivotal role in the process. The story of potato washing is powerful in part because washing seems an unlikely action for monkeys. But is it really? How likely are monkeys to dip objects into water, and how important for the spread of this behavior is a supportive social context? These questions prompted us to do an experimental study of food washing with captive monkeys (Visalberghi & Fragaszy, 1990b).

We presented small groups of capuchin monkeys (*C. apella*; $N = 5$) and crab-eating macaques (*M. fascicularis*; $N = 4$) with basins of water on the floor of their home cages and pieces of cut fruit coated in sand. The monkeys were first familiarized with the pan of water for a few hours on the days before testing. All 5 capuchins and 3 of the 4 macaques began to place the sandy fruit in the water within 2 h of exposure to the fruit and water together. The species differed in the details of their interactions with the water in interesting ways: The macaques ran into and through the basin of water with apparent great pleasure, and the fruit they were holding at the time got wet in the process. Capuchins, in contrast, stayed outside the basin and placed the fruit (and many other objects available in their cage) into it more deliberately. The net result was the same, however: Sand came off the fruit and it became more appealing to the monkeys to eat it.

Our findings suggest that individual exploratory behavior toward objects, coupled with attraction to standing water, made the behavioral pattern identified as food washing extremely probable in our crab-eating macaques. Social processes were not central to the macaques' behavior with food and water, although the social context did contribute generally to high levels of playful behavior. These processes were also evident in capuchins, but to a lesser degree. Given our findings, we are inclined to reverse the usual questions about potato washing by the macaques at Koshima: What elements in the normal social context, the physical setting, and the manner of presenting potatoes inhibited many monkeys at Koshima from taking the potatoes to nearby water? Why did it take years instead of days for others to adopt the same behavior, and why is it that some never did? Potential answers to these questions should become clear as we discuss the range of factors affecting the probability that monkeys will come to do what others around them do.

Juveniles Learning to Use Tools

Taking a developmental slant on the problem of social learning, Fragaszy, Vitale, and Ritchie (1994) looked at how 9 juvenile tufted capuchins in captive groups acquired a specific skill in two different social settings. In one case, the juveniles encountered a task in the company of other juveniles or on their own, but away from adults, in a wire mesh enclosure (hereafter, a *crèche*) that the young animals could enter and leave at will. In the other case, the juveniles encountered a task in the com-

pany of proficient adults in the home cage. In each test session, a group received one kind of task (to dip with sticks for syrup or to pound open walnuts fixed to a surface). Several adults in each group were proficient at both of these tasks, but the tasks were novel for the youngest members of the group (those 2 years old and younger). The expectation was that if the activity of adults supports learning by naive individuals, then youngsters should acquire skills more readily when adults are acting proficiently than they would when they are encountering the same challenges on their own.

The findings provided little support for this prediction. The juveniles were more likely to contact an apparatus at times when the adults also had one. When an apparatus was present at both sites, 4 juveniles (13–22 months old) used the group site more, and the other 4 juveniles (19–31 months old) used the *crèche* site more (1 juvenile had learned to solve the problems in baseline sessions; her data were excluded from this analysis). Five juveniles learned to solve one or both of the problems during test sessions. However, being copresent at the apparatus with proficient adults was not associated with learning to use the tools, and no juvenile in the *crèche* closely monitored adults' actions, nor did any juvenile exhibit any form of behavioral matching at the time the adults were active. The younger animals were more likely to be copresent with an adult, but the older animals were more likely to learn to use the tools. Thus, age and individual practice were better predictors of learning to use the tool than time spent at the adult apparatus or exploring any apparatus at the same time as the adults.

Overall, this study indicated that juveniles are stimulated to explore when adults are active, but they do not gain a strong benefit from being around proficient adults in learning to use an object as a tool. Zuberbühler, Gygax, Harley, and Kummer (1996) report similar findings with captive long-tailed macaques: The dominant adult male in the group spontaneously began to use sticks to sweep in objects from out of reach on the other side of the wire mesh exterior of the enclosure. After they noticed his skill, researchers provided fruit outside and sticks inside the enclosure on a regular basis. The other macaques manipulated bits of wood more frequently when the proficient male was busy sweeping in fruit, but they did not orient their held objects to their targets outside of the enclosure, nor did they select bits of wood that would be suitable for use as a rake—they picked up and handled pieces of bark, for example. While the tool user was using a stick to sweep in objects, the others sat behind or nearby, busily manipulating their own bits of wood, apparently to no particular effect. However, after many months, a few other males in the group began to use sticks to sweep in objects. Zuberbühler et al. conclude that stimulus enhancement may have contributed to their discovery and that the original tool user (the alpha male) may have had greater salience for males in his group than for females. Indeed, the second monkey to learn to use a rake tool, a young male, had a long-

term, strongly affiliative relationship with the original tool user. This case fits well the model for directed social learning proposed by Coussi-Korbel and Fragaszy (1995), which highlighted the supporting role of social affiliation and tolerance between expert and learner in fostering learning by individuals in the presence of particular others.

Juveniles Learning to Operate a Dispenser

Perhaps learning to use a tool is so challenging for capuchins that this kind of task reduces the probability of wide success among group members. If this is the case, presenting other kinds of tasks would be a more effective strategy for finding social contributions to acquisition of skill in experimental studies of problem solving. Fragaszy, Landau, and Leighty (2001, 2002) presented simpler manipulative problems to 20 juvenile (< 2-year-old) capuchin monkeys living in two captive groups. In the first phase of the experiment, the youngsters encountered an apparatus containing juice in a crèche that the adults could not enter but that the juveniles could enter and exit at will. The youngsters could obtain juice in two ways: by putting a finger into a small opening and turning a small, scalloped wheel that passed through a reservoir filled with juice, or by pushing a lever down and releasing it for a pulse of juice. Although there were a few ambiguous, isolated solutions, none of the juveniles solved the task in the crèche using either method in 20 half-hour sessions. Immediately thereafter, Fragaszy et al. (2001, 2002) presented the same apparatus to each of the two groups for 22 half-hour sessions at two locations: in the crèche with both solutions enabled, and in the group enclosure with either the lever (Group 1) or the finger wheel (Group 2) enabled. Most of the adults learned to obtain juice within these sessions. In Group 1, in which the juveniles could be near adults demonstrating the lever solution, 4 of the 6 youngsters solved the lever task, but only 2 youngsters used the finger wheel in the crèche, where they had no demonstrators (except, eventually, each other). In Group 2, 9 of the 14 youngsters routinely used the finger wheel—the solution demonstrated by the adults in that group—but only 2 used the lever in the crèche (see Table 1). Thus, immature animals did not manage to solve these tasks on their own, but they did

learn to do so when they had adult models and, moreover, they tended to adopt the solution style of adults in their groups.

Fragaszy et al.’s (2002) study, like those of Visalberghi (1993), Fragaszy et al. (1994), and Zuberbühler et al. (1996), suggests that adults’ activity with an object particularly stimulates younger animals’ activity with similar objects. In Fragaszy et al.’s (2002) study, manipulating objects directly was sufficient for the naive individuals to achieve the goal (obtaining juice). This is the normal situation in natural settings, in which monkeys act directly on objects enclosing or bearing food. It seems likely that social enhancement of exploratory activity with specific objects or substrates, particularly in socially tolerant settings, is an important aid to youngsters learning how to access and process difficult foods. In particularly tolerant settings, young individuals may coact with others, and this seems a powerful aid to learning to solve a mechanical problem, such as how to open a container or how to perform direct insertion (Westergaard & Fragaszy, 1987; see Coussi-Korbel & Fragaszy, 1995).

Learning About Food With Others

Capuchin monkeys are moderately neophobic toward potential new foods (Visalberghi & Fragaszy, 1995; Visalberghi, Janson, & Agostini, 2003). If social context aids naive monkeys in learning about a novel food, capuchins should be a promising genus in which to study the phenomenon because they show marked tolerance toward each other during feeding. Particularly in captive situations, individual capuchins routinely sit near each other while feeding, and they frequently closely attend to the foods others are eating; these characteristics are especially evident in young animals (Fragaszy, Feuerstein, & Mitra, 1997; Fragaszy, Visalberghi, & Galloway, 1997). A monkey possessing food routinely allows others to take small bits of the food that it has dropped nearby, and occasionally larger pieces (de Waal, 1997; de Waal, Luttrell, & Canfield, 1993; Fragaszy, Feuerstein, & Mitra, 1997). The strong interest of monkeys in the foods of other monkeys and the frequent transfers of food among individuals give the casual human observer the strong impression that they learn something about the palatability of foods from each other.

Attending to others while they eat a food novel to the viewer could promote acceptance of novel foods in capuchins in at least three ways. The simplest mechanism could be that seeing others eating anything promotes eating by the viewer, without regard to the specific items eaten by the viewer or by others. The second mechanism is more specific: Seeing others eating a new item could promote the spectator’s interest in or acceptance of that particular item. A third mechanism, and the most specific, is that naive individuals might attend closely to others’ behaviors toward a potential new food before sampling it themselves.

We have the most positive evidence for the first mechanism. For example, satiated capuchins recommence eat-

Table 1
Number of Juvenile Capuchin Monkeys (6–24 Months Old)
Obtaining Juice in One of Two Ways When Adults in
Their Groups Modeled One Solution

Group	Age Class	Solution	
		Wheel	Lever
1	Adults	NA	5 of 6
	Juveniles	2 of 6	4 of 6
2	Adults	5 of 5	NA
	Juveniles	9 of 14*	2 of 14*

Note—Data were collected during twelve 30-min sessions, when both solutions were available to the juveniles. *Significant within-group difference by juveniles in solution of wheel task versus solution of lever task ($p < .05$, Fisher’s exact test).

ing if familiar individuals begin eating (Galloway, 1998). Monkeys more readily eat novel foods when other monkeys nearby are eating (Galloway, 1998; Visalberghi & Addessi, 2000a; Visalberghi & Fragaszy, 1995) than without group members nearby. In initial presentations of a novel food, other group members that are feeding promote an individual's acceptance of the novel food. Addessi and Visalberghi (2001) evaluated feeding behavior of individual capuchin monkeys encountering a novel food alone, with a partner when only the subject could eat, and when a fellow member of their group was also eating. In the presence of a group member, individuals ate 22% more (by weight) of a novel food than when they were alone. When the group member was present and eating, the individuals ate 64% more than when they encountered the food alone. However, after just a few encounters, consumption of the previously novel food reaches similar levels regardless of whether individuals had previously encountered it alone or with other members of their group (Visalberghi, Valente, & Fragaszy, 1998). Altogether, it is clear that capuchin monkeys can facilitate eating by others when they are eating.

There is also some support for the second mechanism: that seeing others eat promotes interest in the food that the other is eating, especially if the food is novel. Capuchins show interest (inspection at distances of less than 5 cm) in other individuals' novel food far more often than in familiar food (Fragaszy, Visalberghi, & Galloway, 1997). This holds true when a food with a familiar aspect has a novel odor (Drapier, Addessi, & Visalberghi, 2003). Interest in others' novel food is especially evident among immature animals (Fragaszy, Feuerstein, & Mitra, 1997; Fragaszy, Visalberghi, & Galloway, 1997), even though juvenile and infant capuchins in captivity do not display neophobia; they are as likely to eat novel as familiar foods (Fragaszy, Visalberghi, & Galloway, 1997).

We have no evidence of the third mechanism: that capuchins are more likely to accept a specific novel food after seeing others eat that food. Although capuchins pay close attention to others' food, this does not seem to influence what they eat next. Capuchin monkeys consume more of a novel food (as measured by the duration of feeding and by weight of food consumed) when group members are also eating, but the amount (by weight) of food ingested is not affected by whether the observer eats food of the same color or of a strikingly different color than that which the group members are eating (Visalberghi & Addessi, 2000a, 2001; see Galloway, 1998, for the same result with familiar foods of varying colors). A similar finding is obtained if the observer can choose between novel food of two different colors (when the two colors match the colors of the two foods presented to the demonstrator) and the demonstrator is eating only one of them. Even in this experimental setting, when the observer witnesses the demonstrator choosing food of just one color, the observer does not preferentially sample the food with the same color as that chosen by the demonstrator (Addessi & Visalberghi, 2002). Instead, the observer

samples the two novel foods equally. The same finding holds when odor, but not color, varies between the two food sources (Drapier et al., 2003).

Just as capuchins do not rely on others' actions toward novel foods to sample them themselves, they do not rely on others' behavior to assess the current palatability of familiar food (Visalberghi & Addessi, 2000b). In Visalberghi and Addessi's (2000b) study, capuchins, both individually and within their group, encountered familiar palatable food for five sessions, then the same food rendered unpalatable by the addition of white pepper for five sessions, and, finally, the familiar palatable form of the same food again in a final five sessions. Whether tested individually or in a group, capuchins quickly responded to the change in palatability; there was no difference in behavior between those that encountered the altered foods by themselves and those that encountered them in the group.

During this study, as during previous studies concerning acceptance of novel foods by captive capuchin monkeys (Addessi & Visalberghi, 2002; Fragaszy, Visalberghi, & Galloway, 1997; Visalberghi & Addessi, 2000b; Visalberghi & Fragaszy, 1995; Visalberghi et al., 1998), we never observed a more knowledgeable individual attempting to prevent a naive individual from eating unpalatable or novel foods or encouraging a young individual to eat a novel food. In contrast, cotton-top tamarins (*Saguinus oedipus*) living in family groups did avoid palatable foods made unpalatable by the addition of pepper after just one individual in the family had sampled and rejected it (Snowdon & Boe, 2003; see Hikami, 1991, for a related study with macaque mother-infant dyads). Cotton-top tamarins produced highly salient behaviors, vocalizations, and facial expressions when they rejected unpalatable food. Capuchins, in contrast, simply spat out the unpalatable food.

Elements Influencing Social Bias on Learning in Capuchin Monkeys

Overall, the findings of the studies reviewed above illustrate that socially biased learning is always framed within the social and physical setting of behavior and is influenced by the characteristics of the individual, and that all these elements are interrelated. Individual characteristics include behavioral repertoire, general attraction to others, salience of specific partners present at that moment, responsiveness to objects, motivation to engage in new activity, prior experience with the setting, and ongoing experience (e.g., current activities; current internal state). Social elements that bear on an individual's likelihood of learning while with another include the composition of social partners, tolerance of these individuals for the focal learner, the value added to an object or a place by another's actions there and by expressions of affect while performing them (e.g., vocalizations associated with food), and residuals that remain from the others' activity (e.g., bits of food; altered substrates). The physical setting includes the abundance of sites in

which to act, the accessibility of these sites, and so on. The physical setting also affects risks for action. For example, predatory risk pervasively influences the activity of nonhuman primates (Boinski, Treves, & Chapman, 2000); assessment of predatory risk depends on familiarity with the place and with many physical details that one might initially not consider relevant to the issue of social learning (such as the density of foliage cover, ambient acoustics, the elevation of the site, and the variety, position, and abundance of travel routes to and from the site). Monkeys are unlikely to explore a new opportunity for action in a setting in which perceived risk of predation is high. From this ecological perspective, we must look beyond dyadic interactions to understand the course of socially biased learning, whether in natural circumstances or in contrived experimental circumstances. We need an inclusive model of socially biased learning that incorporates individual, social, and physical elements. Network models would be one approach to this problem. We anticipate that modeling studies will assume greater importance in the field of comparative cognition in the next decade.

We see two strong benefits of pursuing modeling of socially biased learning as the outcome of an adaptive network. First, developing and testing models (via both simulations and empirical work) helps move science forward, and there is a clear need for model testing in the area of socially biased learning (Laland & Kendal, 2003). Simulation studies of the formal properties of adaptive networks are a point of advancement for biology as a whole (Bray, 2003; Jasny & Ray, 2003) and, of particular interest in our context, in studies of behavior of group-living animals (Fewell, 2003). Second, network models of socially biased learning can provide a conceptual link with other areas of biology using the same explanatory principles and the same language to describe dynamic biological systems, including (going down a level) the nervous system (e.g., Elman et al., 1996) and (going up a level) the behavior of groups (e.g., Camazine, 2001; Hemelrijk, 2002). As Kamil (1998) suggests, the more links we can make with other areas of biology, the more scientifically vigorous the field of comparative cognition will become.

Callitrichid Counterpoint

Callitrichid monkeys (*Callithrix*), marmosets (*Leontopithecus*), lion tamarins, and tamarins (*Saguinus*) provide a useful comparative counterpoint to capuchins. Callitrichids are small-bodied diurnal monkeys that live in family groups in which all group members participate extensively in caring for offspring (Rylands, 1993). Capuchins, in contrast, are medium-sized monkeys that live in larger groups with multiple breeding females and males. Although capuchins are relatively tolerant toward one another, especially toward young individuals, they do not stay as close to one another as do callitrichids. Overall, callitrichids organize their behavior to a greater extent than do capuchins around the task of maintaining spatial and behavioral cohesion with their social part-

ners. Callitrichids feed on insects and small vertebrates, fruits, and tree sap, with the various genera specializing to some degree in the manner in which these foods are obtained (Dietz, Peres, & Pinder, 1997). Capuchins also feed on animal prey and fruit, but their foraging is distinctive in the extent to which these monkeys extract hidden foods from tough embedding matrices (e.g., wood, husks, and shells) through vigorous action with teeth and hands (see Fragaszy et al., 2004, for a review). Some callitrichids search for and extract hidden food, and differences in some other behaviors across species in these genera parallel differences in the reliance on extraction and opportunism in feeding (Day, Coe, Kendall, & Laland, 2003). By virtue of their size, callitrichid monkeys are more vulnerable to predation than are capuchins, and, correspondingly, they are more cautious than capuchins toward novel spaces and objects (cf. Fragaszy & Adams-Curtis, 1990, and Westergaard & Fragaszy, 1985, with Day et al., 2003, and Hardie & Buchanan-Smith, 2000).

These differences in behavioral ecology correspond to marked differences in the behavior of callitrichids and capuchins in similar experimental settings designed to assess socially biased learning. For example, as we have reviewed above, cotton-top tamarins can learn to avoid unpalatable food by once observing a group mate display disgust when sampling that food (Snowdon & Boe, 2003). Snowdon and Boe suggest that the strong social relationships present in cooperatively parenting species, such as callitrichid primates (marmosets and tamarins), can support learning to avoid foods sampled by others and to prefer foods chosen by others, although this kind of learning is not evident in less cooperative species (such as capuchins). This suggestion is in line with Coussi-Korbel and Fragaszy's (1995) prediction that strong prior social relationships positively impact the likelihood of social learning. Queyras, Scolavino, Puopolo, and Vitale (2000) showed that individual marmosets, conditioned to avoid a familiar food made unpalatable by the addition of table salt, immediately readopted the familiar food preference when tested together with members of their family groups that did not avoid the food. When tested by themselves, they continued to avoid the familiar food, although it was no longer adulterated with salt.

Callitrichids transfer food to offspring more directly and more frequently than all other nonhuman primates (Feistner & McGrew, 1989). Price and Feistner (1993) showed that in captive groups of lion tamarins (*Leontopithecus* spp.), infants begged more and received more food from adults when food was difficult for infants to obtain independently or was presented singly (rather than in abundant quantities), but adults were less likely to share novel foods than familiar foods. Thus, these authors concluded that food sharing did not necessarily contribute to young lion tamarins' learning about a safe diet. Rapaport (1999) reported discrepant results for captive golden lion tamarins (*L. rosalia*). In Rapaport's study, adults transferred novel foods to their offspring more often than fa-

miliar foods, and youngsters were more likely to consume a novel food if it was provided to them by an adult than if they encountered it on their own. The discrepancies may reflect species differences; Price and Feistner included just one *L. rosalia* in their sample of 17 infant *Leontopithecus*. Even more striking than the bias to transfer novel foods is the practice of wild adult golden lion tamarins, which have been seen, three separate times, to give a food-transfer call after they searched briefly in a crevice or hole, wait there until the offspring arrived at the site, then move aside and let the offspring search for, find, and consume the prey item at that site (Rapaport & Ruiz-Miranda, 2002). This species, which among callitrichids relies the most on extracting hidden animal prey (Dietz et al., 1997), seems particularly likely to show strong social bias in learning what to eat and where to find it.

Callitrichid species are often found in mixed-species associations in nature (see Rylands, 1993, for a review). Hardie and Buchanan-Smith (2000) showed that tamarins living in mixed-species groups approached novel objects more quickly than those living in single-species groups. More generally, Hardie and Buchanan-Smith suggest, individual callitrichids can bias the activities of others—even individuals of other species—by indicating the presence of food, the means to obtain it, and the presence of predators. Mixed-species groups of callitrichids, in captivity and in the wild, afford an interesting opportunity to study the occurrence and ecological value of socially biased learning in diverse ways (Buchanan-Smith & Hardie, 1997; Prescott & Buchanan-Smith, 1999).

Caldwell and Whiten (2003) investigated the contribution of two types of social context on how well common marmosets learned to slide a small door horizontally to gain access to food. Overall, the most effective situation for a marmoset to learn how to open the door was to be present with a skilled individual (9 of 12 learned in one group, and 8 of 11 in another group), although experience at taking the food from the box may provide some benefit for learning (more than 20% of the individuals with this experience solved the problem). Neither observation alone nor being present with another naive individual had a measurable effect on the probability of success. The authors note that the naive individuals present with a skilled individual paid close attention to the actions of the skilled individual as it slid the door (and, one assumes, also to the movement of the door). In terms of the above-listed elements contributing to social learning, we suggest that what differentiated this group from the other groups was the value added to the door of the apparatus and its movement, which this group viewed and, perhaps, heard and felt at close range. Thus, in callitrichids, which exhibit pronounced tolerance of others during feeding, being close to another can aid in learning a new skill, even when the learner gains food without itself acting on the problem during this period (i.e., when it scrounges). This system can support directed social learning, in which particular individuals support learning

in particular others by acting together with them in close proximity (Coussi-Korbel & Fragaszy, 1995). Caldwell and Whiten also point out that, so long as individuals can continue to scrounge, they do not have a strong reason to act themselves. It is necessary to test individuals in the absence of skilled solvers to determine if naive individuals have learned to solve a problem themselves.

Day et al. (2003) examined the behavior of three genera of callitrichids—*Leontopithecus* (three species), *Callithrix* (two species), and *Saguinus* (two species)—presented with a novel extractive foraging task (retrieving raisins from a small opaque box). Lion tamarins (*Leontopithecus* spp.) contacted the boxes more quickly, manipulated the boxes the most, were most successful at retrieving the raisins, and (most important for our purposes) were most visually attentive to others acting on the boxes. Marmosets were intermediate between lion tamarins and tamarins in these measures. Although the authors of this study did not assess socially biased learning directly, they suggest that visual attentiveness during exploration and exploitation of the food box by others is an indicator of the relative contribution of social partners to learning. They suggest that the behavioral differences across genera observed in their study, including social attentiveness to others feeding, most likely reflect the foraging strategies (extractive vs. nonextractive), extent of environmental variability (e.g., seasonality) in food resources, and home range size (reflecting dispersal of food) characteristic of these species in nature.

Our quick review suggests that callitrichids and capuchins experience similar sources of social bias in learning about the physical environment. Callitrichids, like capuchins, learn most effectively when they can act jointly with an experienced partner and when there is minimal risk of social conflict in doing so. Acting jointly with an experienced partner helps the naive individual overcome fear of the novel item or situation (particularly important for the more neophobic individuals), and close observation of relevant actions on relevant targets aids the naive individual to act in the right place itself, perhaps by increasing the value of these particular places to the individual. This is an adequate recipe for effective socially biased learning in most situations that these monkeys encounter in nature. The differences across the genera are also clearly evident: Callitrichids are more tolerant of the close proximity of others in their group than are capuchins, and they are more attentive to group members that are feeding. These are differences in degree, not in kind: Capuchins display the same characteristics as callitrichids, but social relationships and risk of social conflict play a larger role in determining which individuals will approach others.

Conclusions

Monkeys are unlikely to imitate, and watching another monkey use an object as a tool does not directly lead a naive individual to the same discovery. However, when direct action on an object or substrate is sufficient to

solve a problem, then copresence with others solving the problem in a tolerant setting aids learning, primarily, it appears, by promoting investigation of the appropriate object. Social influence is likely to aid monkeys in learning about new foods in an indirect manner, by promoting sampling of any food in the vicinity where others are eating. Differences across individuals, settings, groups, species, and genera in the likelihood of social bias in learning reflect the degree of attention individuals devote to group mates and the degree to which individuals coordinate their behavior with each other in time and space.

Findings with callitrichids and capuchins illustrate these differences. When working to produce food, callitrichids are more likely than adult capuchins to exhibit close tolerance among group members. Callitrichids are more neophobic than capuchins; they are less likely to explore new places and new spaces and, therefore, less likely to discover new foods or to solve new manipulative problems on their own. Social coordination of activity thus has a stronger influence on individual discovery and subsequent learning in callitrichids than in capuchins.

The most general lesson we take from this work is that socially biased learning is not a unitary capacity; we cannot rank species according to the degree or complexity of social learning. Instead, we must consider variations in socially biased learning across species and populations in relation to the physical and social contexts in which animals are observed, and characteristics of the animals themselves that contribute to the likelihood that they will attend to others' actions and will attempt to act in the same way or in the same place (cf. Fragasz & Visalberghi, 2001). In agreement with Lefebvre (2000) and West, King, and White (2003), we suggest that social influences on learning are best understood as part of a wider network of immediate influences on behavior and as grounded in individual development and ecology. Modeling social bias in learning as an outcome of an adaptive network may be a useful way to develop these ideas.

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