SOCIAL LEARNING
IN ANIMALS:
THE ROOTS
OF CULTURE

Edited by

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Social Enhancement of Food Preferences in Norway Rats: A Brief Review [1]

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For more than 25 years, my students, coworkers, and I have been engaged in experiments designed both to analyze the behavioral processes that permit one Norway rat (*Rattus norvegicus*) to influence another's selection of foods and to determine how such social influences might facilitate the development of adaptive feeding repertoires by free-living rats.

The relative ease with which social influences on selection of food by rats can be studied in the laboratory has made social transmission of food preferences in rats a particularly fruitful model system in which to study social-learning processes at all stages in the life cycle (For reviews see Galef, 1977, 1985b, 1988, 1994): odor-bearing chemicals in a rat dam's food enter her bloodstream and cross placental membranes to infiltrate the circulation of any fetuses she is carrying. Consequently, late in gestation, fetal rats can detect the scents of at least some of the foods that their dam has eaten and will respond positively to those foods shortly after birth (Hepper, 1988). A few days after parturition, when infant rats are still totally dependent on their dam for nutriment, they receive information through their

mother's milk about flavors of foods that she is ingesting (Bronstein, Levine, & Marcus, 1975; Galef & Sherry, 1973; Galef & Henderson, 1972; Martin & Alberts, 1979). Still later in ontogeny, when weaning rats leave the safety of their natal burrow to seek their first meals of solid food in the open, they use adults of their colony as guides, foraging either at sites where adults are eating (Galef, 1971, 1981; Galef & Clark, 1971a,b) or at locations that adults have previously marked with residual olfactory cues (Galef & Beck, 1985; Galef & Heiber, 1976; Laland & Plotkin, 1991, 1993). In adolescence (and into adulthood), when rats frequently forage relatively independently, their food choices can be influenced by social interactions that occur at the home burrow at some distance from feeding sites (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983). The scent of foods recently eaten, carried on the fur, vibrissae, and breath of a successful forager, can profoundly influence the food choices of other rats with whom the forager interacts.

Here, I first describe relatively briefly our previously reviewed (Galef, 1988), early work describing changes in rats' food preferences following social interactions at a distance from a feeding site with conspecifics that have recently eaten. I then describe in greater detail work on the phenomenon completed since the previous review was written.

OVERVIEW (1982–1986)

The Phenomenon

In 1982, Steven Wigmore and I, pursuing a lead generously provided by Barbara Strupp (See Strupp & Levitsky, 1984; Galef, 1991c), demonstrated that after a naive rat (an observer) interacted with a recently fed conspecific (a demonstrator), the observer exhibited a substantial enhancement of its preference for whatever food its demonstrator had eaten (Galef & Wigmore, 1983). Simultaneously (and independently) Posadas-Andrews and Roper (1983) discovered the same phenomenon.

Such social influence on diet selection by rats proved surprisingly robust (Galef, Kennett, & Wigmore, 1984); it is seen in a variety of situations, in rats of all postweaning ages, both sexes and several different strains (Galef et al., 1984; Richard, Grover, & Davis, 1987), as well as in house mice (*Mus domesticus*) (Valsecchi & Galef, 1989).

Social influence on the food choices of rats is also an unexpectedly powerful influence on diet selection, sometimes as powerful as learned aversions and congen-

ital flavor preferences (Galef, 1986, 1989a): Observer rats taught a profound aversion to some food (as a result of experiencing gastrointestinal distress immediately after eating it) often completely abandoned their aversion after interacting with a demonstrator rat that had eaten the food to which the observers had learned the aversion (Galef, 1986, Galef et al., 1990). For weeks after interacting with demonstrator rats fed a diet flavored with cayenne pepper, observer rats offered a choice between a base diet and an unpalatable modification of that base diet flavored with cayenne pepper preferred the pepper-flavored diet, while control observer rats that had not interacted with demonstrators fed pepper-flavored diet strongly preferred the unflavored version of the base diet (Galef, 1989a).

Limitations on Rats' Communications about Foods

My coworkers and I were surprised to find that observer rats that interacted with unconscious demonstrators or with demonstrators that were experiencing an acute, experimentally induced, gastrointestinal distress exhibited preferences for, rather than aversions to, whatever foods their ill demonstrators had eaten. Indeed, several years of research, both in our laboratory and elsewhere (Galef, Wigmore, & Kennett, 1983; Galef, McQuoid, & Whiskin, 1990; Grover et al., 1988), have produced no evidence consistent with the view that food preferences induced in observer rats by demonstrators are influenced by the state of health of those demonstrators. Such repeated failure to find any sensitivity of observers to the well being or illness of demonstrators (coupled with the ease of finding enhanced preference for foods that demonstrators have eaten) suggests that the function of social transmission of food preferences in rats is to help them to identify potential foods, rather than to aid directly in their identification of potential poisons (Galef, 1985a).

The Analysis

Results of several of our experiments were consistent with the view that observer rats used olfactory cues emitted by demonstrators to identify foods that demonstrators had eaten: Rats developed a preference for a food fed to a demonstrator if separated from that demonstrator by a screen partition, but not if separated from a demonstrator by a transparent Plexiglas partition (Galef & Wigmore, 1983). Observers whose sense of smell had been blocked (by application of zinc sulfate solution to the nasal mucosa) failed to acquire enhanced preferences for foods their demonstrators had eaten, while intact control rats reliably exhibited such preferences (Galef & Wigmore, 1983).

Direct observation of the conditions under which observer rats acquired the food choices of their respective demonstrators indicated that for a demonstrator rat to influence the subsequent food preference of its observer, the observer had to bring its nose close to its demonstrator's mouth while they interacted (Galef & Stein, 1985). Presumably, approach to the mouth of a demonstrator rat was necessary for an observer rat to experience the scent of the food that the demonstrator had eaten.

Further experiments revealed that for an observer rat's food preferences to be affected by interaction with a demonstrator, the observer had to experience more than simple exposure to the smell of foods that their respective demonstrators had eaten, (Galef, Kennett, & Stein, 1985); observer rats that either smelled or ate a food did not develop an enhanced preference for it, while observer rats that smelled a food brushed onto the head of an anesthetized demonstrator rat did develop such a preference (Galef & Stein, 1985; Galef, Kenneth, & Stein, 1985).

I interpreted such findings as suggesting that the olfactory cues altering the food preferences of observer rats have two components: (1) a diet-identifying component (the smell associated with a food) and, (2) a contextual component (an odor produced by rats) that, acting together, were responsible for alterations in observers' food choices. We found that the diet-identifying component of the olfactory signal necessary to alter observer rats' food choices could be provided either by small amounts of food clinging to the fur and vibrissae of demonstrator rats or by the odor, escaping from the digestive system, of portions of food that had been introduced directly into the stomachs of demonstrator rats (Galef et al., 1985; Galef & Stein, 1985).

Yet other experiments showed that the contextual component of the olfactory signal necessary to modify the diet choices of observers was emitted from the anterior of anesthetized rats, but not from either the posterior of anesthetized rats or the anterior of rats recently sacrificed by anesthetic overdose (Galef et al., 1985; Galef & Stein, 1985).

RECENT DEVELOPMENTS (1986–1994)

Causal Analyses

Contextual Cues

The observation that effective contextual cues were localized at the anterior of live rats (Galef et al., 1985; Galef & Stein, 1985) led us to hypothesize that such cues might be contained in rat breath. Mass spectrographic analysis of rat breath re-

vealed the presence, in significant quantities, of both carbonyl sulfide and carbon disulfide (CS_2) (Galef, Mason, Preti, & Bean, 1988). A subsequent test of the ability of CS_2 to provide a context within which exposure of a rat to a food odor would enhance its later preference for foods bearing that odor were successful. Both naive observer rats that we exposed to an anesthetized demonstrator rat that had eaten cinnamon-flavored diet and naive rats that we exposed to a piece of cotton batting that we had both powdered with cinnamon-flavored diet and moistened with a few drops of a dilute CS_2 solution exhibited significant (and roughly equivalent) enhancement of their subsequent preferences for cinnamon-flavored food. On the other hand, observer rats exposed to a piece of cotton batting that we both powdered with cinnamon-flavored diet and moistened with a few drops of distilled water exhibited no subsequent preference for cinnamon-flavored diet (Galef et al., 1988).

We have also asked whether experience of an odor on a conspecific produces a general enhancement of preference for that odor or enhances response to the odor only when it is associated with food. In a series of experiments (Galef, Iliffe, & Whiskin, 1994), we first exposed observer rats to demonstrator rats scented with either cinnamon or cocoa and then offered their observers choices between cinnamon- or cocoa-scented foods, cinnamon- or cocoa-scented nest materials and cinnamon- or cocoa-scented nest sites. Although, as expected, observer rats preferred food scented with the flavor they had experienced in association with a demonstrator rat, the same observers did not prefer either nest materials or nest sites bearing those same scents.

Of course, failures to find effects must always be interpreted with caution. Still, our data are not consistent with the view that the susceptibility of rats to social influences on their food preferences reflects a general enhancement of their preferences for odors experienced in association with conspecifics. Rather, experiencing an odor in association with a conspecific seems specifically to enhance rats' preferences for foods bearing that odor.

Development of Response to Demonstrators

It seemed likely that the experiences of young rats as they interacted with their dam and siblings would prove to be important in either the development or maintenance of rats' susceptibility to social influences on their food preferences. However, when we reared rat pups in total social isolation (Hall, 1975) from Day 2 or 3 postpartum to weaning and then tested them for susceptibility to social influence on food preference, we found that the effects of demonstrator rats on the food preferences of isolation-reared pups were as great as were their effects on the food

preferences of pups reared by their dam and with siblings (Galef & Smith, 1994). Social enhancement of food preference developed and was maintained without interaction with conspecifics.

Extrapolation beyond the Laboratory

In all the experiments described above, observer rats interacted with demonstrators that had relatively simple recent histories of food intake; each demonstrator rat with which an observer rat interacted ate only a single food in the 24 h before interacting with its observer and each observer interacted with only a single demonstrator before it was tested for diet preference. It seems reasonable to suppose that in the world outside the laboratory: (1) free-living Norway rats often eat several different foods before interacting with colony mates, and (2) each rat interacts frequently with several of its fellows. Consequently, in natural circumstances, a rat interacting with conspecifics is likely to be exposed to an extended series of complex, food-related messages.

My students and I have carried out a number of experiments in which we fed demonstrator rats fairly complex diets before we allowed them to interact with observer rats. We then looked to see whether the observers could extract usable information from the complex, food-related olfactory signals their demonstrators provided (Galef, 1991b; Galef, Attenborough, & Whiskin, 1990; Galef & Whiskin, 1992, 1995). Rather than recount the entire history of our exploration of communications concerning food complexes, I shall describe here only two of the more elaborate situations we have examined to date.

Whiskin and I (Galef & Whiskin, 1992) first fed rats powdered rat chow to which we had added one of two combinations of four spices: either Combination A (cinnamon, anise, thyme, and cloves) or Combination B (cocoa, marjoram, cumin, and rosemary). Next we allowed individual rats that had eaten Combination A to interact for 1/2 h with individual rats that had eaten Combination B. Finally, we offered each rat a choice, for 22 h, between one of four pairs of flavored diets: (1) cinnamon-flavored vs cocoa-flavored diet, (2) anise-flavored vs marjoram-flavored diet, (3) thyme-flavored vs cumin-flavored diet, or (4) clove-flavored vs rosemary-flavored diet. (Note that one flavor in each of the four pairs of diets offered to subjects was a constituent of Combination A, the other was a constituent of Combination B.) Additional subjects that we had assigned to a control group each ate either Combination A or Combination B, but did not interact with a conspecific before we offered them a choice between one of the same four diet pairs we offered to subjects that did interact with conspecifics before testing.

During testing, the food preferences of control subjects that had eaten Combi-

nation A did not differ from the food preferences of control subjects that had eaten Combination B. However, when tested for food preference, subjects that had both eaten Combination A and interacted with a partner that had eaten Combination B, ate more of those diets flavored with a spice present in Combination B than did subjects that had eaten Combination B and interacted with a partner that had eaten Combination A. In sum, subjects developed preferences for flavors that their partners had eaten, even when those partners had eaten quite complex diets.

Other experiments revealed that observer rats can respond not only to complex single messages, but also to a succession of simple messages received from a series of demonstrators (Galef, Attenborough, & Whiskin, 1990). On each of nine occasions spread over 23 days, we allowed observer rats assigned to an experimental group to interact for 1/2 h with a demonstrator rat that had just eaten a diet unfamiliar to its observer. Each observer in a control group interacted at the same time with a demonstrator rat that we fed the same diet on which both demonstrators and observers had been maintained throughout life.

Figure 1 shows the days on which demonstrators and observers interacted, the diets fed to demonstrators in the experimental group before they interacted with their observers, and the food choices given to all subjects for 23.5 h on each day of the experiment. As can be seen in Fig. 1, on each day of the experiment when subjects interacted with demonstrators, subjects in the experimental group exhibited a significant enhancement of their preferences for the foods that their demonstrators had eaten.

Functions of Social Learning about Food

It is one thing to know that olfactory messages passing from demonstrator rats to their observers can alter the observers' later food preferences. It is quite another to understand how such socially induced changes in food choice might facilitate development of adaptive feeding repertoires in rodents living outside the laboratory. In the present section, I review several experiments the results of which suggest that olfactory communications about foods help Norway rats to decide: (1) what foods to eat, (2) what potential foods to learn to avoid eating, and (3) where to go to find food.

Learning What to Eat

Although individual rats can sometimes learn to select a single nutritionally adequate food embedded in an array of nutrient-deficient foods (Galef & Beck, 1990; Richter, Holt, & Baralare, 1938; Rozin, 1969), it is relatively easy to create
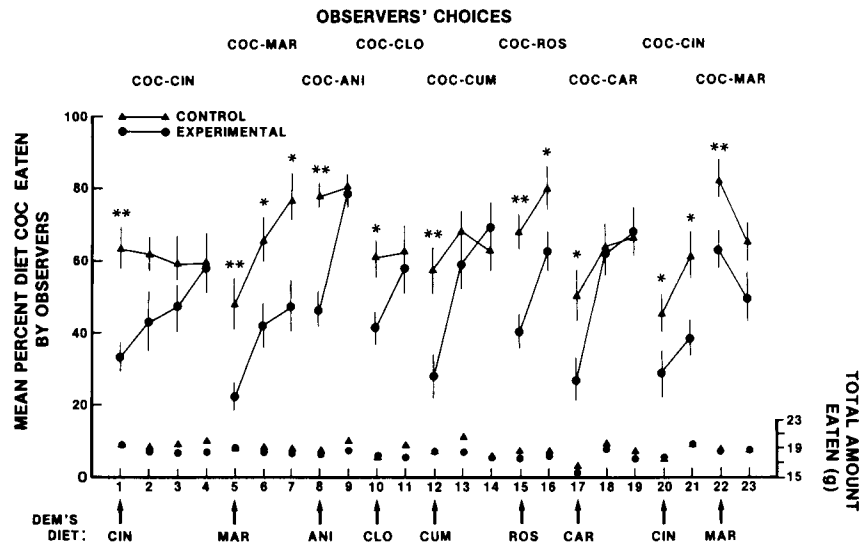
Fig. 1. Mean percentage of Diet Coc eaten and total amount eaten by observer rats in experimental and control groups. Pairs of diets shown at the top of the figure indicate the choices offered to observers on each day. Diets shown at the bottom of the figure indicate foods presented to demonstrators on days indicated by the vertical arrows. Flags indicate $\pm$ 1 SEM. * = $p < .05$, ** = $p < .01$. CIN = cinnamon-flavored diet; MAR = marjoram-flavored diet, ANI = anise-flavored diet, CLO = clove-flavored diet; CUM = cumin-flavored diet; ROS = rosemary-flavored diet; CAR = cardamom-flavored diet. Reprinted from Galef, Attenborough, & Whiskin (1990) by permission of the American Psychological Association.

situations in which naive rats have great difficulty in focusing their feeding on the sole nutritionally adequate food present in an array of foods (Beck & Galef, 1989; Galef, 1991a; Galef, Beck, & Whiskin, 1991).

Beck and I (Beck & Galef, 1989) placed individual rats in enclosures containing three protein-deficient foods (Diet, Cin, Coc, and Thy) and a single relatively unpalatable food (Diet Nut) that contained adequate protein (and all other nutrients) to support normal growth and development. Each subject was either placed alone in a cage or shared its enclosure with one or more conspecific demonstrators that we had trained to eat the protein-rich Diet Nut and to avoid eating the three, protein-deficient alternative diets present in the enclosure. Observer rats that shared their enclosures with trained demonstrators were able to grow rapidly, while rats maintained in isolation failed to thrive in the experimental situation (Beck & Galef, 1989).

To determine how trained demonstrator rats were affecting the feeding behavior of naive subjects in the test situation, we used enclosures arranged in the three ways illustrated in Fig. 2. As can be seen in the figure, we varied the diet eaten by demonstrators (protein-rich Diet Nut or protein-deficient Diet Cin) and the location of the demonstrator's food cup relative to those of their observers (whether demonstrator's ate from a cup adjacent to the cup in the observer's side of the enclosure that contained protein-rich Diet Nut or protein-deficient Diet Cin). Only observers whose demonstrators ate Diet Nut grew rapidly and the rate of growth of observers was not affected by whether demonstrators ate near the food cup containing Diet Nut or elsewhere (Fig. 3). Clearly, information obtained by observers about the food that their respective demonstrators were eating was used by naive rats to locate the most valuable of several available foods.

We have also found that the degree to which the food choices of observer rats are affected by the food choices of their demonstrators is determined by the state of health of the observers themselves. Food choices of protein-deficient observer rats were significantly more profoundly influenced by foods eaten by demonstrator rats than were food choices of protein-replete observer rats (Galef et al., 1991).

Learning What Not to Eat

The ability to use conspecifics as sources of information about which foods are safe to eat might be particularly helpful to individuals that have eaten several different unfamiliar foods (as might a weaning rat) before becoming ill. It seems reasonable to assume that it would be adaptive for a rat to act as though foods that
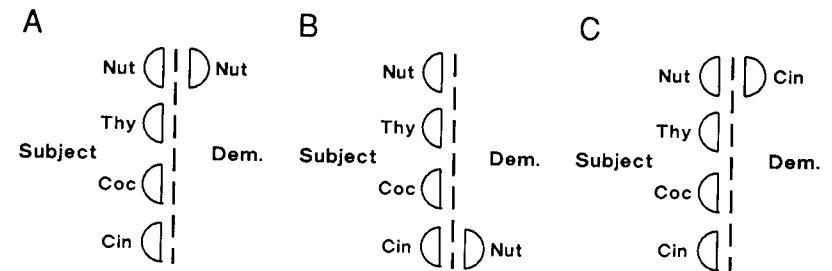

Fig. 2. Overhead schematic of the positions of food cups presented to subjects and their respective demonstrators in the Same-Food, Same-Place, Same-Food, Different-Place and Different-Food, Same-Place conditions. Nut = nutmeg-flavored diet (high in protein); Cin = cinnamon-flavored diet; Thy = thyme-flavored diet; Coc = cocoa-flavored diet (all three low in protein); Dem. = demonstrator. Reprinted from Beck and Galef (1989) by permission of the American Psychological Association.
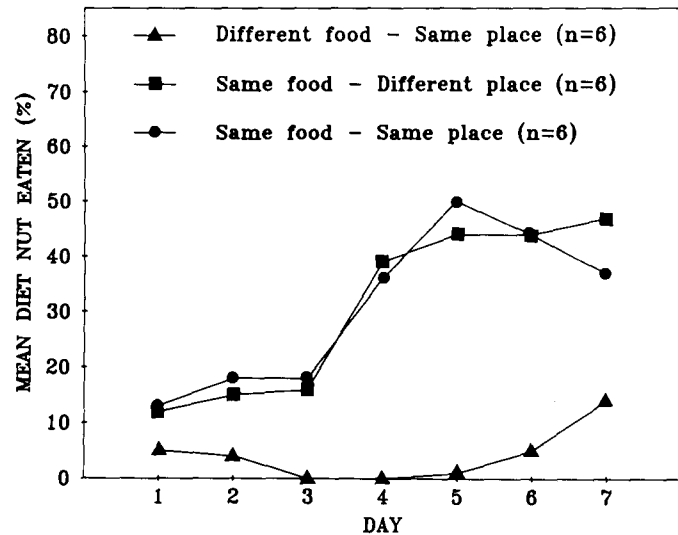
Fig. 3. Mean amount of high-protein nutmeg-flavored diet ingested by subjects as a percentage of their total intake. Reprinted from Beck and Galef (1989) by permission of the American Psychological Association.

other rats are eating are less likely to be toxic than are foods that other rats are not eating.

To allow observer rats to learn what diet another rat was eating, I fed demonstrator rats either cocoa-flavored diet (Diet Coc) or cinnamon-flavored diet (Diet Cin) and then allowed each demonstrator to interact with an observer. I next fed observer rats Diet Cin and Diet Coc in succession, then poisoned the observers with lithium-chloride. To determine whether observers had learned an aversion to Diet Cin or Diet Coc, I offered them a choice between Diet Cin and Diet Coc (Galef, 1987). Observer rats were far more likely to form an aversion to whichever food their respective demonstrator had not eaten than to the food that their respective demonstrators had eaten (See also Galef, 1989b).

Learning Where to Look for Food

Galef, Mischinger, and Malenfant (1987) found that rats will spontaneously follow trained conspecific leaders through a maze and that they will follow potential leaders that have eaten a "safe" food significantly more frequently than they will follow potential leaders that have eaten an "unsafe" food. We trained follower

rats to enter the same goal box as their respective leaders. Once the followers were performing reliably in the maze, we offered each of them, in their home cage, a sample of a novel diet and poisoned them. We subsequently gave followers the opportunity to follow leaders that had eaten either the followers' standard maintenance diet or the food to which the followers had learned an aversion. We found that followers entered the same goal box as their leaders on 90% of the trials when the leaders had eaten maintenance diet on only 58% of trials on which leaders had eaten the diet to which followers had learned an aversion.

Using Studies of Causation to Elucidate Function

Because one might expect natural selection to have shaped processes supporting social learning about foods, discovery of limits on the situations in which such social learning occurs should provide some insight into the functions that social induction of food preference might serve in natural circumstances. We hypothesized that if social induction of food preference is a behavioral process evolved to permit rats to expand their feeding repertoires without incurring some of the risks inherent in sampling previously untasted potential foods, then one might expect social exposure to unfamiliar foods to be more effective in altering the food preferences of rats than social exposure to familiar foods.

In a series of experiments investigating the social induction of rats' preferences for familiar and unfamiliar foods, we found repeatedly that observer rats learned a preference for the unfamiliar rather than the familiar diet that their demonstrators were eating (Galef, 1993). Such findings are consistent with the notion that social induction of diet preference serves rats as a means of reducing the cost of adding totally new foods to their feeding repertoires. The results of subsequent experiments showed that individual experience of a food interfered with social induction of a preference for that food for only a few days after the food was eaten (Galef & Whiskin, 1994). These latter results suggest that the combined effects of individual and social learning about foods should result in free-living rats exhibiting preferences both for totally unfamiliar foods that it learns that conspecifics are eating and for foods that it learns that conspecifics are eating that it has not eaten recently.

CONCLUSIONS

Studies of social influence on food preference in rats have resulted in the discovery of a previously unsuspected major determinant of diet choice. Such studies have

also provided a useful model system in which to explore the many ways in which social interactions can modulate behavioral development (Galef, 1991a; Hill, 1995). Our findings, together with those of others working in the area, have revealed multiple systems that permit naive rats to extract information from their more experienced fellows thus increasing the probability that the food choices of the naive will be beneficial.

As many other chapters in this volume make clear, neither rats nor foraging animals are unique in using socially acquired information to guide their behavior. Although the details of the processes supporting social influence on the food choices of rats may be of interest only to experts in feeding behavior, the general message that a complex of nonimitative social-learning processes can play a central role in development of locally adaptive patterns of behavior should be of importance to all with an interest in the causes and functions of the behavior of animals. Whether one's interests are in the mate choices of guppies (See Dugatkin, this volume), predator recognition by rhesus macaques (Mineka & Cook, 1988), or the spread of novel means of food extraction by European titmice (Fisher & Hinde, 1949; Sherry & Galef, 1984) investigations of social-learning processes are likely to provide insight into how locally adaptive patterns of behavior are acquired.

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Social Learning in Monkeys: Primate "Primacy" Reconsidered

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INTRODUCTION

The recognition that humans share many traits with other primates can have as an unintended correlate an uncritical willingness to ascribe human traits to other primate species (Kennedy, 1992). Behavioral researchers are more likely to provide higher-order "cognitive" explanations for behaviors in primates than members of other orders, perhaps reflecting some intuitive notion that cognitive continuity extends from humans to other primates, but not to other orders. These two tendencies are as misleading for primatologists as they are for the general public (Visalberghi & Fragaszy, 1990); and they extend to our views of social learning. They are apparent, for example, in the cognitive slant to explanations for behaviors in nonhuman primates (such as dietary choices or skilled foraging actions) that we assume are either learned socially, or are socially modulated in humans. In this chapter, we make the case that the apparently natural inclination to attribute a special character to social learning in monkeys, relative to social learning in other animals, is unwarranted. This is not to say that social influences are not important to primates, as to other orders. Rather, the comparative psychological issue is whether a different set of underlying mechanisms supports social learning in primates than in other orders.

We draw on some recent research in our laboratories to illustrate how homo-