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ANALYSES OF SOCIAL LEARNING PROCESSES AFFECTING ANIMALS' CHOICES OF FOODS AND MATES[1]

ANÁLISIS DE LOS PROCESOS DE APRENDIZAJE SOCIAL QUE AFECTAN ELECCIONES ALIMENTICIAS Y SEXUALES EN ANIMALES

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ABSTRACT

Social interactions can profoundly influence the stimuli to which an individual animal is exposed and, consequently, can determine the direction in which learning by individuals proceeds. My laboratory has been examining a few of the many ways in which social influences can bias development of behavioral repertoires of animals. Here, I briefly review our work of the last 30 years on social effects on the food choices of Norway rats and mate preferences of Japanese quail. I show that both the foods that rats ingest and the members of the opposite sex that quail select as sex partners can be profoundly biased by interaction with or observation of conspecifics and analyze behavioural processes that support social learning in these two model systems.

Key words: social learning, food choice, mate choice, Norway rat, Japanese quail, mate-choice copying.

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RESUMEN

Las interacciones sociales pueden influir profundamente sobre los estímulos a los cuales un animal individual está expuesto, y por consiguiente pueden determinar en qué dirección el aprendizaje individual procede. Mi laboratorio ha examinado algunas de las muchas maneras en las cuales influencias sociales pueden sesgar el desarrollo de los repertorios conductuales animales. Aquí reviso rápidamente nuestro trabajo de los últimos 30 años sobre los factores sociales que influyen en las elecciones alimenticias de la rata de Noruega y las preferencias sexuales de la codorniz japonesa. Demuestro que tan los alimentos que las ratas ingieren como los individuos del sexo opuesto que la codorniz elige como parejas sexuales pueden ser profundamente sesgados por interacciones con, o la observación de, miembros de la misma especie; analizo los procesos conductuales que soportan el aprendizaje social en estos dos sistemas modelos.

Palabras clave: aprendizaje social, elección alimenticia, elección sexual, rata de Noruega, codorniz japonesa, imitación de elección sexual.

Satisfying analysis of the processes underlying social behavior both in animals and in humans have proven considerably more difficult than might have been anticipated, in part because of the difficulty of knowing what variables to measure and how to measure them. However, in studies of social influences on learning dependent variables with high face validity are easy to both specify and calibrate. As a possible consequence of this mastery of dependent variables, considerable progress has been made during the past decade in analyzing behavioural processes supporting social learning in animals.

Here, I briefly review two research programs currently in progress in my laboratory. The first is concerned with social influences on food choices of Norway rats' (*Rattus norvegicus*) and the second with social influences on mate choices of Japanese quail (*Coturnix japonica*). The results of both series of studies demonstrate not only that social learning can profoundly affect biologically meaningful activities of animals but also provide some insight into the behavioral process supporting such social learning. I conclude that analyses of social behavior are not only possible, but also necessary, if we are to fully understand behavioral contributions to the survival, reproduction, and possibly, even the evolution of animals both nonhuman and human.

WHY STUDY SOCIAL LEARNING IN ANIMALS?

The last decade has seen a phenomenal increase in interest in animal social learning (Galef, 1998). Psychologists, behavioral ecologists, anthropologists, primatologists, evolutionary biologists, neural network modelers, even economists, have been increasingly active in the field. In studies of social influences on learning measuring the consequences of social interaction is relatively straightforward. Perhaps as a consequence of the ease of specifying and quantifying dependent variables in studies of social learning, behavioural analyses of instances of social learning have often achieved levels of understanding comparable to those typical in investigations of behavioral processes supporting individual learning.

Studies of social learning are not only tractable, such studies are also necessary if we are to understand fully the development of behavioral repertoires in animals. Animals, especially young animals, living outside the laboratory must learn many things rapidly, if they are to survive: A fledgling bird or weaning mammal venturing from its nest for the first time has to learn to avoid predators before it is eaten by one. It has to find water before it dehydrates. It has to learn to select and ingest a nutritionally balanced diet before it exhausts its internal reserves of any critical nutrient.

Naive, young animals faced with such problems would be well advised to take advantage of opportunities to interact with knowledgeable adults. Survival to adulthood demonstrates unequivocally that adults have learned to avoid predators, to find water, to select safe, nutritious substances to ingest, and so on. Most important, adults have done all of these things in the same environment where juveniles with whom they interact are struggling to acquire the behavioural repertoire needed for survival. Consequently, at least in principle, juveniles do not have to learn independently to overcome each of the many challenges posed by the environment they share with their parents and any other adults with whom they come in contact. Attending to the behaviour of older or more knowledgeable others can facilitate acquisition of necessary responses to environmental demands by speeding the laborious process of trial-and-error learning at a time when error can be particularly costly. Hence, from a biological or ecological perspective, as well as from a psychological one, social learning would seem to be worth studying (Galef, 1996a).

SOCIAL INFLUENCES ON THE FOOD PREFERENCES OF NORWAY RATS: A MODEL SYSTEM

My students and I have spent the last 30 years using the acquisition of adaptive patterns of food choice by Norway rats (*Rattus norvegicus*) as a model system in which to explore ways in which a developing animal can incorporate into its own behavioral repertoire the behavior of more knowledgeable conspecifics. The food choices of Norway rats provide particularly appropriate material for investigations of social learning in animals because there is a reasonable amount of field data consistent with the hypothesis that wild Norway rats living outside the laboratory show important social influences on their feeding behavior (Galef, 1976; Steiniger, 1950).

Colonies of free-living rats Norway rats are highly social animals. They live in colonies that inhabit burrow systems from which colony members emerge to forage and to which they return between foraging bouts (Calhoun, 1966). There are sound theoretical reasons to believe that members of social species that, like Norway rats, forage from a fixed location would benefit from social exchange of information about foods (Ward & Zahavi, 1973). If, for example, one member of a colony of rats were to discover a new source of food, eat some and then return to its burrow, it would be advantageous to other colony members, particularly to ignorant juveniles, if they could extract information from the returning successful forager that might facilitate their own identification and location of the newly discovered food (Galef, 1990).

Multiple Processes for Social Learning about Food

My coworkers and I have explored a variety of mechanisms, each able to bias the feeding behavior of young rats (for review see Galef, 1996b): (1) Foods eaten by a lactating rat flavor her milk, and experience of flavors in mother's milk causes weanlings to prefer to eat the foods that their mother ate while lactating (Galef & Clark, 1972; Galef & Henderson, 1972; Galef & Sherry, 1973). (2) The simple physical presence of an adult rat, even an anesthetized one, at a feeding site causes juveniles to approach that site and to begin to eat whatever foods are to be found there (Galef & Clark, 1971a, 1971b). (3) Adult rats mark both foods and feeding sites with residual chemical cues that make marked sites and foods more attractive to juveniles than unmarked ones (Galef & Beck, 1985; Galef & Heiber, 1976; Galef & Muskus, 1979). (4) Adult rats lay scent trails from feeding sites to harborage sites that others follow to food (Galef & Buckley, 1996). The very multiplicity of behavioral processes involved in Norway rats' learning from others about foods and feeding sites suggests that in rats, as in honey bees (von Frisch, 1967; Lindauer, 1961; Seeley, 1995), socially acquired information contributes significantly to foraging efficiency.

A case history

Suppose a foraging rat eats a food at some distance from its burrow, rejoins its colony, and interacts with burrow-mates that, sometime later, leave the burrow to find food. We wanted to know what effect, if any, such interaction between a successful forager and burrow-mate, occurring at some distance from a feeding site, has on the burrow-mate's subsequent choice of foods. Simple observation of free-living animals in uncontrolled environments would never provide a convincing answer to the question, so we designed a laboratory procedure that captured the important elements of the natural situation (Galef & Wigmore, 1983).

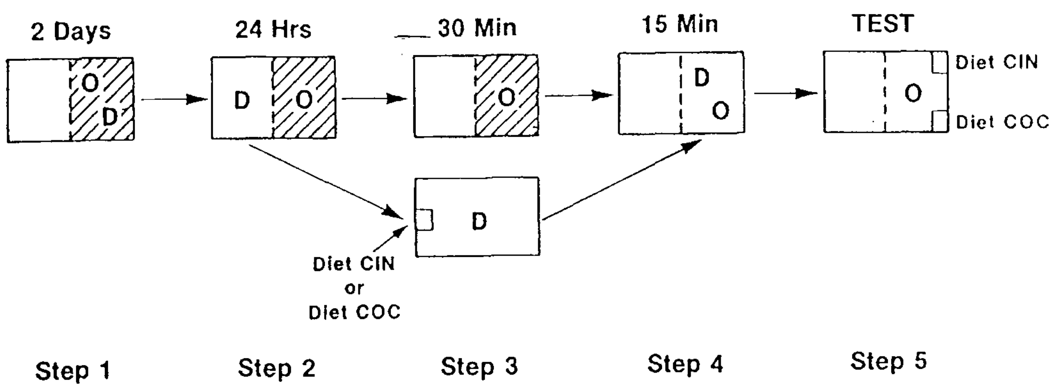

Figure 1. *Schematic of procedure used to study social influence on diet choice in Norway rats. Diet Cin = cinnamon-flavored diet; Diet Coc = cocoa-flavored diet. Reprinted by Permission of the American Psychological Association.*

The basic procedure

We housed and tested our subjects (referred to below as either demonstrators or observers) in pairs in cages divided into two equal parts by a screen partition (see Figure 1). To begin the experiment, we allowed each pair 2 days to become familiar with one another and with the apparatus. Next, we food deprived one of the pair members (the demonstrator) so that it would eat when given access to food. Then, we moved the demonstrator to a separate room and fed it either a cinnamon- or cocoa-flavored diet for 30 min, and, immediately afterwards, placed the demonstrator back with its pair mate (the observer) for 15 min. Last, we removed each demonstrator from the experiment and offered each observer, for 23 hr, a choice between weighed samples of cinnamon- and cocoa-flavored diets.

We found that during the 23-hr choice test, those observer rats whose demonstrators had eaten cinnamon-flavored food ate far more cinnamon-flavored than cocoa-flavored food, whereas those observers whose demonstrators had eaten cocoa-flavored food ate far more cocoa-flavored than cinnamon-flavored food (Galef & Wigmore, 1983). Clearly, the flavor of the food fed to demonstrators affected the food choices of their observers.

Robustness of the phenomenon

A frequent problem with presumed laboratory analogues of behavioral events, such as social learning of a food preference, assumed to occur in nature, is that in the laboratory a behavior of interest occurs only under a restricted set of experimental conditions. Social learning of food preferences, to the contrary, is surprisingly robust to parametric variation.

Over the years, my students and I have repeated the basic experiment dozens of times: with many different diets (Galef, 1983), with wild rat demonstrators and observers as well as domesticated ones, with demonstrator-observer pairs familiar with one another and with pairs that had never met prior to their interaction during Step 4 of the procedure (see Figure 1), with old demonstrators and observers and young ones, with male demonstrator-observer pairs and female ones (Galef, Kennett & Wigmore, 1984). In every case, we saw profound influence of demonstrator rats on their observers' later food choices. In fact, in 15 years, we have not discovered any circumstance where one might reasonably expect observers to acquire information from demonstrators as to the diets those demonstrators have eaten, in which observers did not exhibit a preference for their respective demonstrators' diets. Social influence on the food choices of rats is clearly not dependent on a restricted set of experimental parameters for its expression.

How information is communicated

To look at the mode of communication from demonstrator to observer, we had to gain some control over their interaction. To do so, we used a procedure that differed from that illustrated in Figure 1 in only one important respect; during the 15 min when demonstrator and observer interacted (Step 3 in Figure 1), they were separated by a 1/2-in (1.25-cm) screen.

We found (Galef & Wigmore, 1983) that separating demonstrator and observer with a screen while they interacted did not interfere with communication between them. Observers continued to prefer the food that their respective demonstrators had eaten in Step 5. However, social influence of demonstrators on observers' food choices broke down totally, when we separated them while they interacted with a transparent Plexiglas rather than a screen partition. Clearly, some sort of non-visual contact, perhaps olfactory, perhaps gustatory, perhaps 'linguistic', is necessary if food choices of observer rats are to be influenced by interaction with conspecific demonstrators.

Excluding gustatory cues

If, after a demonstrator rat has eaten and before it interacts with an observer, it is anesthetized, taped to a Petri dish, and left separated from its observer by a screen so that no physical contact between demonstrator and observer is possible (see Figure 2), the observer still prefers the food that its demonstrator ate. Successful extraction of information from an unconscious demonstrator that an observer cannot touch tells us two things: First, the message is emitted in a passive way by the demonstrator, not produced by a demonstrator in response to

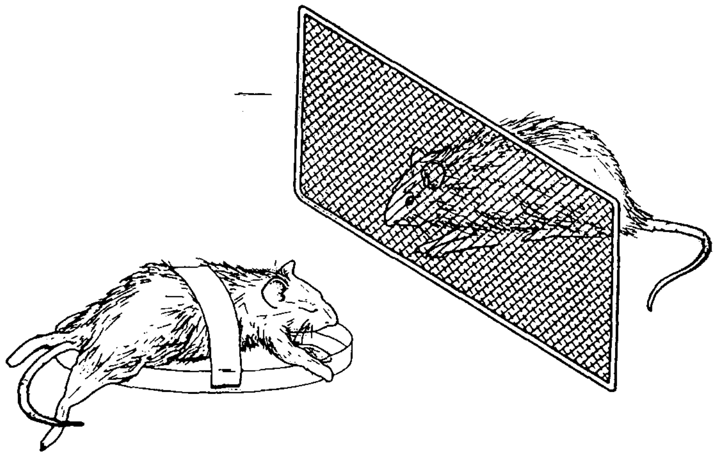

Figure 2. Illustration of anesthetized demonstrator and observer separated by a screen partition. Reprinted by permission of the American Psychological Association.

the presence of an observer. Second, no physical contact between demonstrator and observer is required for information transfer to occur.

The important cue is, as we know from the Plexiglas-barrier experiment, not visual, yet it can be transmitted over some distance. Therefore, it is not gustatory. The important cue is emitted by unconscious rats, which rules out the 'linguistic' hypothesis. We are left with only olfactory cues to carry the message from demonstrator rats to their observers.

Evidence of a role of olfactory cues

Consistent with the hypothesis that olfactory cues carry the message passing from demonstrator to observer, when we rendered observers anosmic (that is unable to smell) before they interacted with their respective demonstrators, the observers failed to exhibit a preference for their demonstrators' diets during a subsequent 22-hr choice test (Galef & Wigmore, 1983).

Also, not only rats but humans as well can tell what diet a rat has been eating using olfactory cues emitted by recently fed rats. When we fed six rats cocoa-flavored diet and another six rats cinnamon-flavored diet, then present all 12 rats in random sequence to a human observer instructed to sniff the rats' breath, the human observer identified the diet the rat had eaten with 85 to 90 percent accuracy (Galef & Wigmore 1983).

Causes of Change in Preference

It's not, of course, too surprising that an observer, either human or rodent, who sniffs a rat's breath can tell which of two foods the sniffed rat has recently eaten.

The more difficult question is why, in a proximal sense, an observer rat that has determined that a conspecific has, for example, just eaten cinnamon-flavored food should suddenly exhibit an enhanced tendency to eat cinnamon-flavored food.

Fear of novelty

Rats, particularly wild rats, are often quite hesitant to eat unfamiliar foods (Barnett, 1963; Galef, 1971). Consequently, at least under some circumstances, simple prior exposure to a food will substantially increase rats' intake of it. If rats are unwilling to eat unfamiliar foods, and if simple exposure to the smell of a food on a demonstrator rat increases an observer rat's familiarity with a food that its demonstrator has eaten, then observers might develop enhanced preferences for their respective demonstrators' diets as a result of simple familiarity with the odor of the diet a demonstrator had eaten. If this were the case, demonstrators would be acting simply as passive carriers of food particles or food odors.

However, results of a number of studies carried out over the years offer no support whatsoever for the hypothesis that changes in observer rats' food preferences result from simple exposure of an observer rat to the smell or to the taste of the diet eaten by its demonstrator (e.g. Galef, 1989; Galef & Stein, 1985; Galef & Kennett & Stein, 1985).

For example, when we gave one group of naive rats access to cinnamon-flavored diet and another group of rats access to cocoa-flavored diet for 30 min/day for 5 consecutive days, and further, offered both groups of rats a choice between cinnamon- and cocoa-flavored diets for the remaining 23 1/2 hr of each day, we saw no effect of this 1/2-hr, daily exposure to and eating of either cinnamon- or cocoa-flavored diet on subjects' food choices (Galef, 1989). If we then gave the same rats 30 min/day to interact with demonstrator rats fed either cinnamon-or cocoa-flavored diet, we saw massive effects of the diet fed demonstrators on the food choices of observers during daily 23 1/2 hr choice tests (Galef, 1989). Simple exposure to a diet did not affect the food preferences of observers. Exposure to a demonstrator that had eaten a diet did affect observers' food preferences. Changes in observers' food preferences, thus, seem to require more than simple exposure to a diet. Changes in observers' food preferences require exposure to food-related cues in the social context that is provided by the presence of a demonstrator.

If, in fact, changes in observers' food preferences depend on exposure to food-related cues in a social context, we are left with two important questions: First, where do the food-related olfactory cues emitted by demonstrators and detected by their observers that permit observers to identify the foods their respective demonstrators ate come from? Second, what are the contextual cues, the social cues, that make exposure to food-related cues effective in altering observers' food preferences?