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Social Influences on the Food Choices of Animals

Bennett G. Galef, Jr., PhD
Department of Psychology
McMaster University
Hamilton, Ontario, Canada

Three sources of information interact to determine the food preferences of animals.[1] First, information transmitted through parental genes guides development of physical substrates (e.g., taste buds, sensory cortex) that underlie sensory-affective responses to flavors. Second, experience of the consequences of ingestion results in learned aversions to toxic substances and preferences for nutritive ones. Third, information acquired during social interaction with others can bias subsequent food choices. This presentation considers the social learning of food preferences and the interaction of such social learning with both congenital taste preferences and individually learned responses to foods.

My coworkers and I have explored several social processes that are each able to bias the food choices of rats.[2–6] This article briefly touches on five such social influences on food choice to indicate that social learning about foods continues throughout life,[7] is complex, and is multifaceted. The sixth process for social learning about foods, which has been a focus of work in my laboratory for many years, is discussed in more detail.

SIX TYPES OF SOCIAL INFLUENCE ON FOOD CHOICE

1. Flavor cues that reflect the flavor of a mother's diet are present in her milk. Such flavor cues allow suckling young to identify foods their dam is eating, and flavors experienced in mothers' milk bias pups' food preferences at weaning, causing weanlings to prefer foods their mother has eaten.[8]
2. When young rats wean to solid food, the simple physical presence of an adult rat, even an anesthetized one, at a potential feeding site induces hungry juveniles to approach that site and to begin eating foods that are found there.[9]
3. While eating, adult rats mark foods and feeding sites with residual chemical cues, and marked foods and feeding sites are far more attractive to juveniles than are unmarked ones.[10,11]
4. Adult rats lay scent trails as they travel between feeding sites and harborage sites, and juveniles follow the trails that adults have created to foods that adults have eaten.[12]
5. Young rats snatch food from the mouths of their elders, and pups show an enhanced preference for a food they have stolen and eaten that they do not have if they ate the same food after simply picking it up off the ground and eating it.[13]
6. When two rats interact at a distance from a feeding site, each can tell what food the other has eaten and subsequently shows enhancement of its preference for that food.[14]

SOCIAL LEARNING ABOUT DISTANT FOODS: A CASE STUDY

Figure 1 illustrates our basic procedure that served as a laboratory analogue of a situation that free-living, wild Norway rats frequently encounter: A rat leaves its communal burrow to forage, succeeds in finding food, and returns to its burrow and interacts with its burrow mates. We wanted to know whether interaction between a returning successful forager and its social group occurring far from where the forager found food would influence the later food choices of colony members with whom the forager had interacted.

The Basic Experiment

We housed subjects in pairs (a demonstrator and an observer) in cages divided by a screen partition:

- **Step 1:** To habituate subjects to the experimental situation, we left pairs undisturbed in their cages for 2 days.
- **Step 2:** We then moved demonstrators to the opposite side of the screen partition from their observers and deprived the demonstrators of food for 24 hours to ensure that they ate when next given access to food.
- **Step 3:** Demonstrators were then moved to a room separate from observers and fed each demonstrator for 30 minutes either cinnamon-flavored diet (Diet Cin) or cocoa-flavored diet (Diet Coc).
- **Step 4:** Next, we placed each demonstrator with its observer and allowed them to interact for 15 minutes.

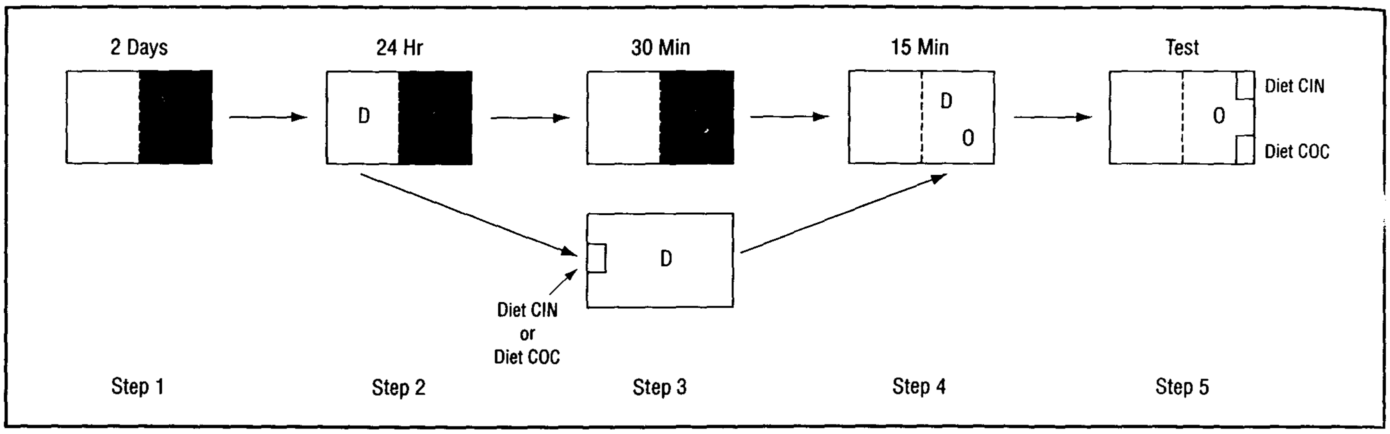

FIGURE 1. Schematic of the procedure used to examine social influence on food choice in Norway rats. (D = demonstrator; Diet Cin = cinnamon-flavored diet; Diet Coc = cocoa-flavored diet; O = observer.)

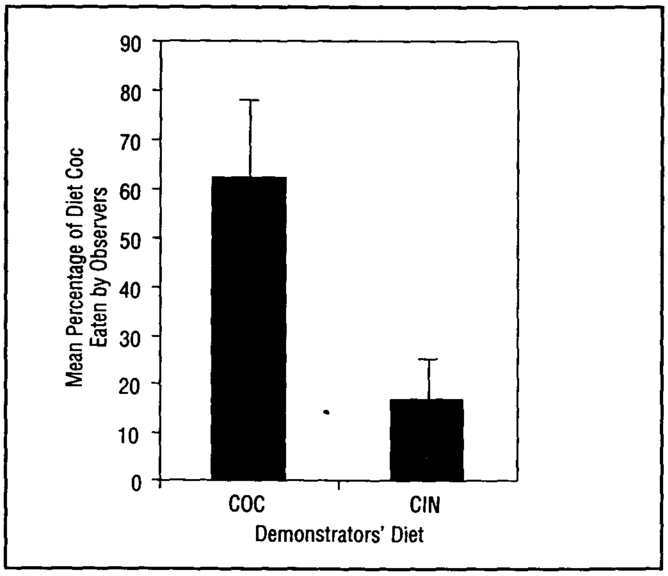

FIGURE 2. Mean (+ SEM) amount of Diet Coc eaten, as a percentage of the total amount ingested over 24 hours by observer rats after interacting with demonstrator rats fed either Diet Cin or Diet Coc.

- Step 5: Finally, we removed demonstrators and for 22 hours offered each observer two food cups, one containing Diet Cin and the other Diet Coc. At the end of the choice test, we determined the percentage of each observer's total intake that was Diet Coc. Observer rats whose demonstrators had eaten Diet Coc ate far more Diet Coc than did observers whose demonstrators had eaten Diet Cin (Figure 2).[14]

Variants on a Theme

We repeated this basic experiment many times—with different diets, with wild and domesticated rats, with old and young rats, with male and female rats, and so forth, and have invariably found profound influence of demonstrator rats on their observers' later food choices.[15] In fact, we have not discovered any circumstance in which an observer might be reasonably expected to acquire information from its demonstrator as to the diet the demonstrator ate where observers have not shown enhanced preferences for their respective demonstrator's diets. Others have found similar social effects on food choice in voles, mice, Mongolian gerbils, hamsters, hyenas, fruit bats, and others.[16]

How Does an Observer Rat Know What Food Its Demonstrator Ate?

We have developed several converging lines of evidence, each consistent with the hypothesis that olfactory cues passing from demonstrator to observer rats allow social learning of flavor preferences to occur.[14] Here, I describe only the most direct of these. An observer rat rendered anosmic (i.e., unable to smell by bathing its olfactory mucosa with zinc-sulfate solution) before it interacts with a demonstrator fails to exhibit enhanced preference for its demonstrators' diet during testing (Figure 3). Control observer rats whose nasal passages were rinsed with a benign saline solution increased their preferences for the diet their demonstrators ate.[14]

Food-Related and Contextual Olfactory Cues

Food-related olfactory cues. The scent of food clinging to the fur of a recently fed demonstrator rat and escaping from its gastrointestinal tract allows an observer rat to learn what food its demonstrator ate. However, neither simply eating a food nor smelling a food increases observer rats' preferences for that food. For exposure to a food scent to change an ob-

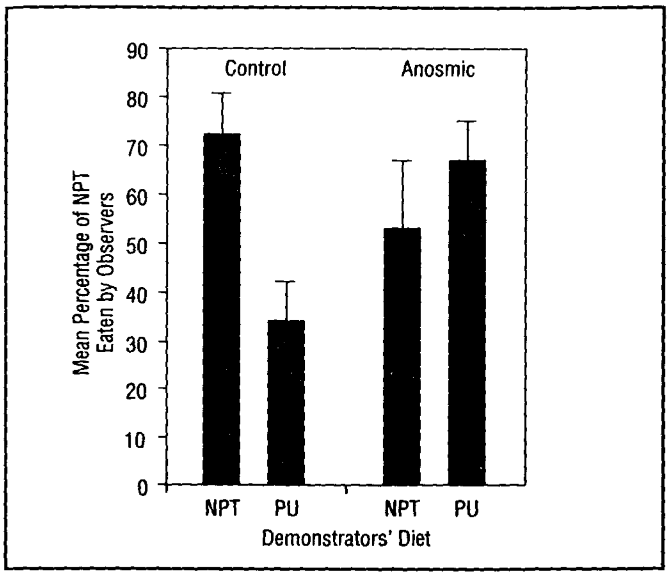

FIGURE 3. Mean (+ SEM) amount of normal-protein test (NPT) diet (Harlan-Teklad) eaten, as a percentage of the total amount ingested over 24 hours by anosmic and control observer rats after interacting with demonstrator rats fed either Diet NPT or Purina rodent laboratory chow (PU) and then offered a choice between those two diets for 24 hours.

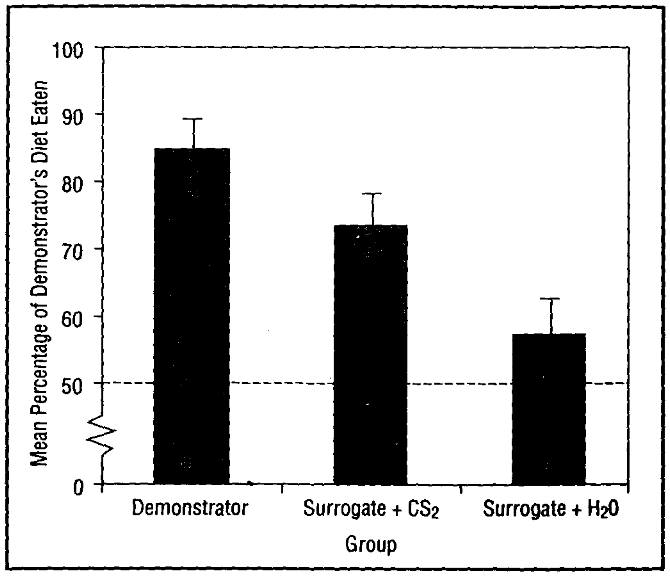

FIGURE 4. Mean (+ SEM) amount of the diet eaten by observer rats as a percentage of their total intake over 24 hours of choice that was the same diet that each observer's demonstrator had eaten. Observer rats interacted with anesthetized demonstrator rats powdered with either Diet Cin or Diet Coc or a piece of cotton batting (Surrogate) powdered with either Diet Cin or Diet Coc and moistened with either carbon disulfide (Surrogate + CS_2) or water (Surrogate + H_2O).

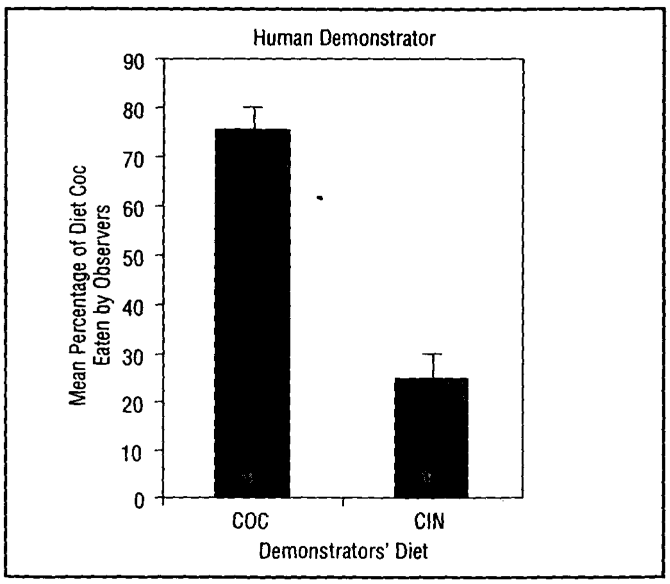

FIGURE 5. Mean (+ SEM) amount of Diet Coc eaten as a percentage of the total amount ingested by observer rats after interacting with human demonstrators fed either Diet Cin or Diet Coc.

server's subsequent preferences, that scent must be experienced together with chemicals carried on the breath of rats.[17]

Contextual cues. Mass spectrograms of rat breath provide evidence of significant concentrations of both carbonyl sulfide and carbon disulfide.[18] Adding a few drops of carbon disulfide, but not of water, to a piece of cotton batting powdered with food makes that piece of cotton batting almost as effective as a demonstrator rat in altering observers rats' subsequent food preferences (Figure 4).[18] Sulfur compounds in rat breath provide a context that allows exposure to food-related scents to alter rats' food preferences.

A Test of the Hypothesis That Carbon Disulfide Provides Necessary Context

Like rats, humans have trace amounts of carbon disulfide on their breaths. If the combination of food odor and carbon disulfide can produce a change in flavor preferences in rats, then human demonstrators who eat a food and breathe on a rat should increase the rat's preference for the food that its human demonstrator ate. In fact, observer rats breathed on by human demonstrators that ate either Diet Cin or Diet Coc have an increased preference for whichever food their human demonstrator ate (Figure 5).[6]

Interaction of Social Learning with Congenital Flavor Preferences

For 23.5 hr/day for 25 consecutive days, we offered rats a choice between Diet Coc and a diet flavored with cayenne

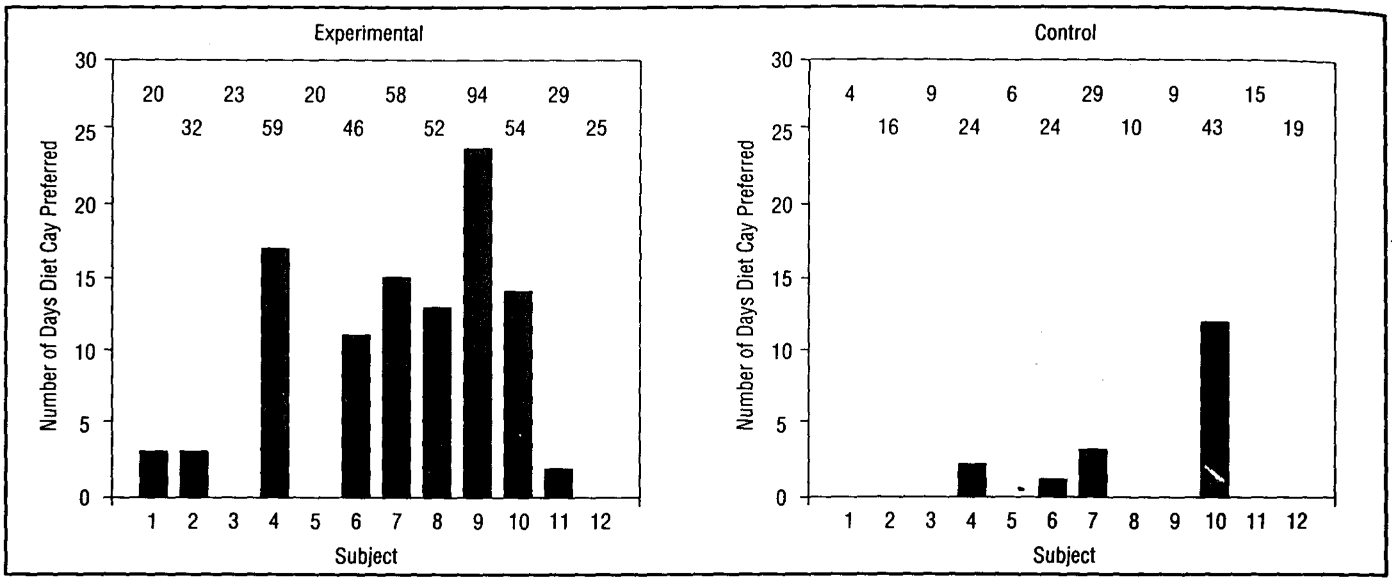

FIGURE 6. ***Number of days (of 25) each subject assigned to experimental and control conditions ate more Diet Cay than Diet Coc. Numbers above each bar indicate the mean percentage of Diet Cay eaten by each observer during 25 days of diet choice.***

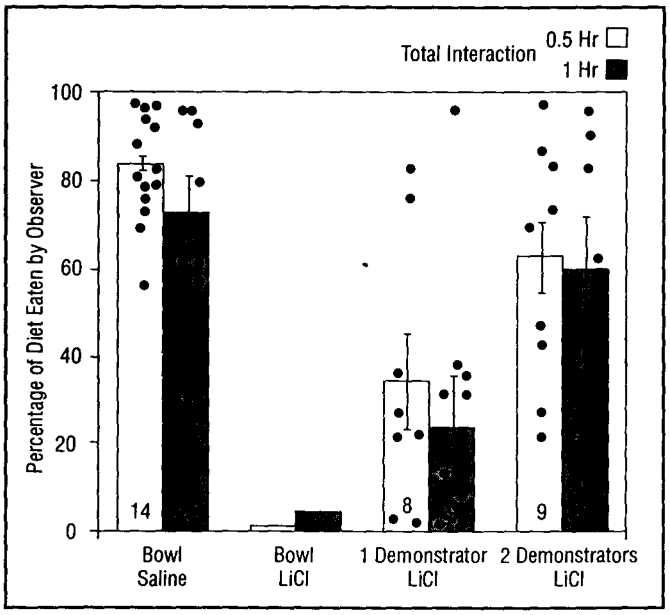

FIGURE 7. ***Mean (+SEM) amount of Diet NPT eaten as a percentage of the total amount ingested by rats first poisoned after eating Diet NPT and then permitted to interact with either a bowl containing Diet NPT or either one or two demonstrators fed Diet NPT and by control rats either injected with saline solution after eating Diet NPT and interacting with a bowl containing Diet NPT following poisoning. Points are scores of individual subjects. (LiCl = lithium chloride)***

pepper (Diet Cay), a substance that rats find aversive. For the remaining 30 minutes of each day, we provided rats assigned to the control group a bowl of Diet Cay and rats assigned to the experimental group a demonstrator rat that had been fed Diet Cay. Exposure to a demonstrator rat fed Diet Cay caused some observers to prefer Diet Cay to Diet Coc (Figure 6).[19]

Interaction of Social Learning with Poison Avoidance

A rat fed an unfamiliar food and then made ill by injection with a toxin shows a strong aversion to eating the food it ate before falling ill. We fed naïve observer rats an unfamiliar, diet (Diet NPT), made them ill by injecting them with lithium-chloride solution, and 24 hours later let the subjects interact for 1 hour with either (1) a bowl of diet NPT, or (2) either one or two rat demonstrators that ate diet NPT. We injected rats assigned to a control group with a harmless saline solution before they interacted for 1 hour with a bowl containing diet NPT. Many observers poisoned after eating diet NPT that later interacted with two demonstrator rats fed diet NPT acted as though they had never been poisoned (Figure 7).[20] Social learning totally reversed the most powerful known experiential determinant of food choice.

CONCLUSIONS

The take-home messages from these experiments are straightforward:

1. The food choices of rats and of many other mammals are profoundly affected by information acquired from others as to what foods they have eaten.

2. We know how such social learning of food preferences proceeds.
3. Social learning can reverse the effects of other major determinants of which foods animals choose to eat.

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