

Social Transmission of Food Preferences: An Adaptation for Weaning in Rats

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Comparison of the extent of social influence on the feeding site selection of adult and weanling domesticated rats revealed that social interaction is a far more potent factor in determining the diet selection of weanlings than of adults. The social transmission of diet preferences is discussed as an adaptation of greatest importance during the weaning period.

Weanling rat pups, both wild and domesticated, prefer to ingest a relatively unpalatable diet that the adult members of their colony have been trained to eat rather than a more palatable alternative diet that the adults of their colony have been trained to avoid (Bronstein, Levine, & Marcus, 1975; Capretta & Rawls, 1974; Galef, 1977; Galef & Clark, 1971, 1972). I have suggested previously that this ability of rats to transmit acquired food preferences socially from individual to individual might be particularly adaptive when the transmitter of the food preference is an adult and the recipient of the transmission a weanling juvenile (Galef, 1976, 1977; Galef & Clark, 1971). Young rats seeking their first meals of solid food in the general environment are relatively ignorant of the location and identity of nutritious food stuffs and must seek out these foods at a time when they are particularly vulnerable to environmental stress. Adults rearing young have learned the identity and location of necessary, safe foods during their own exploration in the area in which they reproduce. It would clearly be advantageous to the young (and, hence, to the

reproductive advantage of their parents) if juveniles could make use of the experience of adult conspecifics in locating solid foods. Thus, consideration of the problems faced by weanling rats undertaking the transition from dependence on mother's milk to independent acquisition of solid food in the general environment suggests that weanling rat pups are far more needful of socially transmitted information than are experienced adults.

If weanling rats are more dependent than adult ones on social interaction in selecting foods for ingestion, then one would expect weanling rats selecting foods for ingestion to make greater use than adult rats of cues emitted by conspecifics. Informal observations in our laboratory have indicated that adult rats are, in fact, far less profoundly influenced in their diet selection by the food choices of conspecifics than are weanlings. In this article these observations are formalized, and the mechanisms underlying the difference in the importance of social factors in the dietary selection of weanling and adult rats are explored.

Experiment 1

The present experiment was undertaken to determine the relative influence of a colony of adult rats, trained to eat at a location at which the less palatable of the two available diets was presented, on the feeding patterns of untrained conspecific adults and juveniles.

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Method

Colony. A colony of four 3-mo-old female Long-Evans rats was established in the $.9 \times 1.9 \times .3$ m enclosure illustrated in Figure 1a. The enclosure was constructed of slotted angle iron and hardware cloth, and its galvanized sheet-metal floor was covered to a depth of .4-.8 cm with woodshavings. Four wooden nest boxes ($5 \times 5 \times 2.5$ cm) were provided. Water was available ad lib and food was presented for 3 hr/day in two aluminum food bowls located approximately .8 m apart.

Each food bowl was securely fixed to a Plexiglas disk attached to the center of a $.5\text{-m}^2$ sheet-metal plate. Each plate was in turn placed in $.5\text{-m}^2$ Plexiglas tray. The aluminum bowl and metal plate of the feeding apparatus presented to the colony in the position labeled Bowl B in Figure 1a could be connected through a shock generator, which allowed the experimenter to deliver a 1.6-mA current to colony members attempting to eat at the Bowl B location (see Galef & Clark, 1972, for a detailed description of the apparatus).

Colony members were trained to eat the diet, powdered Purina Laboratory Chow, consistently presented in Bowl A and to avoid the more palatable diet, Teklad fat-sufficient diet (Teklad Mills, Madison, Wisconsin), consistently presented in Bowl B, by shocking them whenever they ate from the latter source. Colony members rapidly learned to avoid Bowl B and to feed at Bowl A and continued to do so in the absence of application of shock for some weeks.

Experimental subjects. Nine pairs of Long-Evans female rats (five 12-wk-old pairs and four 25-day-old pairs) served as experimental subjects. These animals, born in the McMaster colony, had been maintained as sibling pairs in $36 \times 31 \times 16$ cm cages on ad lib Purina Laboratory Chow and water from weaning at 21 days of age. For the 4 days prior to introduction into the colony enclosure, each pair was placed on a 3 hr/day (powdered Purina Laboratory Chow) feeding schedule synchronized with that of the colony enclosure. At the end of the fourth of these scheduled feeding periods, a single pair of experimental rats was placed in the colony enclosure, left there for 4 days, and then removed. The experimenter observed the colony enclosure by closed circuit television throughout the four 3-hr colony feeding periods during which each experimental pair was cohabiting with the colony and recorded the number of times the members of that experimental pair fed at each of the two colony food bowls. No shock was administered while experimental subjects were in the colony enclosure.

Results and Discussion

The main results of Experiment 1 are presented in Figure 2 which shows the mean percentage of experimental pair feeding bouts occurring at the colony-utilized Bowl A. A feeding bout was defined as an uninterrupted period of feeding during which a subject neither turned away from nor moved more than 1 in. (2.54 cm) from a food source. As is clear from examination of the figure, adult experimental pairs ate far more frequently at the colony-avoided Bowl B than did juvenile experimental pairs (Mann-Whitney U and associated p values for Days 1-4, respectively: $U = 1, p < .03$; $U = 2, p < .05$; $U = 0, p < .01$; and $U = 0, p < .01$).

Colony members were not observed to exhibit overt aggressive behavior (chase, box, or laterally display) toward either adult or juvenile experimental pair members, which suggests that differences in the aggressive behavior of colony members toward the two classes of experimental pairs did not mediate differences in their feeding behavior. Of course, the difference between adult and juvenile experimental subjects in utilization of the colony-avoided bowl and the novel diet it contained could be totally independent of any influence of the behavior of colony members on that of experimental subjects. It is

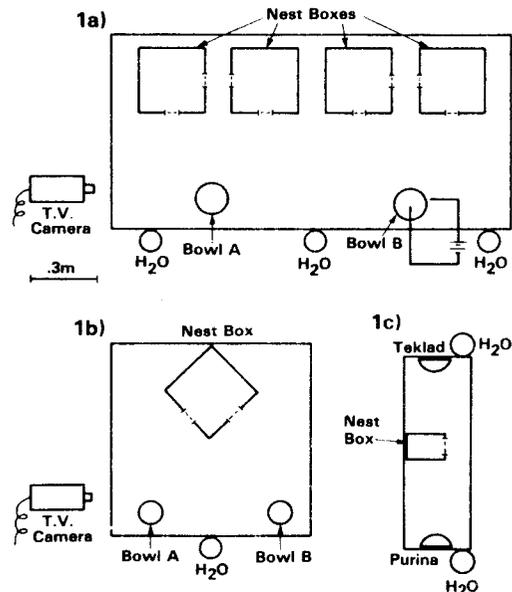


Figure 1. Overhead schematic view of the enclosures used in (1a) Experiment 1, (1b) Experiment 3, and (1c) Experiment 2.

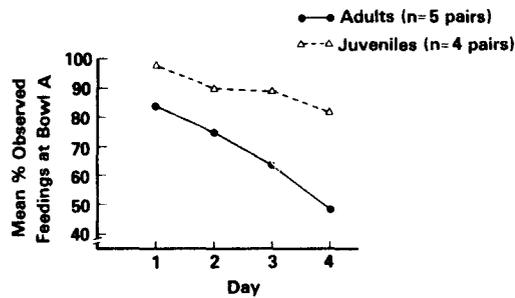


Figure 2. Mean percentage of feeding bouts directed toward the colony-utilized food bowl (Bowl A) by adult and juvenile experimental pairs in Experiment 1.

possible that juvenile rats are simply more hesitant to transfer feeding to a novel diet than are conspecific adults. Experiment 2 investigates this possibility.

Experiment 2

The present experiment investigates the relative hesitancy of adult and juvenile domesticated rats to ingest an unfamiliar diet, independent of social interactions.

Method

Subjects. Fifteen 14-wk-old and fifteen 21-day-old Long-Evans rats from 10 litters born in the McMaster colony, maintained on ad lib Purina Laboratory Chow and water from weaning at Day 18 postnatally, served as subjects.

Procedure. All 30 subjects were individually caged in enclosures like that illustrated in Figure 1c and were presented with powdered Purina Laboratory Chow for 3 hr/day for seven consecutive days at the location indicated in the figure. Beginning on the eighth day of scheduled feeding, and for the subsequent 3 days, each subject was presented for 3 hr/day with two food cups, one containing powdered Purina Laboratory Chow and the other containing Teklad fat-sufficient diet. The experimenter determined the amount of each diet eaten by weighing food cups before and after each feeding session. Spillage, which was minimal, was returned to the appropriate food cup prior to weighing.

Results and Discussion

Figure 3 presents the mean amount of the familiar Purina chow eaten by adults and juveniles as a proportion of their total intake. As evident from examination of the figure, adult rats did not differ from juveniles in their hesitancy to ingest a

novel diet in a novel location. These data suggest that the results of Experiment 1 cannot be attributed to differences in the neophobia (Barnett, 1958; Galef, 1970) of adult and juvenile domesticated rats.

Comparison of the data presented in Figure 2 with those of the present experiment reveals a considerable effect of conspecifics on adult rate of transfer of feeding to a novel diet. As has been previously shown (Galef & Heiber, 1976), an adult rat can be influenced in its choice of feeding location by residual olfactory cues deposited near a feeding site by others. However, as noted in the discussion of Experiment 1, the effect of social influence is clearly far more pronounced in juvenile than in adult rats.

Experiment 3

The present experiment avoids the confounding of colony-avoided and novel diet present in Experiment 1. It directly examines the possibility that the difference found in Experiment 1 between juveniles and adults in rate of transfer of feeding to a novel food was due to a difference in the effectiveness of social influence in determining the feeding site selection of rats of different ages.

Method

Subjects. Subjects were 24 adult (11–14 wk-old) and 24 juvenile (27–31 day-old) Long-Evans female rats weaned to Purina Laboratory Chow at 18 days

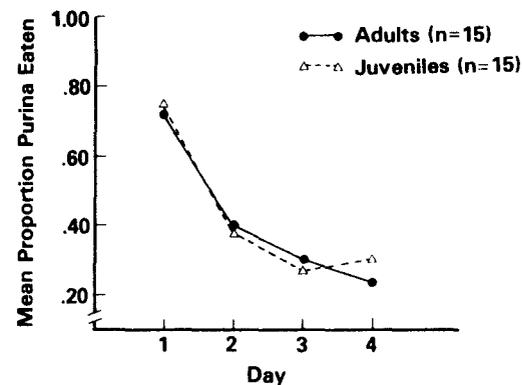


Figure 3. Mean amount of familiar Purina diet eaten as a proportion of total food eaten by adults and juveniles in Experiment 2.

of age and maintained as sibling pairs in $36 \times 31 \times 16$ cm cages until testing.

Procedure. Twenty-two hours prior to the initiation of testing, a pair of sibling juveniles ($n = 8$ pairs) or of sibling adults ($n = 8$ pairs), or a pair composed of one adult and one juvenile ($n = 8$ pairs) was placed in the enclosure illustrated in Figure 1b in the absence of food. At the commencement of testing two food bowls containing powdered Purina Laboratory Chow were placed in the positions indicated in the figure. For the next 2 hr the experimenter observed the feeding behavior of the subjects by closed circuit television, recording the location, time of initiation, and time of termination of each feeding bout of each subject. Individual animals in each pair were distinguished by pelage markings. The member of each pair of adults and each pair of juveniles that had a broader stripe on its back was arbitrarily designated the first member of that pair and the one with the narrower stripe, the second member of the pair. At the end of the 2-hr test period the food bowls were removed, and 22 hr later the test procedure was replicated.

Data analysis. To determine whether the animals were influencing one another's choice of feeding site, we examined those instances in which one animal of a pair initiated feeding while the other pair member was feeding. The former animal could, of course, choose to feed together (T) with its pair mate or separate (S) from it. The ratio of the number of times each member of a pair chose to eat together with its pair-mate divided by the total number of instances of initiation of feeding when a pair-mate was at a food bowl, $T/(S + T)$, provides one measure of the extent of social influence on each animal when choosing a feeding location. The $T/(S + T)$ ratios were calculated separately for the first and second members of each of the eight pairs composed of two adults or two juveniles, and $T/(S + T)$ ratios were calculated separately for juveniles and adults in the adult-juvenile pairs.

Such measures of social influence on feeding site selection could obviously be distorted by a strong position bias on the part of the subjects. If, for example, all subjects ate only at the right-hand bowl, each would exhibit a ratio of $T/(S + T) = 1$, even though no social influence existed. As a control for such bias, the ratio $T/(S + T)$ was calculated from the data of randomly composed pairs of animals. The data collected from each animal, indicating the location, time of initiation, and time of termination of each of its feeding bouts, were randomly paired with those of another animal from a similar type pair, and the ratio $T/(S + T)$ was calculated for this randomly constituted pair.

Results and Discussion

The results of Experiment 3 are presented in Figure 4 which shows the mean $T/(S + T)$ values for juvenile, adult, and adult-juvenile pairs and their random controls. As can be seen in the figure, all

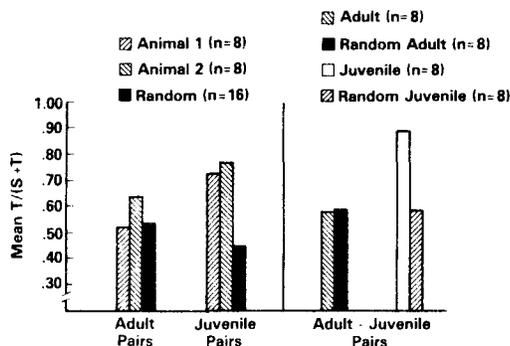


Figure 4. Mean amount of eating together as a proportion of total instances of eating together and separately.

randomly paired animals ate together about as frequently as they ate apart, $T/(S + T) \approx .50$. Similarly, members of true adult pairs did not attract one another to a feeding site. Juveniles, however, were very strongly influenced in their choice of feeding site by the presence there of an adult or juvenile conspecific. These data strongly suggest that the difference found in Experiment 1 between adult and juvenile rats in rate of transfer of feeding to a site avoided by conspecifics was the result of differences in their susceptibility to social influence during the process of feeding site selection.

General Discussion

The results of the preceding experiments indicate that selection of a feeding site, and consequently selection of a diet (Galef & Clark, 1971), are more profoundly influenced socially in juvenile than in adult rats. These data suggest that the tendency of rats to make use of information provided by conspecifics in the selection of a diet is best treated as a behavioral adaptation of greatest importance during the weaning stage when the young rat is dependent on conspecific adults to direct its activities in potentially profitable directions (Galef, 1977).

As Adolph (1957, p. 131) proposed in his monograph on the ontogeny of regulatory systems, "each stage of development is functionally complete in its own right." The data of the present studies suggest

that a dependence on social interaction in the selection of foods is a specific adaptation in response to the problems posed to rat pups by the necessity to transfer the orientation of their feeding responses from their dam to specific locations in the larger environment.

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