Susceptibility of Artificially Reared Rat Pups to Social Influences on Food Choice

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Using techniques developed by Hall (1975) and modified by Diaz (1991), we maintained rat pups in total social isolation from the time they were 2 or 3 days of age until they were 42 days old. We found that rat pups reared in social isolation exhibited susceptibility to social enhancement of food preference indistinguishable from that exhibited by normally reared rat pups. These data suggest that development of a tendency to use conspecifics as sources of information about what foods to eat does not depend upon previous experience either of interaction with conspecifics or of feeding in social situations. © 1994 John Wiley & Sons, Inc.

Experiments conducted both in our laboratory and elsewhere have shown repeatedly that after a naive young rat (an observer) interacts with a recently fed conspecific (a demonstrator), the observer exhibits an enhanced preference for whatever food its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Heyes & Durlach, 1990; Winocur, 1990). Although both causes and functions of such socially induced modifications of food preference in rats have been the subject of numerous studies (see Galef, 1988, 1989, 1990 for reviews), the ontogeny of susceptibility to social influence on food choice in rats has seldom been explored.

Common sense suggests that rat pups' experiences early in life might play an important role in their developing susceptibility to social influences on their food choices. Infant rats feed exclusively during periods of intense social interaction (milk intake is possible only when infant rats are in contact with a lactating female, and infants almost always suckle simultaneously with siblings). Even during and after weaning, juvenile rats frequently feed with others of their species (Galef, 1981; Galef & Clark, 1971). Such early experiences of feeding in social circumstances might be necessary for young rats to learn that conspecifics can provide important clues about the location and nature of foods.

Further, in a study of effects of early experience on rats' susceptibility to social influences on feeding site selection, Galef (1981) found that, unlike rat pups reared by a dam and with siblings, rat pups reared without social contact did not prefer feeding sites occupied by conspecifics to feeding sites with no rats near them. Rat pups reared in social isolation might well exhibit deficits in their use of conspecifics as sources of information about what to eat, just as they exhibited deficits in their use of conspecifics as sources of information about where to eat (Galef, 1981).

Experiment 1

In the first experiment, we compared the magnitude of social influence on the food preferences of isolation-reared and normally reared 42-day-old rat pups. It was our expectation that normally reared animals would exhibit more profound social influence on their diet selection than would animals reared in social isolation.

Method

Subjects

Thirty 42-day-old male and female Long-Evans rat pups born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario) to breeding stock acquired from Charles River Canada (St. Constant, Quebec) served as observers in the present experiment. Fifteen of these 30 observers were assigned at birth to an experimental group and the remaining 15 to a control group.

An additional 30 normally reared juvenile rats served as demonstrators. Each demonstrator rat was 7–10 days older than the observer rat with which it interacted during the experiment.

Apparatus

Food preferences of individual observer rats were tested in large, wire-mesh hanging cages (43 × 25 × 18 cm) divided into two equal compartments (21.5 × 25 × 18 cm) by a hardware-cloth partition (1.25-cm mesh).

Procedure

Normal Rearing

The 15 observer rats assigned to the control group were reared by their respective dams ($n = 8$) in normal fashion and weaned at 21 days of age. After weaning, these observers were maintained on ad-lib pellets of Purina Rodent Laboratory Chow #5001 and water in groups of three or four same-sex littermates in polycarbonate shoe-box cages (37 × 30 × 17 cm).

Isolation Rearing

The 15 pups reared in isolation were taken from their dams ($n = 6$) 24 to 36 hr after birth. They were then anesthetized with ether and, using methods developed by Hall (1975), were each implanted with a chronic intragastric cannula. Following

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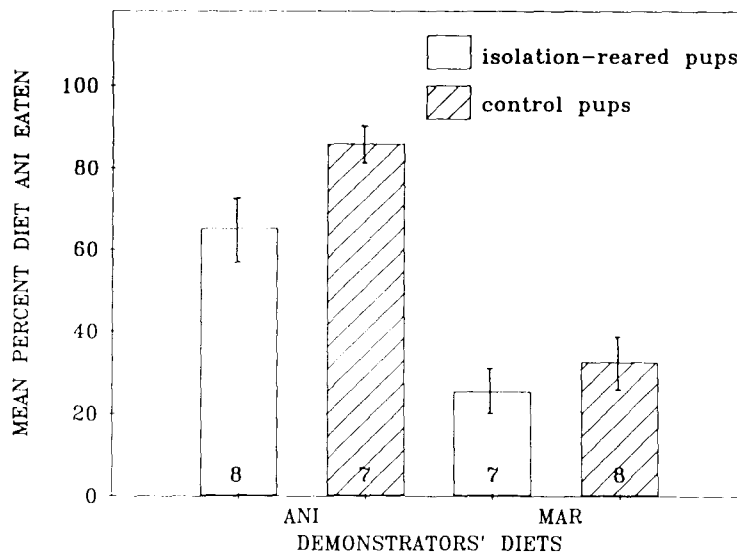
Fig. 1. Mean amount of Diet Ani eaten, as a percentage of total amount ingested, by observer rats reared either in social isolation or normally. Numbers inside histograms = n/group. Flags = ± 1 SE.

cannulation, each pup was maintained in a polystyrene cup floating in a constant-temperature bath (Hall, 1975) and fed an enriched milk diet (Diaz, 1991) through its cannula until it was 18 days old.

When each pup was 18 days of age, its cannula was removed and the pup was placed alone in a small, shoe-box cage (27.5 × 17.5 × 12.5 cm) where it was first fed a mash of powdered Purina Rodent Laboratory Chow #5001 and water and then gradually weaned, first to dry, powdered Purina chow and finally to pellets of Purina chow. Pups in the experimental group of observers remained in tactile and visual isolation from conspecifics until the end of the experiment, except during the 30-min period of social interaction described in Step 4 below.

Inducing and Testing Social Influences on Food Choice

We attempted to induce socially enhanced food preferences in each of our observer rats at 42 days of age. The procedure employed with all 30 observers was identical and consisted of six steps:

1. Each observer rat was introduced into one compartment of a hanging cage, provided with ad-lib access to pellets of Purina chow and water and left undisturbed for 2 days to become familiar with the experimental apparatus.
2. While observers were becoming familiar with the apparatus, their demonstrators were placed in individual cages in a separate room, where they were accustomed to a 1 hr/day feeding schedule. On each of 2 consecutive days, each demonstrator rat was food-deprived for 23 hr, then offered powdered Purina chow for 1 hr.
3. Following a third, 23-hr period of food deprivation, each demonstrator was fed one of two diets composed by adding either 1 g of ground anise (Diet Ani) or 2.4 g of ground marjoram (Diet Mar) to 100 g of powdered Purina Rodent Laboratory Chow #5001.

4. Immediately after eating either Diet Ani or Diet Mar for 1 hr, each demonstrator was placed in a hanging cage on the other side the hardware-cloth barrier from its observer, and demonstrator and observer were left undisturbed to interact for 30 min.
5. At the end of this 30-min period of interaction, demonstrators were removed from the experiment, and each observer was offered a choice, for 22 hr, between two weighed food cups, one containing Diet Mar and the other containing Diet Ani.
6. At the end of the 22-hr test period, the experimenter determined the amount of each of the two diets eaten by each observer and calculated: (1) the percentage of each observer's total intake that was Diet Ani and (2) the percentage of each observer's total intake that was the diet that its respective demonstrator had eaten.

Results and Discussion

The 15 observer pups reared in social isolation grew at an almost normal rate. They weighed 30.3 ± 0.5 g when 18 day old, while the 15 normally reared control observer pups weighed 33.0 ± 0.5 g at the same age, $t(28) = 3.80, p < .01$.

The main results of the experiment are presented in Figure 1, which shows the mean amount of Diet Ani eaten during testing by observers whose demonstrators ate either Diet Ani or Diet Mar when fed for 1 hr in a room separate from observers. As is clear from examination of Figure 1 and as statistical tests confirmed, during the 22-hr test those observers in the control group whose demonstrators ate Diet Ani ate a greater percentage of Diet Ani than did those observers in the control group whose demonstrators ate Diet Mar, Mann-Whitney U test, $U = 0, p < .0001$. Similarly, those observers in the isolation-reared group whose demonstrators ate Diet Ani ate a greater percentage of Diet Ani than did those observers in the isolation-reared group whose demonstrators ate Diet Mar, $U = 7, p < .01$. Further statistical analyses revealed that: (1) observers assigned to both control and isolation-reared conditions ate a greater percentage of the diet that their respective demonstrators had eaten than one would expect by chance, Wilcoxon tests: control observers, $t = 4, p < .0001$; isolation-reared observers, $t = 18, p < .01$; and (2) control observers and isolation-reared observers did not differ significantly from one another in the mean percentage of their respective demonstrators' diets eaten during testing , Mean percent $\pm SE$ demonstrator's diet eaten by: control observers, 76.0 ± 5.7 percent; isolation-reared observers 65.8 ± 5.9 percent; Mann-Whitney U test, $U = 82$, ns.

Experiment 2

Although the results of Experiment 1 are consistent with the hypothesis that rat pups reared in social isolation are as sensitive to social influences on their food choices as are normally reared rat pups, there is at least one alternative explanation of the outcome of Experiment 1. Galef and Kennett (1987) have reported that 21-day-old, normally reared rat pups, unlike either their 28- or 38-day-old fellows, exhibit enhancement of their preferences for a food following a 30-min period of simple exposure to that food.

It is possible that the development of rat pups reared in isolation was slowed so that 42-day-old, isolation-reared rat pups, like 21-day-old, normally reared rat pups, respond to simple exposure to a food by increasing their later preference for that food. If so, then the isolation-reared pups in Experiment 1 might have exhibited enhanced preferences for the foods that their respective demonstrators had eaten, even if they were not susceptible to specifically social influences on their food

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The present experiment was undertaken to determine whether simple exposure of 42-day-old, isolation-reared rats to the taste and smell of foods would suffice to enhance their later preferences for those foods.

Method

Subjects

Fourteen isolation-reared and 14 normally reared Long-Evans rat pups, maintained as described in Experiment 1, served as subjects in the present experiment.

Apparatus

The apparatus used was the same as in Experiment 1.

Procedure

The procedure of Experiment 2 was similar to that of Experiment 1 except that: (1) we used no demonstrators and (2) during Step 4 of Procedure, subjects were exposed for 30 min to a 10-cm diameter, semicircular, stainless-steel dish containing either Diet Ani or Diet Mar rather than to a conspecific demonstrator that had eaten either Diet Ani or Diet Mar. To maximize subjects' simple exposure to diets in the present experiment, the dish containing Diet Ani or Diet Mar was on the same side of the screen partition as a subject.

Results and Discussion

The main results of Experiment 2 are presented in Figure 2, which shows the mean amount of Diet Ani eaten during Step 5 of Procedure by isolation-reared and control subjects simply exposed either to Diet Ani or to Diet Mar during Step 4 of Procedure. As is evident from inspection of Figure 2, simple exposure of 42-day-old, isolation-reared rat pups to either Diet Mar or Diet Ani, like simple exposure of normally reared, 42-day-old pups to the same diets, failed to enhance preference for the exposed diet, Mann-Whitney U tests, $Us > 16$, ps = ns. Further, as one might expect given the failure of simple exposure to a diet to alter preference for that diet, isolation-reared and control subjects that were simply exposed to a diet: (1) did not eat a greater percentage of the diet to which they had been exposed than would be expected by chance, Wilcoxon tests: $ts > 42$, ps = ns, and (2) did not differ from one another in the mean percentage of the diet to which they had been exposed that they ate (Mean percent $\pm$ SE exposed diet eaten by: control subjects = 48.4 $\pm$ 8.6%; isolation-reared subjects = 59.3 $\pm$ 9.5%; Mann-Whitney U test, U = 83, ns.

The results of Experiment 2 indicate that the finding in Experiment 1 of preferences by pups reared in isolation for the diets eaten by their respective
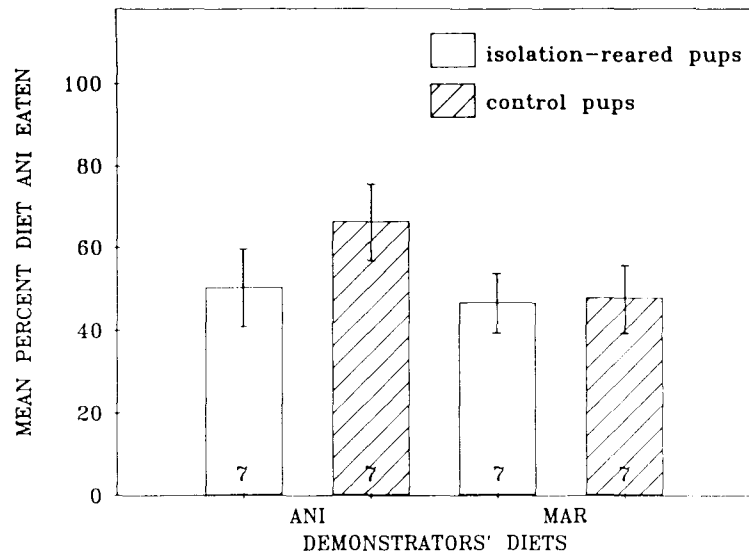
Fig. 2.   Mean amount of Diet Ani eaten, as a percentage of total amount ingested, by subjects raised either in social isolation or normally and simply exposed to either Diet Mar or Diet Ani. Numbers inside histograms = n/group. Flags = ± 1 SE.

demonstrators cannot be explained in terms of simple exposure to diets during the period of interaction of demonstrators and observers.

General Discussion

Frankly, we were surprised to find that rat pups reared in isolation from conspecifics were as susceptible to social influence on their food choices as were normally reared rat pups. We had anticipated major disruption of social influence on food preference following rearing in isolation similar to the disruption of socially induced feeding-site preference exhibited by isolation-reared rat pups described elsewhere (Galef, 1981).

Perhaps we should have anticipated the present result. In an article conceptually very similar to the present one, Hofer, Shair, and Murowchick (1989) compared the behavior of pups reared in social isolation with that of pups reared by their dams and concluded that many social experiences that normally occur during ontogeny are not necessary for development of species-typical attachment responses in rats. When placed in an unfamiliar environment, normally reared and artificially reared rat pups exhibited similar reductions in vocalization, rearing, and locomotion in response to contact with a conspecific adult female. The study by Hofer et al. (1989), like the study reported here, provides an example of an ability of rat pups to respond in species-typical fashion to cues associated with conspecifics despite having been reared in conditions providing an abnormally restricted range of social interactions (See also Galef & Kaner, 1980).

Of course, experiences other than those that we manipulated may prove important for normal development of susceptibility to social influence on food choice in rats. For example, [and as discussed in considerable detail by both Hofer et al. (1989) and Galef & Kaner (1980)], exposure of rat pups reared in isolation either to social stimulation during the first 2 or 3 days of life or to stimuli they generate themselves while held

in isolation from conspecifics might be necessary to sustain normal development of susceptibility to social influences on feeding behavior in pups lacking the opportunity to participate in social interactions during most of their early lives.

As Hofer et al. (1989, p. 564) stated, one useful feature of null outcomes of experiments that use isolation-reared animals to identify stimuli important in the ontogeny of species-typical behaviors is that negative findings "allow us to focus on a much simpler environment in which to search for the interactions underlying development of . . . behavior."

Still, it is surprising to find a complex social behavior as resistant to disruption by developmental manipulation as susceptibility to social influence on food choice has proven to be. Almost every aspect of the early experience of artificially reared rat pups is abnormal, and the absence of any obvious effects of so deviant an early life on social learning about foods was totally unexpected. Social experiences that, intuitively, would seem important for emergence of a capacity for social learning do not appear to play a major role in development of a tendency to use conspecifics as sources of information about what foods to eat.

Notes

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