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Groups of naive rats learn to select nutritionally adequate foods faster than do isolated naive rats

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Abstract. Naive juvenile Norway rats, *Rattus norvegicus*, were housed either individually or in groups of six and were given 10-days ad libitum access to three palatable, protein-deficient diets and a single, less palatable, protein-rich diet. Although subjects housed in groups ate the same amount of food as did subjects housed alone, group-housed animals both ate more protein-rich diet and grew more rapidly than did individually housed subjects.

The young of many mammalian species face a severe challenge to survival at weaning. As milk flow from its dam wanes, each juvenile must learn to choose appropriate foods to eat from among myriad ingestible substances with which it comes into contact (Galef & Beck 1990).

Beck & Galef (1989) have reported that individual weanling rats offered a choice of four foods (three both relatively palatable and protein-deficient and one relatively unpalatable but protein-rich) were slow to learn to eat the protein-rich food and failed to grow at a normal rate. On the other hand, individual weanlings that shared their enclosures with adult demonstrator rats that had been trained to eat only the protein-rich diet, quickly learned to eat that diet and grew normally (Beck & Galef 1989; Galef et al. 1991).

The procedure used by Beck & Galef (1989) provided a laboratory analogue of a situation (presumably common outside the laboratory) in which juvenile rats that are learning to select an adequate diet have opportunities to interact with adult conspecifics that have already learned what foods to eat. However, Beck & Galef's (1989) procedure failed to capture a second, potentially important social feature of the weaning environment; in natural circumstances, most rat pups are weaned as one of a sibling group each of whose members must learn to find a nutritionally adequate diet in an unfamiliar environment.

EXPERIMENT 1

Experiment 1 was undertaken to determine whether rat pups weaned in groups would be more efficient at learning to select a nutritionally adequate diet from an array of adequate and deficient foods than would rat pups weaning in isolation. We offered both groups of juvenile rats and individual juvenile rats four distinctively flavoured foods, only one of which contained sufficient protein for normal growth. We then determined whether members of groups of animals were more successful than were their isolated fellows in learning to select the protein-rich diet. Thus, we asked not whether a naive animal could use a knowledgeable conspecific as a source of information to solve a foraging problem, but whether members of groups of naive animals could solve a foraging problem more rapidly than could isolated naive animals.

Methods

Subjects

One hundred and twenty experimentally naive, 42–49-day-old, female Long-Evans rats, 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 subjects. When we had a group of 24 42–49-day-old pups, we weighed them and assigned each pup to one of four groups of six that we equated for mean weight. The six subjects in some groups were housed together ($N=11$ groups of six subjects), while the six subjects in remaining groups ($N=9$ groups of individual subjects) were housed in individual cages.

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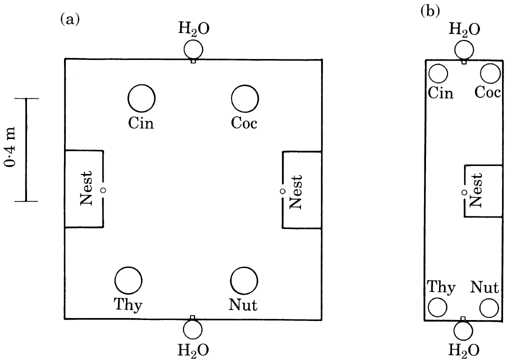

Figure 1. Overhead schematic drawing of the apparatus used to house (a) groups of six subjects and (b) individual subjects in experiment 1.

Apparatus

We housed groups of six animals in cages (1 × 1 × 0·3 m) constructed of angle iron, hardware cloth and galvanized sheet metal and housed individual animals in enclosures (1 × 0·3 × 0·3 m) constructed by placing two sheet-metal partitions (0·3 × 1 m) at 0·3-m intervals in 1 × 1 × 0·3-m cages (see Fig. 1). Each group cage contained two wooden nestboxes (30 × 15 × 15 cm) and four ceramic food bowls (10 cm diameter), while cages housing individuals contained a single nestbox (20 × 15 × 15 cm) and four Pyrex food bowls (7 cm diameter).

Diets

On each of the 10 days of the experiment, we placed four food bowls in each enclosure for 23 h/day. Three of these four bowls contained diets that were both relatively palatable and relatively poor in protein (4·4% protein by weight). The fourth bowl contained a diet that was both relatively unpalatable and relatively rich in protein (17·5% protein by weight). A 12% protein diet is considered adequate for young rats (Guide to the Care and Use of Experimental Animals 1980).

The three protein-poor diets were composed (in g/kg) by mixing 800 g protein-free, basal mix (Teklad Diets, Madison, Wisconsin, Catalogue No. TD 86146; in g/kg, 808·5 g corn starch, 108·1 g vegetable oil, 27·0 g cod liver oil, 54·1 g mineral mix, and 2·7 g vitamin mix) with 100 g corn starch, 50 g granulated sugar, and 50 g high-protein casein (Teklad Diets, Catalogue No. 160030). Protein-deficient diets were flavoured with either 10 g/kg McCormick's fancy ground cinnamon (Diet Cin), 20 g/kg Hershey's pure cocoa (Diet Coc), or 10 g/kg Club House ground thyme (Diet Thy).

The single protein-rich diet (Diet Nut) was composed by mixing (in g/kg) 800 g protein-free, basal mix with both 200 g of a high-protein casein, which is unpalatable to rats (Kon 1931), and 10 g/kg of Club House ground nutmeg.

When the four diets were offered in a 2-h simultaneous choice test to young rats that had been deprived of food for 20 h, Diet Nut proved to be the least preferred of the four. Furthermore, as expected, during the first 24 h of the experiment described below, Diet Nut accounted for less than 8% of the total food intake by both subjects housed individually and subjects housed in groups.

Procedure

To begin the experiment, we placed both individual subjects and groups of six subjects in their respective cages with two bowls, both containing a powdered form of their normal maintenance diet (Purina Laboratory Rodent Chow No. 5001). The subjects were left undisturbed for 2 days to become familiar with the experimental situation.

At the end of this 2-day familiarization period, we removed the bowls containing Purina chow from each cage and replaced them with four bowls, one containing each of either relatively palatable, protein-poor Diets Cin, Coc and Thy or relatively unpalatable, protein-rich Diet Nut.

For the next 10 days, we weighed each food bowl and each subject daily and determined both the intake of each diet and the rate of growth of each pup.

Data analysis

Because each group of six subjects shared a single set of food bowls, we could measure only the total amount of Diets Cin, Coc, Thy and Nut eaten by groups. To equate the variance in amounts of diets eaten by individual subjects with the variance in the amounts of diets eaten by subjects in groups, we combined the food intakes of the six members of each group of pups assigned to individual cages. Thus, we always compared the total amounts of foods eaten by six isolated

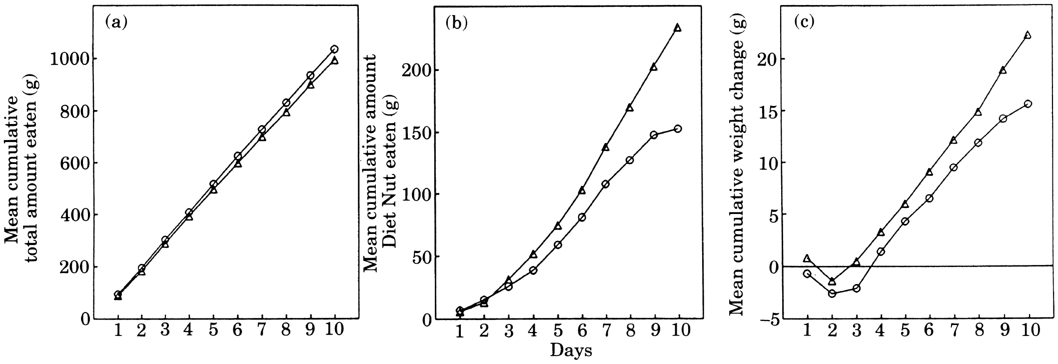

Figure 2. (a) Mean cumulative amount of food eaten/subject, (b) mean cumulative amount of protein-rich, Diet Nut eaten/subject and (c) mean cumulative weight gain/subject during the 10 days of experiment 1. △: Group-housed subjects; ○: individually housed subjects.

subjects with the total amounts of foods eaten by groups of six subjects. For consistency, data on subjects' weight gains were treated similarly.

Results

Although subjects housed in groups and subjects housed in isolation ate roughly the same amount of food during the 10 days of the experiment (Student's *t*-test, $t=0{\cdot}51$, $df=18$, $P=0{\cdot}31$), subjects in groups ate 53·4% more relatively unpalatable, protein-rich, Diet Nut ($t=1{\cdot}93$, $df=18$, $P<0{\cdot}05$) and gained 42·3% more weight than did isolated subjects ($t=2{\cdot}42$, $df=18$, $P<0{\cdot}03$; Fig. 2).

For individually housed subjects, correlational analyses of the relationship between: (1) total intake of Diet Nut across the 10 days of the experiment and total change in body weight and (2) total intake of foods other than Diet Nut and total change in body weight revealed that a far greater proportion of variance in the weight gain of individual pups could be accounted for by variance in their intake of Diet Nut ($r^2=0{\cdot}74$) than by variance in their intake of the other three diets combined ($r^2=0{\cdot}10$). These correlations are consistent with the view that the relatively high growth rate of pups maintained in groups resulted from their eating relatively large amounts of protein-rich diet.

The results of experiment 1 provide evidence that naive young rats living in groups can be more successful than similar animals living in isolation both in selecting a nutritionally adequate diet and in maintaining a normal growth trajectory. However, the data of experiment 1 provide no insight into the behavioural interactions responsible for induction of enhanced intake of the relatively unpalatable, protein-rich Diet Nut by rats housed in groups.

Experiment 2 was undertaken to explore one of the more interesting behavioural processes which might support the social influence on diet selection observed in experiment 1.

EXPERIMENT 2

There are many possible explanations for the finding in experiment 1 that groups of naive young rats might differ from their isolated conspecifics in their pattern of food selection. For example, rats living in groups might simply be more likely than rats living in isolation to ingest substantial quantities of unpalatable foods, or the palatability spectra of rats might change as a function of the size of the social group in which they reside.

We, however, were particularly struck by the observation that rats assigned to individual cages in experiment 1 exhibited great variance in their latencies to eat their first substantial meal of the unpalatable, protein-rich Diet Nut. Some subjects housed in isolation came to focus their intake on Diet Nut by the end of the second day of the experiment; others never ate more than a trivial amount of Diet Nut on any of the 10 days of the experiment.

From our measurements of the food intake of individually housed subjects in experiment 1, we also knew that once an animal had eaten a substantial amount of protein-rich Diet Nut and, presumably, experienced the beneficial effects of protein repletion contingent upon eating that diet, it was very likely both to continue to eat Diet Nut and to grow more rapidly than individuals that were avoiding ingesting Diet Nut because of its relatively low palatability.

Previous work in our laboratory has shown that after a subject rat interacts with a conspecific that has eaten several different foods, only one of which was unfamiliar to the subject, the subject rat exhibits greater enhancement of its intake of the unfamiliar food than of the familiar foods that its conspecific ate (Galef 1993). Extrapolating this finding to the situation in experiment 1, one might expect that once the first rat in a group had added Diet Nut to the repertoire of protein-deficient diets that it shared with its fellow group members, each subsequent interaction of the rat eating Diet Nut with one of its fellows should have induced an enhanced preference for the unfamiliar, unpalatable, Diet Nut in those that had not yet eaten it.

In experiment 2 we examined the simplest situation we could devise that would capture what we hypothesized might be the critical interaction producing the social enhancement of intake of Diet Nut in groups of subjects observed in experiment 1. This important interaction would occur whenever a rat eating only cinnamon-, cocoa- and thyme-flavoured diets interacted with another of its group that had started to eat the unpalatable nutmeg-flavoured diet in addition to the diets flavoured with cinnamon, cocoa and thyme that all group members were eating.

Methods

Subjects

Eighty-four experimentally naive, 42-day-old, female, Long-Evans rats from the McMaster University Psychology Department vivarium served as observers. An additional 84 49–56-day-old female rats that had been observers in other experiments served as demonstrators.

Diets

In experiment 2, we used both the same four diets that we had used in experiment 1 and two new diets: Diet A (composed by adding 0·1 g ground cinnamon, 0·8 g pure cocoa, 0·2 g ground thyme and 6·5 g high-protein casein (Teklad Diets, Catalogue No. 160030) to 92·4 g Protein-free Basal Mix (Teklad Diets, Catalogue No. TD86146)) and Diet A + Nut (composed by adding 0·3 g ground nutmeg to each 99·7 g of Diet A). The mixture of ingredients in Diet A + Nut produced a diet roughly equivalent in its constituents to the average intake of constituents by groups of six subjects on the last day of experiment 1.

Apparatus

Demonstrators and observers were each housed individually throughout the 4 days of the experiment in wire-mesh hanging cages (18 × 34 × 19 cm).

Procedure

Treatment of demonstrators and observers during the experiment was as follows.

(1) We, first, randomly assigned each observer to one of two groups that differed only in the foods that we fed to their respective demonstrators during step 2 below.

(2) All 84 observers were fed Diet A ad libitum for the first 3 days of the experiment. While the observers were eating Diet A, we placed all 84 demonstrators on a 23 h/day deprivation schedule during which powdered Purina chow was available for 1 h/day on each of 2 consecutive days. Following a third 23-h period of food deprivation, we fed each of 42 demonstrators Diet A for 1 h and the remaining 42 demonstrators Diet A + Nut for 1 h.

(3) At the end of the demonstrators' 1-h feeding period, we removed all food from the cages of observers and placed a demonstrator in the home cage of each observer. Demonstrators and observers were then left to interact freely for 30 min.

(4) At the end of the 30-min period of interaction between demonstrators and observers, we removed demonstrators from the experiment and offered 24 observers (12 of which had interacted with demonstrators fed Diet A and 12 of which had interacted with demonstrators fed Diet A + Nut) a choice between weighed samples of Diets Cin, Coc, Thy and Nut. At the same time, we offered 10 observers that had interacted with a demonstrator fed Diet A and 10 observers that had interacted with a demonstrator fed Diet

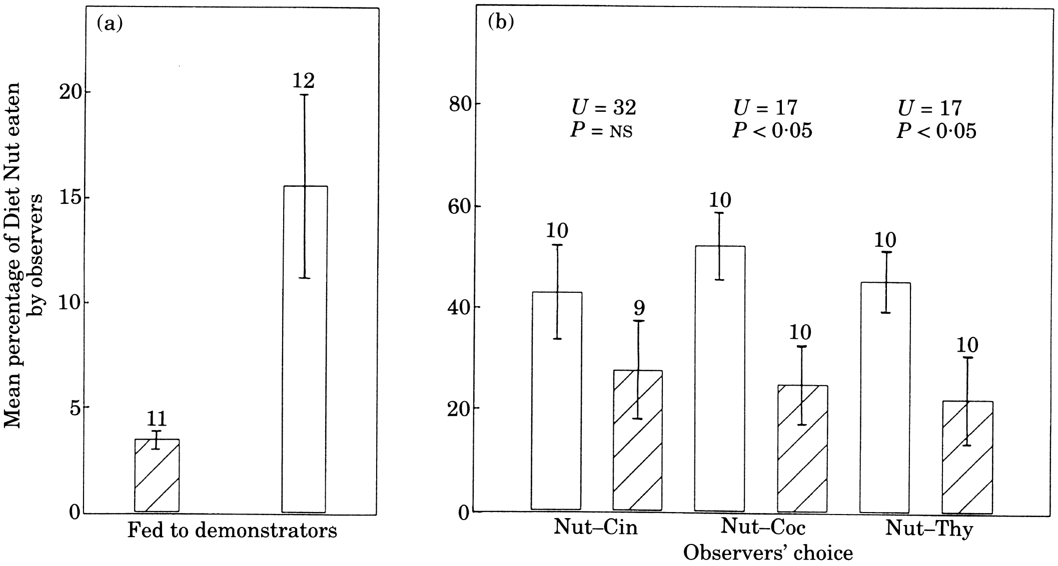

Figure 3. Mean (± SE) percentage of Diet Nut eaten by subjects in experiment 2 that, first interacted with demonstrators fed either Diet A (▨) or Diet A + Nut (☐) and then were offered a choice (a) between Diets Cin, Coc, Nut and Thy or (b) between either Diet Nut and Diet Cin, Diet Coc and Diet Nut or Diet Thy and Diet Nut.

A + Nut a choice between: (1) Diet Nut and Diet Cin, (2) Diet Nut and Diet Coc or (3) Diet Nut and Diet Thy.

(5) Twenty-two hours later, we determined the amount of each diet eaten by each observer.

Results and Discussion

Observers offered a choice between Diets Nut, Thy, Coc and Cin that had interacted with demonstrators fed Diet A + Nut ate significantly more Diet Nut during testing than did observers that had interacted with demonstrators fed Diet A (Mann–Whitney U-test, $U=27$, $P<0{\cdot}01$; Fig. 3a).

Similarly, when offered a choice between Diet Nut and either Diet Coc or Diet Thy, observers that had interacted with a demonstrator fed Diet A + Nut ate significantly more Diet Nut than did the observers that had interacted with demonstrators fed Diet A (Mann–Whitney U-tests, both Us = 17, both Ps < 0·05; Fig. 3b). Observers offered a choice between Diet Nut and Diet Cin that had interacted with demonstrators fed Diet A + Nut tended to eat more Diet Nut than did observers that had interacted with demonstrators fed Diet A, although this tendency was not statistically significant (Mann–Whitney U-test, $U=32$, NS; Fig. 3b).

GENERAL DISCUSSION

Experiments conducted both in our laboratory and elsewhere during the past decade have shown repeatedly that, after a naive young rat (an observer) interacts with a recently fed conspecific (a demonstrator), the observer increases its intake of whatever foods its demonstrator ate (Galef & Wigmore 1983; Posadas-Andrews & Roper 1983; Heyes & Durlach 1990; Winocur 1990; Galef & Whiskin 1992; see also Galef 1986, 1988, 1994).

The general procedure used in all of these studies of social influence on food preference, in which a naive observer interacted with a trained demonstrator and the observer was then tested to determine the effects of social interaction on its behaviour, is the paradigm most frequently used in studies of social learning generally (see Zentall & Galef 1988 for examples).

There are, however, other experimental situations that can provide insight into aspects of social learning that the standard paradigm does not. For example, Krebs et al. (1972) examined the relative success of flocks of naive birds and of individual naive birds searching for food caches concealed in an aviary. When one of a group of birds found food, others in its flock increased the amount of time that they spent searching both in the same area where food had been found and in similar types of foraging sites. Consequently, members of flocks of birds were more successful in finding food than were individuals.

Few other experiments have been undertaken to determine whether life in social groups can facilitate acquisition of adaptive patterns of behaviour by group members. This lack of investigations is unfortunate because groups of animals need not be more successful than isolated animals in solving problems. For example, in those species whose members are more strongly motivated to remain in social contact than to explore, interaction with conspecifics could impede, rather than accelerate, discovery of resources or opportunities not being exploited by group members (Thorndike 1911, page 83; see also Beauchamp & Kacelnik 1991).

We found in experiment 1 that members of groups of naive rats offered both an unpalatable, nutritionally adequate diet and several palatable, deficient diets learned to focus their intake on the nutritionally adequate diet more rapidly than did isolated rats. Thus, we demonstrated, in a situation quite different from that examined by Krebs et al. (1972) that groups of animals can forage more efficiently than can animals in isolation.

The results of experiment 2 provided one plausible explanation for the observed outcome of experiment 1. Once the first of a group of rats began to eat the unpalatable, nutritionally adequate, nutmeg-flavoured diet (in addition to the three palatable, deficient diets that all group members were eating) and interacted with other group members, there would have been a disproportionate increase in the other group members' intake of nutmeg-flavoured diet, the only food that one group member had eaten that other group members had not. The relatively greater potency of unfamiliar foods than of familiar foods to enhance food preferences should have accelerated group exploitation of Diet Nut once one member of a group began to eat that diet.

Although we have identified one behavioural process that might allow groups of naive rats to select foods more efficiently than isolated rats, other behavioural processes could produce the same result. Several different behavioural mechanisms that allow naive rats to exploit more experienced conspecifics as sources of information about which foods to eat are described in the literature (see Galef 1984, 1990 for reviews); each might play a role in allowing groups of naive individuals to perform better than isolated individuals, when faced with a need to select a nutritionally adequate diet from an array of potential foods.

Furthermore, although we have identified a situation in which groups of naive animals learn more rapidly than naive individuals, it cannot be assumed that life in social groups invariably facilitates solution of problems by group members. Much work, both empirical and theoretical, remains to be done to determine the conditions under which group membership facilitates, interferes with or leaves unaffected the ability of individual animals to solve problems posed by their physical environments.

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