

## Information centres of Norway rats: sites for information exchange and information parasitism

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**Abstract.** Results of previous studies have demonstrated that aggregation sites of Norway rats, *Rattus norvegicus*, can provide unsuccessful foragers with opportunities to extract information about available foods from their more successful fellows. The present experiments show that aggregations of rats also allow successful foragers to exchange information about foraging opportunities. After interacting, both members of a pair of rats, each of which had just eaten a different, novel food exhibited enhanced preferences for the food that their respective partners had eaten. These socially induced changes in diet preference did not result from simple exposure of interactants to food-related cues during interaction. Changes in diet preference as a result of information exchange depended on exposure of each interactant to food-related cues in the context provided by the presence of its partner.

In a provocative discussion of the functions of roosting assemblages of unrelated birds, Ward & Zahavi (1973, page 517) suggested that avian aggregations may 'serve principally as information centres wherein knowledge of food or good feeding sites may be obtained by individuals temporarily lacking such knowledge'. From this perspective, interactions at information centres are relatively exploitative; unsuccessful individuals extract useful foraging information from successful individuals and the latter receive nothing in return. Such exploitative aggregations of unrelated individuals would appear to be stable only if opportunities for reciprocal altruism existed: e.g. if (1) the costs to a successful individual of providing information were small relative to the benefits to the unsuccessful of acquiring information, (2) individuals that provided information at aggregation sites on one occasion were likely to receive information there on other occasions, and (3) non-reciprocators could be identified and discriminated against (Trivers 1971, 1985). Because the second and third conditions appear unlikely to be fulfilled at many aggregation sites, it is not clear why successful foragers should enter aggregations.

In a series of laboratory studies of the possibility that the burrows of rats, *Rattus norvegicus*, like the roosts of birds, might serve as information centres for unrelated individuals (see Galef 1989a, 1990, for reviews), my co-workers and I adopted Ward &

Zahavi's (1973) general view of how information centres might function. In all of our previous experiments, we used 'demonstrator' rats (i.e. animals with information to impart about available foods) and 'observer' rats (i.e. naive animals that were given the opportunity to extract useful information from their respective demonstrators). Thus, our experiments produced an exploitative or parasitic interaction between each observer and its demonstrator. Under such circumstances, we found repeatedly, as have others, that, after interacting with a recently fed demonstrator rat, observer rats exhibit enhanced preferences for the foods eaten by their respective demonstrators (Galef & Wigmore 1983; Posadas-Andrews & Roper 1983; Galef 1989b).

There is a complementary view of how information centres might function. Rather than providing a location for exploitative interaction, where unsuccessful animals parasitize information from the more successful, aggregation sites might provide the opportunity for successful individuals to exchange information and thus increase the probability that both participants in an interaction at an aggregation site would forage successfully in the future. For example, two rats eating different foods could exchange information regarding their respective diets. Each could thus be provided with some protection in the event of failure of its current source of nutriment.

In the present series of experiments, I first (experiment 1) show that, while interacting, two Norway rats that have recently eaten different foods can exchange information about the foods that they ate. I then (experiments 2 and 3) explore the behavioural processes that support the socially induced changes in diet preference found in experiment 1.

## EXPERIMENT 1

I undertook the first experiment to determine whether rats would exchange information concerning foods they had recently eaten. Given the results of our previous studies (Galef & Wigmore 1983), I expected that, if exchange of diet-identifying information occurred, it would result in each participant exhibiting an enhanced preference for the food that its partner had eaten. The experiment was also designed to determine whether diet-identifying information acquired during an exchange was any less effective in altering diet preferences than was similar information acquired during simple parasitic exploitation of a demonstrator rat by an observer.

### Methods

#### *Subjects*

Seventy-two experimentally naive, 42-day-old female Long-Evans rats, descended from breeding stock obtained from Charles River Canada (St Constant, Quebec) and reared in the vivarium of the McMaster University Psychology Department on ad libitum water and food (pellets of Purina Rodent Laboratory Chow 5001), served as subjects. Six subjects were randomly assigned to each of eight experimental and four control groups. An additional 24 56-day-old female rats, from the same source as subjects, served as demonstrators for subjects in control groups.

Each subject and each demonstrator was housed individually throughout the experiment in a wire-mesh hanging cage measuring 22 × 24 × 27.5 cm. These cages had solid side walls that prevented any contact between subjects except during step 3 of procedure described below.

#### *Diets*

During the experiment, each subject in experimental groups and each demonstrator in control

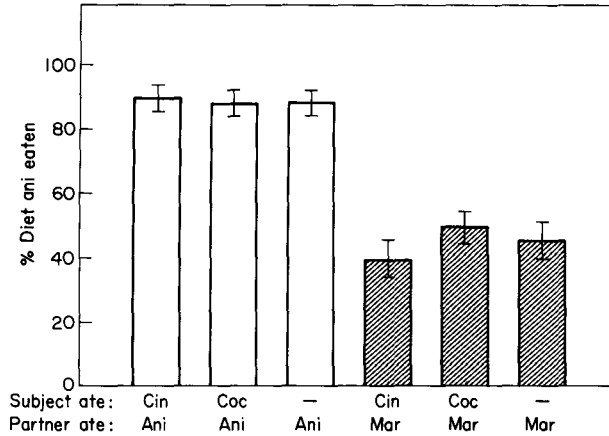
groups was fed one of four diets composed by mixing powdered Purina Rodent Laboratory Chow 5001 with either: 1% by weight McCormick's Pure Ground Cinnamon, 2% by weight Hershey's cocoa, 2% by weight bulk, ground marjoram, or 1% by weight bulk, ground anise. The results of earlier studies indicated that each of the pairs cocoa-flavoured and cinnamon-flavoured diet and anise-flavoured and marjoram-flavoured diet are roughly equipalatable.

#### *Procedure*

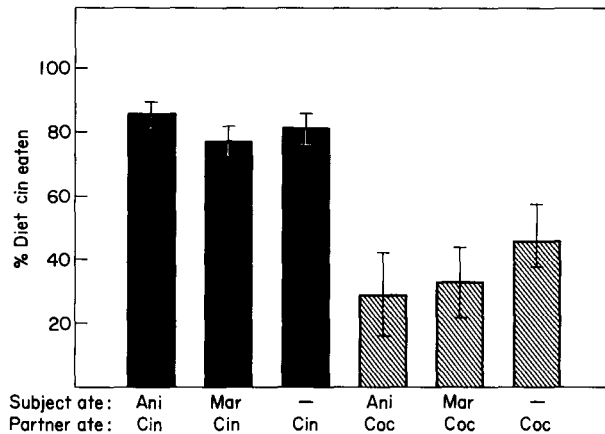
*Experimental Groups.* Subjects in each of the eight experimental groups were treated in five steps as described below. (1) Each subject was placed on a 23-h food-deprivation schedule, receiving powdered Purina Rodent Laboratory Chow 5001 for 1 h/day for 2 consecutive days. (2) Following a third 23-h period of food deprivation, each subject was offered, for 1 h, a food cup containing either cinnamon-, cocoa-, marjoram- or anise-flavoured diet. (3) Immediately following feeding of each subject, pairs of subjects were placed together for 30 min in one of their home cages. Subjects that had eaten either cinnamon-flavoured ( $N=12$ ) or cocoa-flavoured ( $N=12$ ) diets were each placed with a subject that had eaten either anise-flavoured ( $N=12$ ) or marjoram-flavoured ( $N=12$ ) diets. (4) At the end of the 30-min period of interaction, the subject that had been moved to interact with a partner was returned to its home cage and both subjects were then offered, in their respective home cages, a choice between a pair of diets for 23 h.

If a subject had eaten the cinnamon-flavoured diet (diet cin) and had interacted with a partner that had eaten marjoram-flavoured diet (diet mar), it was designated a member of group diet cin/diet mar and so on. Subjects ( $N=6$ /group) in groups diet cin/diet mar, diet cin/diet ani, diet coc/diet mar, and diet coc/diet ani were offered a choice between diet mar and diet ani during the 23-h test (step 4). Subjects in groups diet mar/diet cin, diet mar/diet coc, diet ani/diet coc, and diet ani/diet cin were offered a choice between diet cin and diet coc during the test period (step 4).

At the end of the 23-h test, I first determined the weight of diet eaten by each subject during step 4 and then calculated the percentage of each subject's intake during step 4 that was either diet ani (for subjects in groups diet coc/diet mar, diet cin/diet mar, diet cin/diet ani, diet coc/diet ani and diet coc/



**Figure 1.** Mean ( $\pm$ SE) percentage diet ani eaten during the 23-h choice between diet mar and diet ani by experimental and control subjects in experiment 1 ( $\square$ : partner ate diet ani;  $\text{▨}$ : partner ate diet mar).



**Figure 2.** Mean ( $\pm$ SE) percentage diet cin eaten during the 23-h choice between diet cin and diet coc by experimental and control subjects in experiment 1 ( $\blacksquare$ : partner ate diet cin;  $\text{▨}$ : partner ate diet coc).

diet ani) or diet cin (for subjects in groups diet mar/diet cin, diet mar/diet coc, diet ani/diet cin and diet ani/diet coc).

**Control groups.** Subjects in each of four control groups ( $N=6$ /group) were treated identically to subjects in experimental groups except: (1) subjects in control groups were fed nothing during step 2 and (2) during step 3, instead of interacting with another subject, each subject interacted with a demonstrator that had eaten either diet cin, diet coc, diet ani or diet mar during step 2.

Those observers in control groups that interacted with demonstrators that had been fed either diet coc or diet cin during step 2 were offered a

choice between diets cin and coc during step 4; those observers in control groups that interacted with demonstrators that had been fed either diet ani or diet mar during step 2 were offered a choice between diets ani and mar during step 4.

## Results

The main results of experiment 1 are presented in Figs 1 and 2. Two conclusions can be made. First, during testing (step 4), subjects in experimental groups exhibited an enhanced preference for the diet that their respective partners had eaten during step 2. Those subjects in experimental groups whose partners had eaten diet ani before interaction ate more diet ani during the 23-h test than did those

subjects in experimental groups whose partners had eaten diet mar before interaction (Mann-Whitney *U*-tests, both  $U_s=0$ , both  $P_s<0.001$ ). Similarly, those subjects in experimental groups whose partners had eaten diet cin before interaction ate more diet cin during the 23-h test than did those subjects in experimental groups whose partners had eaten diet coc before interaction (Mann-Whitney *U*-tests, both  $U_s\leq 5$ , both  $P_s\leq 0.02$ ).

Second, as can also be seen in Figs 1 and 2, there was no systematic tendency for subjects in control groups (those subjects that interacted with demonstrators that had been fed an unfamiliar diet during step 2 but that were not themselves fed during step 2) to be more profoundly influenced in their food preferences by interaction with their demonstrators than were subjects in experimental groups by interaction with one another.

### Discussion

While interacting with conspecifics, subjects in the experimental groups of this experiment acted both as 'demonstrators' for and 'observers' of their partners. Comparison of the food choices during testing of subjects in experimental groups with those of subjects in control groups indicates that emission of diet-identifying cues did not interfere in a functionally significant way with detection of diet-identifying cues. The data thus suggest that successful forager rats could benefit from entering aggregation sites if there were some probability that other successful individuals would be encountered there. Each successful forager could both: (1) acquire potentially valuable information and (2) provide equally valuable information to others at little or no cost to itself.

## EXPERIMENT 2

The finding in experiment 1 that while interacting with a conspecific the same individual can act both as a sender and receiver of diet-identifying information offers the opportunity to investigate some important issues in the study of social transmission of diet preferences among rats. In several studies of social transmission of diet preference (Galef et al. 1985; Galef 1989b), I have tried to distinguish between two equally plausible explanations of social influences on the food choices of rats. First, simple exposure of observer rats to the odour of particles of food carried by a demonstrator might result in enhancement of preference for the food

that a demonstrator ate. Second, such changes in food preferences of observer rats may require, not simple exposure to food odours, but exposure to food odours in the context provided by the presence of a demonstrator rat. Only in the latter case would the influence of interaction with conspecifics on food preferences of rats be truly social.

Data from previous studies have led us to conclude that effects of demonstrator rats on the food preferences of their observers resulted from processes more potent than simple exposure to diet-identifying cues (Galef et al. 1985; Galef & Stein 1985; Galef 1989b; Heyes & Durlach 1990). On the other hand, in two pioneering studies of social influences on diet preference, Posadas-Andrews & Roper (1983) provided data consistent with the hypothesis that socially induced changes in diet preference resulted from observer rats simply smelling or eating particles of food carried on the coats of conspecifics.

The methods introduced in experiment 1 above offer an opportunity to examine directly the relative strength of simple exposure to a diet and exposure to a diet eaten by a conspecific on later diet choice. In the present experiment, I first fed subjects one of a pair of diets, then let each subject interact with a second subject that had been fed the other diet in the pair. Last, I offered each subject a choice between the two diets in question: the diet that it had eaten itself and the diet eaten by its partner. Because each subject had greater simple exposure to the diet that it had eaten than to the diet that its partner had eaten, if simple exposure to a diet were responsible for enhancing subjects' preferences, each subject should have preferred the diet that it had eaten to the diet that its partner had eaten. Alternately, if experience of diet-identifying cues in the context provided by the presence of a conspecific was important in enhancing diet preferences of subjects, then one would expect subjects to exhibit enhanced preferences during testing for the diet that their respective partners had eaten rather than for the diet that they had eaten themselves.

### Methods

#### *Subjects*

Forty-eight experimentally naive, 42-day-old female Long-Evans rats from the vivarium of the McMaster University Psychology Department served as subjects. An additional 24 identical rats served as 'demonstrators' for subjects in control groups.

### Procedure

The apparatus and diets were the same as those used in experiment 1. The procedure was identical to that used with subjects in experimental groups in experiment 1 except that, during step 3, subjects fed marjoram-flavoured diet interacted with subjects fed anise-flavoured diet and subjects fed cinnamon-flavoured diet interacted with subjects fed cocoa-flavoured diet. The four groups of subjects ( $N=6$ /group) thus produced can be described, using the notation introduced in experiment 1, as groups diet ani/diet mar, diet mar/diet ani, diet cin/diet coc and diet coc/diet cin.

During testing (step 4) subjects in both groups diet mar/diet ani and group diet ani/diet mar were offered a choice between diet mar and diet ani. Subjects in both groups diet cin/diet coc and group diet coc/diet cin were offered a choice between diet coc and diet cin.

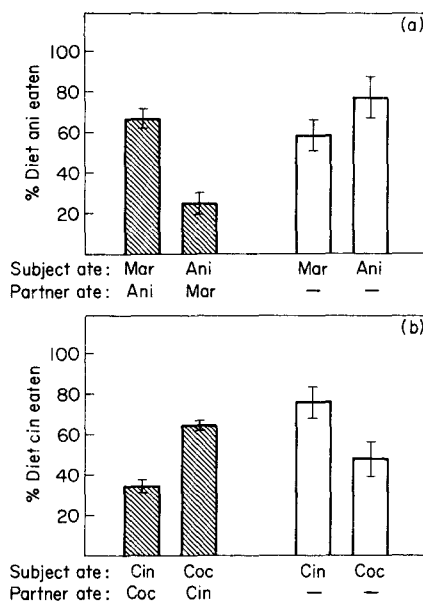
**Control groups.** Subjects in each of four control groups ( $N=6$ /group) were treated identically to subjects in experimental groups except that subjects in control groups all interacted with demonstrators that had eaten unadulterated powdered Purina Rodent Laboratory Chow 5001 during step 2, rather than with partners that had eaten a flavoured diet.

### Results and Discussion

As is evident from Fig. 3 and as statistical tests confirmed, subjects in experimental groups exhibited enhanced preferences for the foods that their respective partners had eaten, not for the foods that they had eaten themselves (Mann-Whitney  $U$ -tests, both  $U_s \leq 1$ , both  $P_s < 0.002$ ).

On the other hand, during testing (step 4), subjects in the four control groups exhibited an enhanced preference for the food that they had eaten themselves during step 2 (Mann-Whitney  $U$ -tests, both  $U_s \leq 7$ , both  $P_s \leq 0.05$ ). The enhanced preference of subjects in experimental groups for the foods eaten by their respective partners cannot, therefore, be attributed to each subject avoiding during testing (step 4), the food that it had eaten during step 2.

Taken together, the results of the present experiment offer strong support for the hypothesis that the enhanced preferences for foods that conspecifics had eaten were not the result of simple exposure to those foods during step 3 of the experiment.

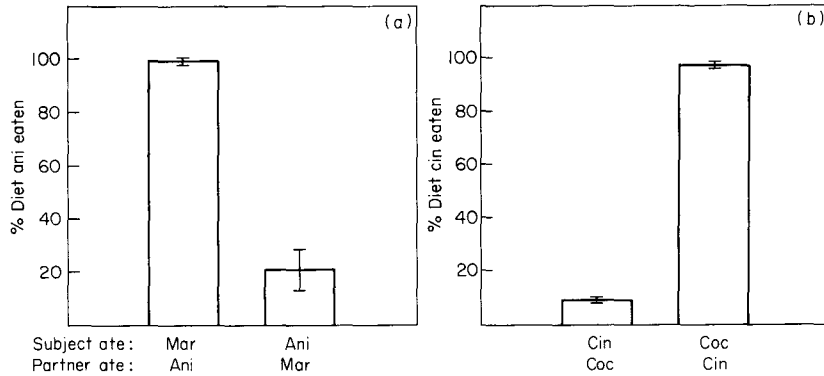


**Figure 3.** (a) Mean ( $\pm$ SE) percentage diet ani eaten by (■: experimental and □: control) subjects in experiment 2 during a 23-h choice between diet ani and diet mar. (b) Mean ( $\pm$ SE) percentage diet cin eaten by subjects in experiment 2 during a 23-h choice between diet cin and diet coc.

### EXPERIMENT 3

It might be argued that the reasons why subjects in experiment 2 exhibited enhanced preference for the foods eaten by their respective partners, rather than for the foods that they had eaten themselves, was that each subject attended more to diet-identifying cues emitted by its partner than to diet-identifying cues emitted by the food that it had eaten itself. If diet-identifying cues emerging from a conspecific were attended to more than were diet-identifying cues emerging directly from a food, then the results of experiment 2 might still be understood in terms of simple exposure effects, as Posadas-Andrews & Roper (1983) suggested.

If experience of food-related cues in the presence of a conspecific acts simply to increase the attention paid to those cues, then one would expect subjects to learn associations to food-related cues emitted by conspecifics more readily than they would learn associations to foods that they ingested themselves (see, for example, Revusky & Bedarf 1967; Kalat & Rozin 1970; Heyes & Durlach 1990; and, for general review, Pearce & Hall 1980). We have



**Figure 4.** (a) Mean ( $\pm$  SE) percentage diet ani eaten by subjects in experiment 3 during a 23-h choice between diet ani and diet mar and (b) mean ( $\pm$  SE) percentage diet cin eaten by subjects in experiment 3 during a 23-h choice between diet cin and diet coc.

shown previously that an observer rat that experiences lithium chloride induced toxicosis after interacting with a demonstrator that has eaten a food unfamiliar to the observer, learns an aversion to the unfamiliar food that its demonstrator has eaten (Galef et al. 1983). Because both (1) olfactory cues emitted by demonstrators and (2) taste cues from ingesting a food are adequate conditional stimuli for taste aversion learning, one might expect a subject that had both eaten a novel food and interacted with a demonstrator that had eaten a novel food immediately before becoming ill to learn a stronger aversion to the conditional stimulus (1 or 2) to which it had paid greater attention.

In this experiment, I first fed each subject one of a pair of diets, then let it interact for 30 min with another subject that had been fed the second diet in the pair. Immediately after interaction, I poisoned both subjects and, finally, offered each subject a choice between the two diets: the diet that its partner had eaten and the diet that it had eaten itself. If subjects were simply attending more to diet-identifying cues emitted by their respective partners than to diet-identifying cues emitted by the foods they themselves had eaten, then one might expect subjects in the present experiment to learn aversions to the foods that their respective partners had eaten, not to the foods that they had eaten themselves.

## Method

### Subjects

Twenty-four experimentally naive, 42-day-old female Long-Evans rats from the vivarium of the McMaster University Psychology Department served as subjects.

### Procedure

The apparatus and diets were the same as those used in experiment 2. The procedure was identical to that of experiment 2 except that immediately after each subject had interacted with its pair mate (step 3) and before it was offered a choice between diets (step 4) it was injected with 1% of body weight 1% weight/volume lithium-chloride solution and then given 24 h to recover from the effects of injection before testing (step 4) was started.

### Results and Discussion

As is evident from Fig. 4, subjects learned an aversion to foods that they had eaten themselves, not to foods that their respective partners had eaten. These data indicate that experience of food-related cues in the context provided by the presence of a conspecific does not simply increase the general salience of, or attention paid to, diet-identifying cues experienced on a conspecific.

## GENERAL DISCUSSION

The results of the present series of experiments demonstrate that aggregation sites can be places for mutual exchange of information of value to all participants, as well as places for information parasitism. The demonstration that aggregation sites can serve as places for information exchange provides a plausible explanation for entry of successful foragers into aggregation sites of non-kin even if successful foragers lack assurance of future reciprocal benefits from members of the aggregation they enter.

In the case of Norway rats, the effects on later feeding behaviour of information acquired during mutual interaction with conspecifics seem to depend on experience of diet-identifying cues in social context, not on simple exposure during social interactions to diet-identifying cues. Thus, the results of the present series of studies indicate that, in rats, exchange of information about distant foods (like parasitism of information about distant foods) is a truly social phenomenon, not the result of simple exposure of animals at aggregation sites to particles of food carried on the fur or in the guts of their fellows (Galef & Stein 1985).

As we have shown previously, socially acquired information about potential foods can assist laboratory rats in: (1) finding nutritionally valuable foods (Beck & Galef 1989), (2) avoiding ingestion of toxins (Galef 1986a, b) and (3) deciding where to seek food (Galef & Wigmore 1983; Galef et al. 1987). Because these phenomena occur in a wide range of laboratory conditions (Galef et al. 1984), it seems reasonable to suggest that social exchange of information about foods can play similar roles in guiding foraging by free-living wild Norway rats in adaptive directions.

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