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A PRIMER OF OLFACTORY COMMUNICATIONS ABOUT DISTANT FOODS IN NORWAY RATS

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INTRODUCTION

During a brief period of social interaction, a naive Norway rat (an observer) can extract information from a recently fed conspecific (a demonstrator) sufficient to allow the observer to identify the diet that its demonstrator ate. In our standard procedure (Galef and Wigmore, 1983), each observer rat first interacted for 15 min with a demonstrator rat that had eaten either cinnamon- or cocoa-flavored diet (Diet Cin or Diet Coc). The observer was then isolated and offered a choice between Diets Cin and Coc for 22 hr. In such experiments, observer rats exhibit enhanced preferences for whatever diet their respective demonstrator ate (Galef et al., 1984).

DURATION AND MAGNITUDE OF SOCIAL EFFECTS ON FOOD PREFERENCE

Socially acquired food preferences are both durable and powerful. Figure 1 presents data describing the feeding behavior of two groups of 12 rats, whose members were each offered a choice between Diet Cin and Diet Coc diets for 23½ hr/day, for 17 consecutive days. During the remaining ½ hr of each of the first 5 days of the experiment, each member of one group of

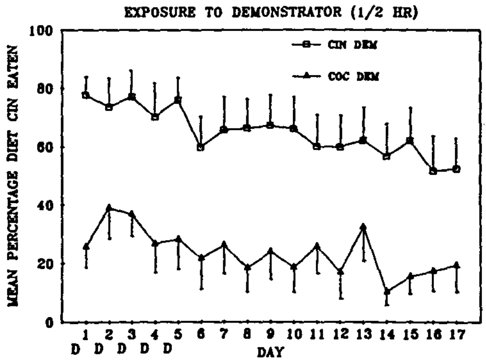

Fig. 1. Mean amount of Diet Cin eaten by observers interacting with demonstrators fed either Diet Cin or Diet Coc, as a percent of total amount ingested (Galef, 1989b).

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subjects interacted with a demonstrator rat fed Diet Cin and each member of the other group of subjects interacted with a demonstrator rat fed Diet Coc. As can be seen in Figure 1, effects of the diet fed to demonstrator rats on the food preferences of their observers lasted for 17 days (Galef, 1989b).

The magnitude of social influence on food choice is, perhaps, most clearly revealed by examining interactions of socially induced diet preferences with the most powerful known experiential determinant of food choice, poison-induced learned aversion (Galef, 1986b). I fed observer rats a palatable, casein-and-cornstarch-based diet (Diet NPT) for 1 hr. After feeding, I injected each rat with either saline solution or LiCl solution. After recovering from the effects of injection, each subject interacted either for ½ hr or for 1 hr with either a bowl containing Diet NPT, a single demonstrator rat fed Diet NPT or two demonstrator rats each fed Diet NPT. Finally, each subject was given a choice between Diet NPT and unfamiliar Diet Coc for 24 hr.

As can be seen in Figure 2, half the observer rats that had learned aversions to Diet NPT and then interacted with two demonstrator rats, each of which had eaten Diet NPT (i.e. subjects in Group 2 - DEM, LiCl), totally abandoned the aversion they had learned to Diet NPT. Social influence profoundly affected food choices of poisoned rats (Galef, 1986b, 1987, 1989c).

IMPLICATION OF OLFACTORY CUES

Results of a number of experiments indicate that the influence of demonstrator rats on their observers' food preferences depends on olfactory cues that pass from demonstrator rats to their observers (Galef and Wigmore, 1983) and that olfactory cues passing from demonstrators to observers and affecting observers' diet preferences have two components: first, a diet identifying component (Galef et al., 1985), which permits an observer to identify the diet that its demonstrator ate; second, a contextual component that is emitted by a conspecific and makes the diet-identifying component effective in altering observers' diet preferences (Galef, 1990b; Galef et al., 1985; Galef and Stein, 1985). As can be seen in Figure 2, simply exposing observer rats to the smell of a diet (Group Bowl-LiCl) did not increase the preference of observers for that diet. We observed social enhancement of observers' diet preferences only when the odor of a diet was experienced by observer rats in the presence of a demonstrator rat (Groups 1-DEM LiCl and 2-DEM LiCl).

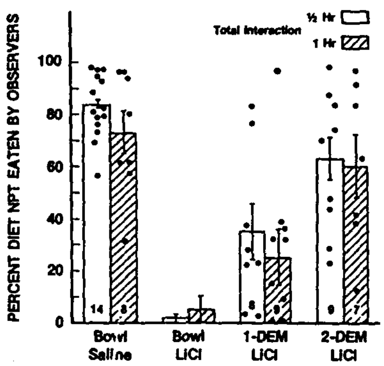

Fig. 2. Amount of Diet NPT eaten, as a percent of total amount ingested by observers during test (from Galef, 1986b).

Results of a series of studies indicate that both diet-identifying olfactory cues and contextual olfactory cues are carried on the breath of demonstrator rats (Galef and Wigmore, 1983; Galef and Stein, 1985). Mass-spectrographic analysis of rat breath revealed that it contains carbon disulfide (CS_2) (Galef et al., 1988) and the results of several experiments (Bean et al., 1988; Galef et al., 1988; Mason et al., 1989) have shown that adding an aqueous solution containing a few parts/million of CS_2 to a food enhances rats' preferences for that food, while adding equal quantities of water to a food does not enhance rats' preferences for it. In sum, our data are consistent with the view that CS_2 in rat breath is an important component of the olfactory context that makes diet-identifying cues, also carried on the breath of demonstrator rats, effective in enhancing the attractiveness of foods to observer rats.

COMPLEXITY AND SOPHISTICATION OF THE COMMUNICATIVE PROCESS

For the remainder of this brief review (for more thorough reviews, see Galef, 1986a; 1988; 1989a; 1990a), I shall focus on the complexity of the messages enhancing food preference that pass between rats. The results of our experiments show that the system for olfactory communication about foods described above can handle more information than one might anticipate.

Information Exchange or Information Parasitism?

The notion of a demonstrator rat providing information to an observer is itself an oversimplification. Naive observer rats do not simply extract information from recently fed demonstrators. Rather, pairs of foraging rats exchange information about foods they have recently eaten (Galef, 1991a).

As illustrated in schematic in Figure 3, I food-deprived pairs of rats for 23 hr, then fed one member of each pair either Diet Cin or Diet Coc and fed the other member of each pair either anise-flavored diet (Diet Ani) or marjoram-flavored diet (Diet Mar). Next, I let the two subjects interact for 30 min. Last, I offered those subjects that had eaten either Diet Cin or Diet Coc a choice between Diets Ani and Mar, one of which had been eaten by each subject's pair mate. Similarly, I offered those subjects that had eaten either Diet Ani or Diet Mar a choice between Diet Cin and Diet Coc, one of which had been eaten by each of these subjects' pair mates.

The 2 x 2 x 2 design of the experiment is easily grasped by examining Figure 4 which shows: (1) the mean percent Diet Ani eaten during the 23-hr test by subjects that ate either Diet Cin or Diet Coc and then interacted with subjects fed either Diet Mar or Diet Ani and (2) the mean percent Diet

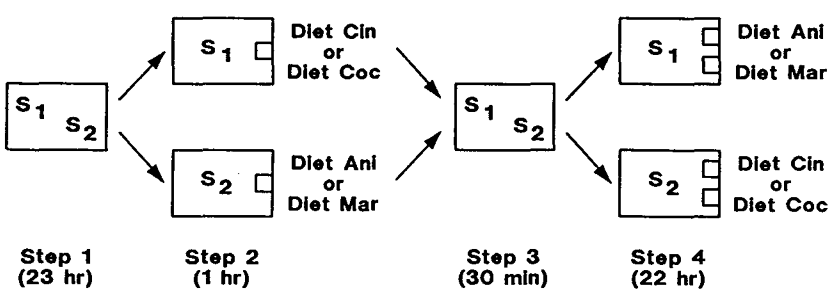

Fig. 3. Schematic diagram of procedure. S_1 and S_2 = subjects.

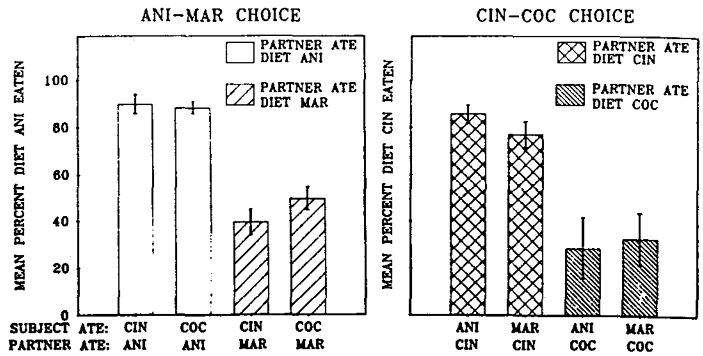

Fig. 4. Mean percentage Diet Ani or Diet Cin eaten by subjects offered a choice between either Diets Ani and Mar or Diets Cin and Coc (from Galef, 1991a).

Cin eaten during the 23-hr test by subjects that ate either Diet Ani or Diet Mar and then interacted with subjects fed either Diet Cin or Diet Coc. Subjects in all four conditions exhibited enhanced preferences for foods of the flavor that their respective partners had eaten. An individual rat is not either a "demonstrator" or an "observer"; rather, an individual rat can act both as a demonstrator for and an observer of its fellows.

Information Complexity

By using the olfactory communicative system under discussion, rats are able to exchange information about rather complex individual histories of recent food intake (Galef et al., 1990; Galef and Whiskin, in press). Indeed, if rats were unable to communicate about complex recent feeding experiences, the system would be of relatively little use. Participants in an exchange of olfactory information would have to eat foods one at a time, if they were to provide a decipherable message to those with whom they interacted.

We (Galef and Whiskin, in press) fed each of 42 rats a food (Combination A) composed of powdered Purina chow to which we had added (in g/100 g of chow) 1.0 g cinnamon (Cin), 0.5 g anise (Ani), 0.5 g thyme (Thy), and 0.5 g cloves (Clo) and a second group of 42 rats a second food (Combination B) composed of Purina chow to which we had added (in g/100 g of chow) 2.0 g cocoa (Coc), 1.0 g marjoram (Mar), 0.5 g cumin (Cum) and 0.5 g rosemary (Ros). We then took one rat that had eaten Combination A and one rat that had eaten Combination B and let them interact for 30 min. Finally, we offered each of the 84 rats in the experiment a choice between a pair of diets: one flavored with an herb or spice from Combination A, the other flavored with an herb or spice from combination B. Each subject thus chose between a food containing a flavor that it had eaten itself and a food containing flavor that its partner had eaten. The experimental design is, perhaps, most easily grasped by examining the four panels of Figure 5.

Figure 5 shows that, during testing, subjects exhibited a preference for the flavors that their partners had eaten, not for the flavors that they had eaten themselves. For example, when, as illustrated in the left-hand panel of Figure 5, subjects were offered a choice between Diet Cin and Diet Coc, those subjects that (1) had eaten Combination A (which contained Cin) and (2) had interacted with partners that had eaten Combination B (which contained Coc) preferred Diet Coc. This pattern of subjects exhibiting preferences for flavors in foods that their respective partners had eaten, rather than for flavors in foods that they had eaten themselves is repeated in each of the other three panels of Figure 5.

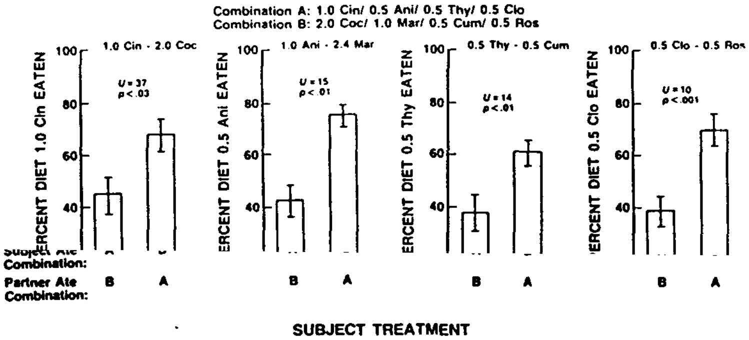

Fig. 5. Panels show the percentage of either Diet Cin, Diet Ani, Diet Thy or Diet Clo eaten by subjects during testing. Flavorants present in Combinations A and B are shown above the figure. Choice of diets offered subjects is indicated at top of panels (from Galef and Whiskin, in press).

Control subjects (whose data is not presented in Figure 5), simply fed either Combination A or Combination B and then offered choices between pairs of foods, one containing a flavor from Combination A and one containing a flavor from Combination B, exhibited no effect of eating a diet combination on their subsequent food preferences (Galef and Whiskin, in press). Consequently, the alterations in experimental subjects' food preferences (shown in Figure 5) must have been the result of interaction with partners rather than of subjects' own feeding experiences.

Last, it is worth mentioning that subjects in this experiment surely experienced more exposure to the flavors in the combination diet which they ate themselves than to the flavors in the alternative combination diet which their respective partners ate. Yet, subjects developed preferences for flavors in the combination diet that their partners ate, not for flavors in the combination diet that they ate themselves. The results of the present experiment thus provide additional evidence that simple exposure to foods is not in itself responsible for the enhanced preference for foods observed following social interactions between rats that have eaten various foods.

CONCLUSIONS

Taken together, the results described above indicate that aggregations of rats can act as "information centres" (Ward and Zahavi, 1973) where successful foragers can exchange information about foods they have eaten and unsuccessful individuals can extract information allowing them to identify foods their more successful fellows have eaten. There is reason to expect that both information exchange among and information parasitism by Norway rats could prove useful, guiding the unsuccessful to sources of nutriment (Galef, 1990a; 1991b) and providing the successful with information they could use if their current sources of nutriment were to fail (Galef, 1991a).

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