

# CHEMICAL SIGNALS IN VERTEBRATES 4

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OLFACTORY COMMUNICATION AMONG RATS: INFORMATION  
CONCERNING DISTANT DIETS

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INTRODUCTION

Animal Communication in the Absence of Display

The study of animal communication has traditionally focused on analyses of conspicuous displays, ritualized (Blest, 1961), or formalized (Smith, 1977) over evolutionary time for the function of intraspecific communication (see McKay, 1972, for discussion of problems of definition). However, particularly among vertebrates, communication need not involve such specialized signals.

As any organism engages in its routine daily activities, it coincidentally provides usable information to others. Stimuli emitted as incidental by-products of behaviors necessary for individual survival can serve communicative functions similar to those of ritualized displays. For example, the rasping sounds an agouti makes while gnawing on a nut, carry dozens of meters through the tropical forest and attract other agouti, as well as the occasional potential predator, to a promising feeding site (Smythe, 1970); a vulture, descending to scavenge from a carcass lying on the Serengeti plain, draws both others of its kind and competing species to a recent kill (Houston, 1979; Schaller, 1972). It does not seem reasonable to suppose that in such cases the discoverer of a resource is emitting signals specialized for communication to announce its find. Yet the feeding behavior of an agouti or vulture provides unambiguous messages to those sufficiently alert and behaviorally flexible to detect and exploit them. Stimuli generated by individuals engaging in life-sustaining activities can be utilized by others to facilitate their own acquisition of resources. Although such unspecialized signals have been discussed at length as contexts modifying the meaning of formalized displays (Smith, 1977), they have not been treated as primary forms of communication. Hence, the potential importance of unspecialized signals in mediating interaction among organisms has been little studied.

In the present chapter, I describe recent work from my laboratory, the results of which are consistent with the view that incidental by-products of ingestion are important media of communication among rats. Olfactory signals, passively emitted by rats following feeding, provide conspecifics with information that both facilitates and orients subsequent foraging by its recipients.

### Communication Among Members of Social Species Foraging from a Central Site

A number of behavioral ecologists have suggested that in social species that forage from a central location, such as a burrow, roost, or nesting area, unsuccessful foragers could enhance their own subsequent foraging efficiency by acquiring information from successful foragers encountered at the central site (DeGroot, 1980; Ward and Zahavi, 1973; Erwin, 1977; Bertram, 1978, Waltz, 1982). Wild Norway rats are social, central-place foragers. In natural circumstances, each rat lives as a member of a colony that inhabits a fixed system of burrows. When foraging, colony members disperse from their burrow, feed, and then return to it (Calhoun, 1967; Telle, 1966).

As part of a long-term study of the behavioral processes underlying social learning in Norway rats (see Galef, 1977; 1983; 1984 for reviews), my students and I have been examining the possibility that rat burrows serve as 'information-centres' (Ward and Zahavi, 1973), i.e., as aggregation sites at which information concerning current availability of foods in the larger environment is exchanged among foragers. As will be seen below, our data indicate that one Norway rat can use information acquired during interaction with conspecifics in orienting its own subsequent foraging excursions. One rat can exploit diet-identifying cues passively emitted by recently-fed others both to determine what to eat and where to seek food.

#### THE LABORATORY PARADIGM

The procedures used in the studies described below were designed to mimic situations in which a foraging rat ingests a food at some distance from its burrow, returns to its burrow, and then interacts with a burrow-mate. Our purpose was to discover whether, as a result of such interaction: (1) the burrow-mate could acquire information concerning the food the forager had eaten and (2) whether the burrow-mate would subsequently use that information either in selecting foods for ingestion or in orienting its own foraging behavior.

Of course, any laboratory analogue of a natural foraging situation will fail to reflect many of the environmental complexities faced by free-living animals. Experimental control frequently requires both reduction in the number of alternative courses of action available to subjects and replacement of spontaneous behavior by experimenter-initiated manipulations. Consequently, experiments such as those described below, though adequate to reveal behavioral capacities that might be employed in natural circumstances, do not provide evidence that these capacities are actually used by free-living animals. Demonstration that rat burrows actually function in nature as information-centres requires field studies that have not yet been undertaken (Galef, 1984; Galef and Wigmore, 1983).

#### The Basic Experiment

During all experiments described below, our subjects were housed in same-sex pairs in cages divided in half by screen partitions. For purposes of exposition I will refer to one member of each pair as a "demonstrator" and the other as an "observer".

The basic experiment, schematized in Figure 1, was carried out in five steps:

Step 1. Demonstrator and observer were maintained together with ad lib access to Purina Laboratory Rodent chow and water for a 2-day period of familiarization with both apparatus and cage-mate.

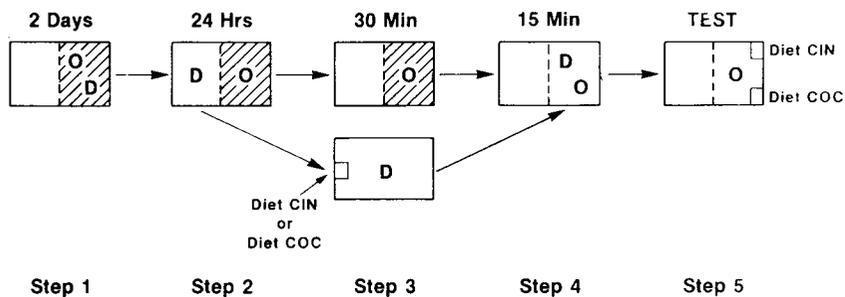


Fig. 1. Schematic diagram of the procedure of the basic experiment. O = observer; D = demonstrator; hatching indicates maintenance diet present in cage. (Galef and Wigmore, 1983. Copyright 1983 by Baillière Tindall. Reprinted by permission of the publisher and authors.)

Step 2. The demonstrator was moved to the opposite side of the screen partition from its observer and food-deprived for 24 hr to ensure that the demonstrator ate when given the opportunity to do so.

Step 3. Chow was removed from the observer's side of the cage (in preparation for testing) and the demonstrator was moved to a cage in a separate room and allowed to feed for 30 min on either cinnamon-flavored diet (Diet Cin) or cocoa-flavored diet (Diet Coc).

Step 4. The demonstrator was returned to the observer's side of the cage and demonstrator and observer were allowed to interact for 15 min.

Step 5. The demonstrator was removed from the experiment and the observer was offered a choice between two weighed food-cups, one containing Diet Cin and one containing Diet Coc.

Figure 2 shows the mean amount of Diet Coc, as a percentage of total amount eaten, ingested during testing (Step 5) by observers whose demonstrators had eaten either Diet Coc or Diet Cin during Step 4 of the experiment. As can be seen in Figure 2: (1) Those observers whose demonstrators ate Diet Coc ate a far greater percentage of Diet Coc than did those observers whose demonstrators ate Diet Cin and (2) effects of demonstrators' diet on observers' diet preference were still observable 48-60 hr after interaction of demonstrator and observer. The results of this first experiment clearly show that an observer rat can extract from a demonstrator information identifying the diet that demonstrator had eaten at a time and place distant from the locus of demonstrator-observer interaction. The data also show that this information is sufficient to bias its recipient's subsequent selection of diet.

#### Variations on a Theme

We have repeated the basic experiment described above many times: with a variety of different diets (Galef and Wigmore, 1983), with hungry and replete observers, with male demonstrator-observer pairs and female ones, with wild and domesticated rats, with demonstrator-observer pairs familiar with one-another and with pairs that had never met prior to their interaction during Step 4 of the experiment, with both old demonstrators and observers and young ones, and with observers selecting distinctively flavored fluids rather than solids for ingestion (Galef, Kennett and Wigmore, in press). In every case, we have seen robust preferences by

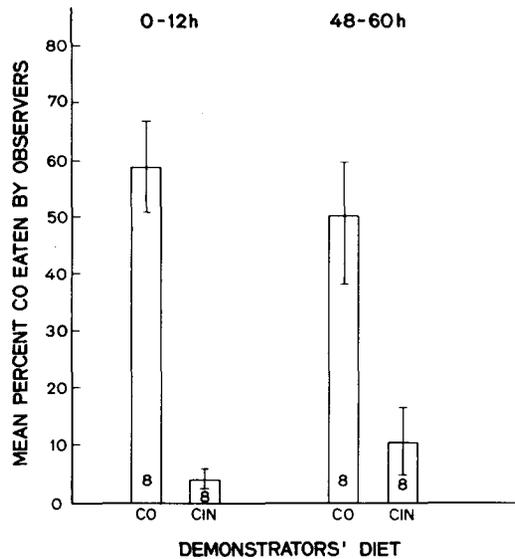


Fig. 2. Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by observers whose demonstrators ate either cocoa- or cinnamon-flavored diet. CO = Cocoa-flavored diet; Cin = Cinnamon-flavored diet. (Galef and Wigmore, 1983. Copyright 1983 by Baillière Tindall. Reprinted by permission of the publisher and authors.)

observers for their respective demonstrators' diets. Similarly, Posadas-Andrews and Roper (1983) and Strupp and Levitsky (1984), using rather different paradigms, have repeatedly observed demonstrator influence on subsequent observer diet preference. The phenomenon of demonstrator influence on observer diet preference seems a general one in Norway rats, not dependent on some restricted set of experimental parameters for its expression.

#### Effects of the Passage of Time

In the basic experiment diagrammed in Figure 1, observers and demonstrators interacted immediately after demonstrators had eaten a diet. Observers had the opportunity to choose between diets immediately following extraction of information from their respective demonstrators. Free-living rats must expend time in returning from a feeding site to their burrows. In the field, foragers departing from their burrows must expend further time in reaching a feeding site. If the capacity of rats to transmit information concerning a food eaten at a distance from their burrow is to function in information exchange in natural settings, communication must occur even if there are delays both between a successful forager's ingestion of a food and its return to its burrow and between the interaction of a successful forager with other rats and the latter's arrival at a potential feeding site. In terms of the laboratory analogue illustrated in Figure 1, rats must be able to tolerate delays between Steps 3 and 4 and between Steps 4 and 5 and still successfully exchange information.

The results of experiments in which independent groups of subjects experienced varying delays (1) between a demonstrator feeding and its interaction with an observer and (2) between an observer interacting with a demonstrator and its choosing between diets are presented, respectively,

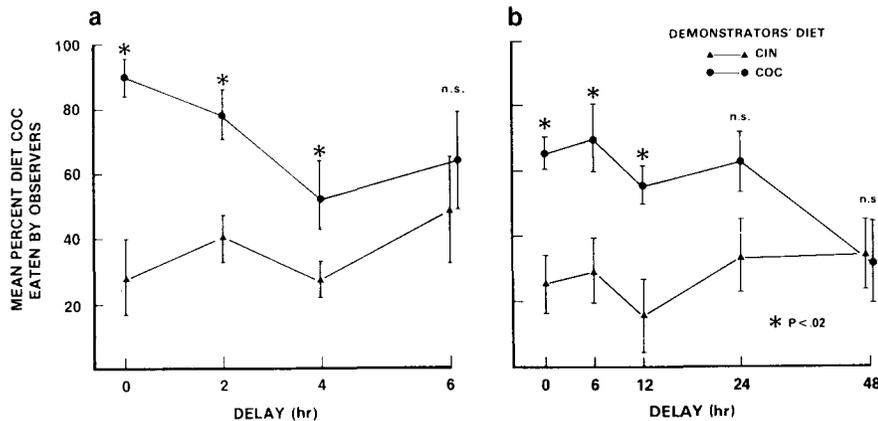


Fig. 3. Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by observers whose demonstrators ate Diet Cin or Diet Coc: (3a) as a function of time between ingestion by demonstrator and interaction with observer (3b) as a function of time between interaction of demonstrator and observer and initiation of testing. (Galef and Wigmore, 1983. Copyright 1983 by Baillière Tindall. Reprinted by permission of the publisher and authors.)

in Figures 3a and 3b. As is clear from examination of the figures, and as statistical tests confirmed (Mann-Whitney U tests, see Figure 3 for *p* values), rats could tolerate considerable delays between Steps 3 and 4 or between Steps 4 and 5 of the basic experiment and still successfully exchange information.

As can be seen in Figure 3a, demonstrators continued to emit, for at least 4 hr after feeding on a diet, cues sufficient to permit an observer to identify its demonstrator's diet (Galef and Kennett, in press). Data presented in Figure 3b indicate that observers can use diet-identifying information obtained from demonstrators for 12 to 24 hr after receiving it (Galef, 1983). Both the time course of emission of diet-identifying information obtained from demonstrators seem appropriate to permit use of the information-transmission system under investigation in natural environments.

#### Handling of Multiple Messages

In natural circumstances, each rat lives within a social group or colony (Telle, 1966). While there is relatively little information available concerning social life in wild rat colonies, it seems reasonable to suppose that each colony member, prior to departing from its colony's burrow system on a foraging expedition, might have an opportunity to acquire information from several conspecifics about foods they had recently ingested. It is possible that an individual rat, remaining in its burrow and interacting with a succession of colony-mates returning from successful foraging trips, could collect information concerning the entire range of foods the returning foragers had exploited.

If rats in their burrows are to make use of information received from a succession of returning colony-mates, they must be able to distinctively encode and store information extracted from each informant. The results of several studies indicate that rats have such a capacity (Galef, 1983).

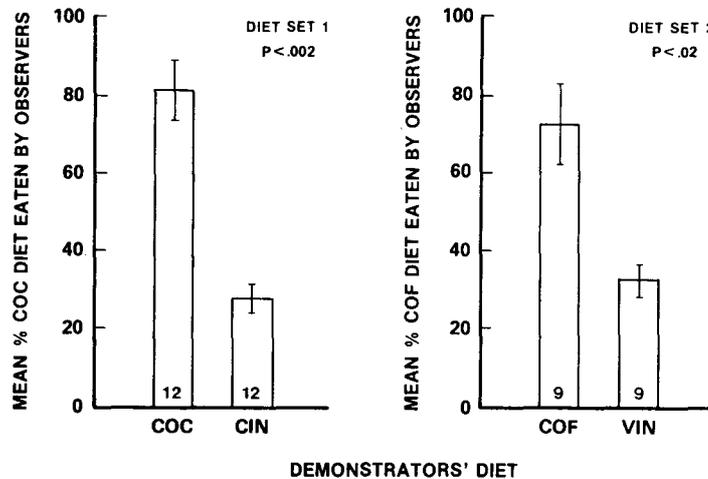


Fig. 4. Mean percent Diet Coc (left-hand panel) or Diet Cof (right-hand panel) eaten by observers one of whose demonstrators ingested, respectively, either Diet Cin or Coc, or either Diet Cof or Vin. (Galef, 1983. Copyright 1983 by the American Psychological Association. Reprinted by permission of the author and publisher.)

Our method was similar to that outlined in Figure 1. However, in the present experiment, each observer, instead of interacting during Step 4 with a single observer that had eaten either Diet Cin or Coc, interacted for 15 min with each of a series of four demonstrators, one of which had eaten vinegar flavored-diet (Diet Vin), one of which had eaten coffee-flavored diet (Diet Cof), one of which had eaten a casein and cornstarch based diet (Diet NPT), and one of which had eaten either Diet Coc or Diet Cin. During testing of observers (Step 5 of Figure 1), each observer was offered a choice between Diets Cin and Coc. As can be seen in the left-hand panel of Figure 4, those observers one of whose four demonstrators had eaten Diet Coc preferred Diet Coc, while those observers one of whose four demonstrators had eaten Diet Cin, preferred that diet. Of course, it might have been the case that the two diets selected for testing (Diets Cin and Coc) were simply the most salient of those offered to demonstrators. To control for this possibility, the entire experiment was repeated using Diets Cin, Coc, and NPT, as irrelevant diets and Diets Cof and Vin as critical test items. As can be seen in the right-hand panel of Figure 4, those observers one of whose four demonstrators ingested Diet Cof preferred Diet Cof, while those observers one of whose four demonstrators ingested Diet Vin preferred Diet Vin.

Such preferences for the diet eaten by one demonstrator, embedded in a series of three masking demonstrators, indicate that observers are able to distinctively encode a number of diet-identifying signals sequentially extracted from demonstrators. These findings are consistent with the notion that a rat remaining in its burrow and interacting with a succession of returning successful foragers is able to construct an inventory of foods currently available in the larger environment and exploited by its fellows.

#### Use of Extracted Information in Orientation of Foraging

Although the experiments described above indicate that a successful

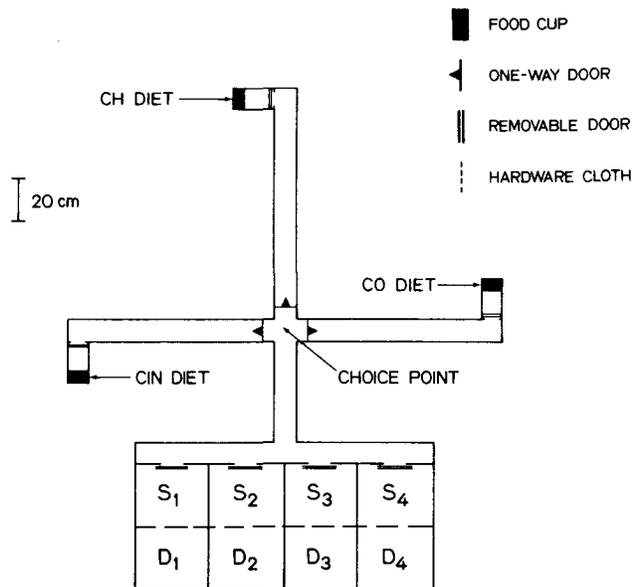


Fig. 5. Plan view of apparatus. Ch = cheese-flavored diet; Cin = cinnamon-flavored diet; Co = cocoa-flavored diet; S = subject; D = demonstrator. (Galef and Wigmore, 1983. Copyright 1983 by Baillière Tindall. Reprinted by permission of the publisher and authors.)

forager can provide information about diets it has ingested far from the locus of information transfer, these studies do not provide evidence that such information can be used by its recipients to facilitate their foraging. To investigate the usefulness of socially-transmitted information in increasing foraging efficiency, we introduced our subjects into the environment depicted in overhead schematic in Figure 5. The rule here was that each of three discriminable foods was available at a different, fixed location: cheese-flavored diet (CH Diet) in the central arm of the maze, cocoa-flavored diet (CO Diet) in the right arm, and cinnamon-flavored diet (CIN Diet) in the left. Only one of the three diets was accessible to each subject on any given day, and the particular diet available to a subject on any day was randomly selected.

Each subject ( $S_n$  in Figure 5) was given four trials/day using a correction procedure. On the first trial of each day, each subject had no information as to which food was available, and therefore had only one chance in three of selecting the correct arm of the maze. If it chose the correct arm, it ate for a few minutes. If it did not, it was locked in the arm it had chosen for a few minutes, and the first trial was repeated until the subject found the food. Trials 2, 3, and 4 of each day were run in the same fashion.

Each subject could, in effect, tell the experimenter when it understood this little world by exhibiting more or less perfect performance in its first choices on trials 2, 3, and 4 of each day. Once a given subject had reached the necessary criterion of performance on trials 2, 3, and 4, testing was instituted.

On each test day, for 15 min prior to Trial 1 of that day, each subject was allowed to interact with a demonstrator rat ( $D_n$  in Figure 5) that

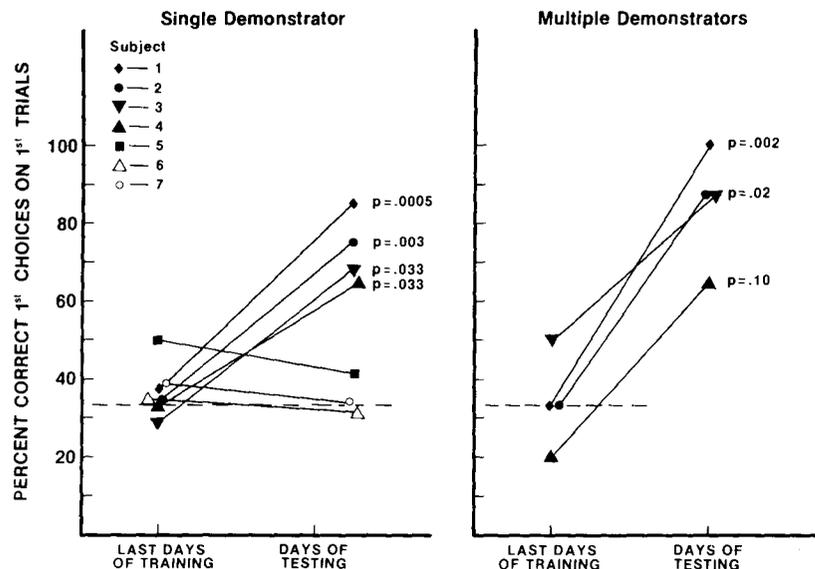


Fig. 6. Percentage of correct first choices on first trials by subjects at the end of training and during testing in the apparatus illustrated in Figure 5. (Galef, 1983; Galef and Wigmore, 1983. Copyrights 1983 by Baillière Tindall and the American Psychological Association. Reprinted by permission of the authors and publishers.)

had eaten the diet that was going to be available to that subject on that day. That is, if cheese-flavored diet was going to be available to S<sub>3</sub> on a given day, S<sub>3</sub>'s demonstrator, D<sub>3</sub>, was fed cheese-flavored diet for 30 min and then allowed to interact with S<sub>3</sub> for 15 min prior to initiating Trial 1 of testing of S<sub>3</sub>.

In order to determine whether subjects were capable of using information acquired from demonstrators to enhance foraging efficiency, we compared the probability of a correct response on the first choice of the first trial of each day of testing (when information from a demonstrator was available to subjects) with the probability of a correct response on the first choice of the first trial of each of the last days of training (when noninformation from a demonstrator was available to subjects). As can be seen in the left-hand panel of Figure 6, four of our seven subjects were able to use the information provided by their respective demonstrators to facilitate location of unpredictable foods (Galef and Wigmore, 1983).

As indicated in the immediately preceding section, rats can distinctively encode diet-identifying information extracted from a series of conspecifics. We have also found that they can use such diet-identifying information, embedded in a series of like messages, to orient foraging trips. During testing, instead of allowing each subject to interact with a single demonstrator predicting the food to be available on a given day, we had each subject interact with four demonstrators, three of which had eaten irrelevant foods (Diets NPT, Vin, and Cof) and one of which had eaten the food to be available to the subject on that day. As can be seen in the right-hand panel of Figure 6, subjects were still able to extract and use the relevant information in selecting an arm of the maze for initial exploration on test days (Galef, 1983).

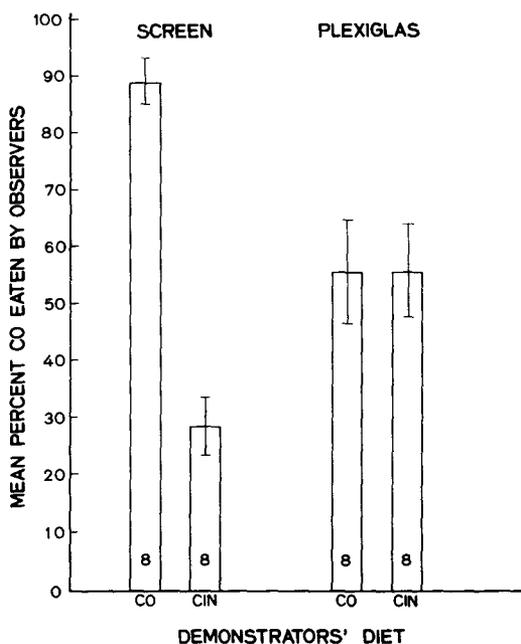


Fig. 7. Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by observers whose demonstrators ate cinnamon- or cocoa-flavored diet. Left-hand bars, observer and demonstrator separated by a screen partition during interaction. Right-hand bars, observer and demonstrator separated by a Plexiglas partition during interaction. (Galef and Wigmore, 1983. Copyright by Baillière Tindall. Reprinted by permission of the publisher and authors.)

Taken together, the results of the experiments described above indicate that rats returning from a successful foraging trip can provide information to conspecifics concerning foods they have exploited. Further, the data indicate that information acquired by one rat from another can be used to facilitate foraging in situations in which a food is available intermittently at fixed locations.

#### THE NATURE OF MESSAGES PASSING FROM DEMONSTRATORS TO OBSERVERS

##### Implication of Olfactory Signals

An obvious question arising from the observations described above concerns the means by which an observer rat acquires information from a demonstrator as to the diet that demonstrator has been eating. We have developed several converging lines of evidence, each consistent with the hypothesis that olfactory cues passing from demonstrator to observer are sufficient to allow observer identification of demonstrators' diets.

In order to examine the mode of communication of diet-identifying information from demonstrator to observer, it was necessary to gain some control over their interaction. We employed a procedure similar to that depicted in Figure 1, but with one important modification. During the period of demonstrator-observer interaction (Step 4 of Figure 1), the members of each demonstrator-observer pair were on opposite sides of the

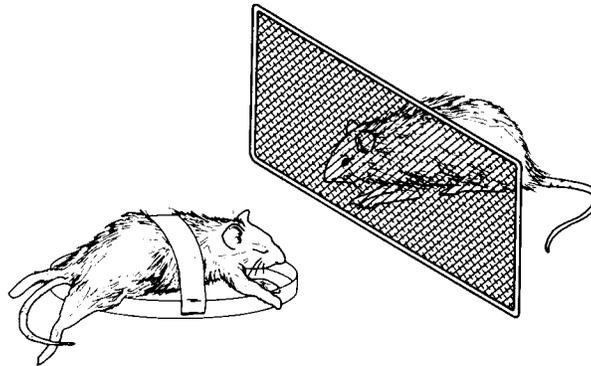


Fig. 8. Illustration of procedure during interaction of anesthetized demonstrator and observer.

screen partition dividing their cage.

As can be seen in Figure 7, observers had no trouble in developing a preference for their respective demonstrators' diets when separated from their demonstrators by a screen during interaction. However as can also be seen in Figure 7, if the screen partition was replaced by a clear Plexiglas partition, demonstrator influence on observer diet preference was completely abolished (Galef and Wigmore, 1983).

Further, we have conducted an experiment in which each demonstrator, after eating either Diet Cin or Diet Coc, was anesthetized and placed 5 cm from and facing a screen partition, with its observer on the other side of the screen (see Figure 8). During subsequent preference testing, observers still exhibited (Figure 9) a robust preference for their respective demonstrators' diets (Galef and Wigmore, 1983). Also, as one would expect if olfactory cues play an important role in information transfer between demonstrator and observer, observers rendered anosmic by passing Zinc-sulfate solution through their nares (Alberts and Galef, 1973) failed to exhibit a preference for their respective demonstrators' diets. Control rats whose nasal passages had been rinsed with saline solution continued to exhibit a preference for their respective demonstrators' diets (See Figure 10).

Last, but not least, humans, as well as rats, can use olfactory cues emitted by a previously-fed rat to tell what diet that rat has been eating. A human observer presented with a dozen rats in random sequence, half of which had eaten Diet Coc and half of which had eaten Diet Cin, could, by sniffing their breaths, tell with better than 85 percent accuracy which rat had eaten which diet (Galef and Wigmore, 1983).

#### CAUSES OF DEMONSTRATOR INFLUENCE ON OBSERVER DIET PREFERENCE

The simplest behavioral explanation of the observed influence of demonstrators on observers' subsequent diet selection would be something like the following. Rats are always somewhat hesitant to ingest unfamiliar foods (Barnett, 1958; Galef, 1970). An observer rat that, as the result of interacting with a demonstrator that has eaten a Diet X, has been exposed to cues associated with Diet X, should be familiar with Diet X. Therefore, an observer rat that has interacted with a Diet-X-fed demonstrator should eat Diet X in preference to other roughly equipalatable,

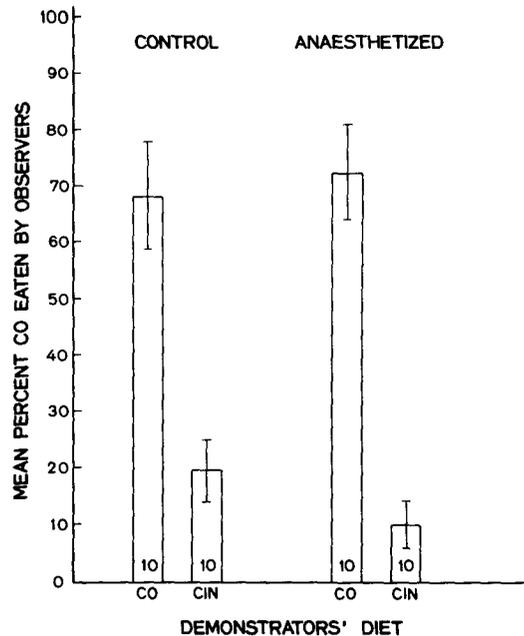


Fig. 9. Mean amount of Diet Coc eaten by observers, as a percentage of total amount ingested. Left-hand bars, observers interacting with intact demonstrators. Right-hand bars, observers interacting with anesthetized demonstrators, as depicted in Figure 8. (Galef and Wigmore, 1983. Copyright 1983 by Baillière Tindall. Reprinted by permission of the publisher and authors.)

but totally unfamiliar, diets. Demonstrator influence on observer diet preference could, thus, be explained as the result of a simple increase in observer familiarity with a demonstrator's diet.

We have conducted a number of experiments designed to test the adequacy of explanations of demonstrator influence on observer diet preference in terms of demonstrator-induced diet familiarity of the sort described above (Galef, Kennett, and Stein, in press). In every case, the results of our studies have been contrary to the most straight-forward predictions from the familiarity hypothesis.

For example, if reduced diet novelty, resulting from observer exposure to diet-identifying cues during interaction with a demonstrator, were responsible for subsequent demonstrator influence on observer diet preference, one would expect observers choosing between two familiar diets for be relatively immune to demonstrator influence in their diet selection. Any additional familiarity with one test diet, resulting from a brief period of interaction with a demonstrator fed that diet, should be overwhelmed by observers' extensive previous experience with both test diets.

We conducted an experiment much like that outlined in Figure 1 except that during the 2-day period of familiarization (Step 1 of Figure 1), observers in a Cin/Coc Pre-exposure Group were left alone in their cages and allowed *ad lib* access to two food bowls, one containing Diet Cin and one containing Diet Coc. Following two days of feeding on Diets Cin and Coc, each observer was exposed for 15-min to an unfamiliar demonstrator that had eaten either Diet Coc or Diet Cin (Step 4 of Figure 1). Each

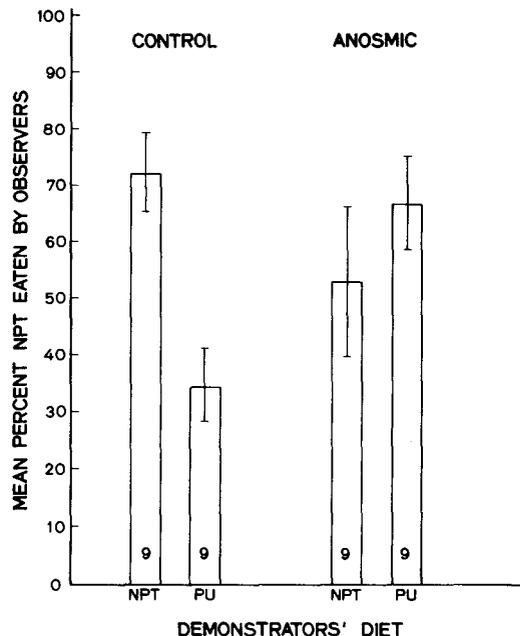


Fig. 10. Mean amount of Diet NPT ingested, as a percentage of total amount eaten, by observers whose demonstrators ate either Diet NPT or Pu. Left-hand bars, observers' nasal cavities rinsed with saline. Right-hand bars, observers' nasal cavities rinsed with ZnSO<sub>4</sub>, i.e., anosmic. (Galef and Wigmore, 1983. Copyright 1983 by Baillière Tindall. Reprinted by permission of the publisher and authors.)

observer was then tested for its preference between Diets Coc and Cin (Step 5 of Figure 1). Observers in the Control group were treated identically to those in the Cin/Coc Pre-Exposure Group except that during familiarization (Step 1 of Figure 1) observers in the Control Group had access to two food bowls containing a powdered form of their standard maintenance diet.

The main results of the experiment are presented in Figure 11 which shows the mean amount of Diet Coc, as a percentage of total amount eaten, ingested by observers in Cin/Coc Pre-exposure and Control Groups. As can be seen in the figure, the diet eaten by demonstrators profoundly affected the food choice of observers in both groups. This finding renders unlikely interpretation of the effects of demonstrator influence on observer diet preference as resulting solely from familiarity with the taste or smell of a diet experienced during 15 min of interaction with a demonstrator. Further, simply feeding a rat either Diet Cin or Coc for 15 min (or, for that matter, 24-hr) prior to offering it a choice between Diets Cin and Coc had no effect on rats' subsequent choice of diet (Galef, Kennett, and Stein, in press).

On the basis of such data, it is difficult to maintain the hypothesis that demonstrator influence on observer diet preference is the result of a simple increase in observers' familiarity with their respective demonstrators' diets. An obvious alternative is that observer experience of diet-identifying cues within a context provided by the presence of a demonstrator is necessary, if experience of diet-identifying cues is to

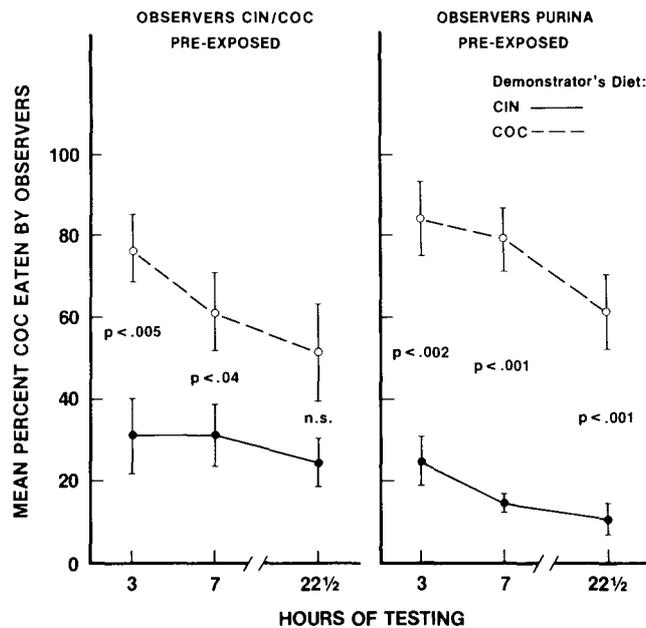


Fig. 11. Mean amount of Diet Coc ingested, by observers either pre-exposed or not pre-exposed to Diets Cin and Coc and whose demonstrators ate either Diets Cin or Coc. (Galef, Kennett and Stein, 1985. Copyright 1985 by the Psychonomic Society, Inc. Reprinted by permission of the authors and publishers.)

alter observers' subsequent diet preference. It is this hypothesis that has been the guiding principle in our recent research.

#### Analysis of Olfactory Cues

Assume, for the sake of argument, that I am correct in asserting that the effects of demonstrator rats on the subsequent dietary preferences of their observers are the result of observers experiencing the smell of a diet within the sensory context provided by a demonstrator, rather than the result of simple exposure to diet-related cues during interaction with a demonstrator. If so, then analysis of the message passing from demonstrator to observer presents two separable problems: (1) determination of the source of the diet-identifying cues emitted by demonstrators and (2) determination of the source and nature of the contextual cues, also emitted by demonstrators, that act in concert with the diet-identifying cues to alter observers' subsequent diet preference.

Diet identifying cues. In order to look more closely at the cues involved in demonstrator influence on observer diet preference, we again changed our experimental procedures slightly. The new procedure was similar to that described in Figure 1, but differed both in the way in which demonstrators were made to emit diet-identifying cues (Step 3) and the treatment of demonstrators and observers during the period of their interaction (Step 4). Rather than feed all demonstrators during Step 3 of the procedure, we employed a variety of techniques for attaching diet-identifying cues to demonstrators. Some demonstrators were allowed to eat Diet Cin or Diet Coc for 30 min, as was done in the basic experiment. Other demonstrators were anesthetized and their faces dusted with either

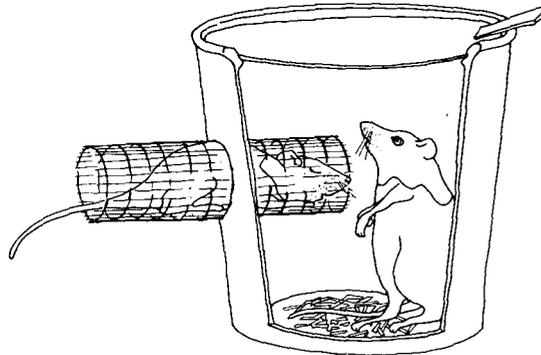


Fig. 12. Illustration of apparatus used to analyze diet-identifying and contextual cues. (Galef and Stein, 1985. Copyright 1985 by the Psychonomic Society, Inc. Reprinted by permission of the authors and publisher.)

Diet Cin or Diet Coc. Yet other demonstrators were anesthetized and tube-fed one of two distinctively flavored fluids. Some observers, instead of interacting with a demonstrator during Step 4 of the procedure, spent 30 min interacting with a surrogate rat (constructed of cotton-battling and surgical gauze) one end of which had been dusted with either Diet Cin or Coc. Further, instead of permitting demonstrator and observer to interact freely during Step 4, each demonstrator was placed, following anesthetization, in the screen tube of the apparatus illustrated in Figure 12. Observers were introduced into the bucket-shaped area of the enclosure, left there for 30 min, then moved back to their respective home-cages for testing (Step 5 of Figure 1).

As can be seen in Figure 13, 30 min observer interaction with a surrogate rat, dusted with either Diet Coc or Cin, failed to affect observer diet preference during testing (Step 5), providing further evidence of the inadequacy of simple exposure to a diet to produce alterations in observer diet preference. In contrast, exposure to a fed demonstrator, an anesthetized demonstrator powdered with diet, or an anesthetized demonstrator tube-fed a flavored solution each had the capacity to alter observers' diet selection during testing.

The finding that diet applied to the face of a demonstrator enhanced diet preference in their observers indicates that ingestion of a diet by a demonstrator is not critical in demonstrator production of diet-identifying cues. The finding that demonstrators stomach-loaded with a flavored solution also induced observers to increase their preference for the solution placed in the stomach of demonstrators indicates that particles of food clinging to the fur and vibrissae of demonstrators are not necessary for transmission of diet-identifying information to observers. Taken together the results of the present study (Galef, Kennett, and Stein, in press; Galef and Stein, in press) indicate that both particles of food on the exterior of rats and portions of diet in the stomach of rats provide cues sufficient to permit observers to identify their respective demonstrators' diets.

Contextual cues. The results of the studies presented in Figure 13 also suggest that a demonstrator rat provides a context within which exposure to diet-identifying cues alters observers' subsequent diet preference. Observer preference was not affected by exposure to a diet

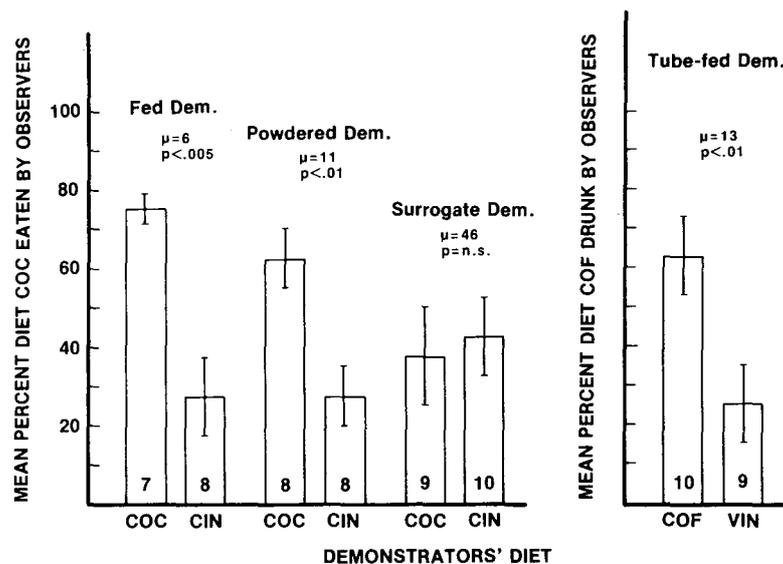


Fig. 13. Left-hand panel: Mean amount of cocoa-flavored diet eaten, as a percentage of total amount ingested, by observers interacting with demonstrators or surrogates. Right-hand panel: Mean amount of coffee-flavored solution, as a percentage of total amount drunk, ingested by observers whose demonstrators were tube-fed with either coffee- or vinegar-flavored solution.

presented on a surrogate, but was affected by exposure to the same diet presented on the face of a rat. Further, the procedure employed in these studies provides an opportunity to define more precisely the nature of the contextual cues which, in combination with diet identifying cues, produce demonstrator influence on observer diet preference.

We allowed observers to interact for 30 min in the apparatus illustrated in Figure 12 with demonstrators treated in one of four ways: (1) Observers in the Powdered-face Group interacted with anesthetized demonstrators whose faces had been rolled in either Diet Cin or Diet Coc. (2) Observers in the Dead-powdered-face Group interacted with demonstrators that had been sacrificed by anesthetic overdose and had their faces rolled in either Diet Cin or Diet Coc prior to the demonstrators introduction into the apparatus. (3) Observers in the Powdered-rear Group, interacted with anesthetized demonstrators whose rear ends were rolled in Diet Cin or Diet Coc. These demonstrators were introduced into the screen tube of the apparatus illustrated in Figure 12 with their rear ends inside the bucket and their heads outside of it. Last, (4) observers in the Surrogate Group were allowed to interact in the apparatus with a rat-size cotton-batting stuffed length of tubular gauze one end of which had been rolled in either Diet Cin or Diet Coc.

Figure 14 presents a measure of the degree of influence of the various sorts of demonstrators on their respective observers' subsequent diet preferences during testing (Step 5 of Figure 1). The greater the Cocoa-demonstrator/Cinnamon-demonstrator ratio the greater the influence of demonstrators' diets on observers' subsequent diet preference.

To summarize the results of a series of statistical analyses discussed in detail elsewhere (Galef and Stein, in press): (1) Observers in

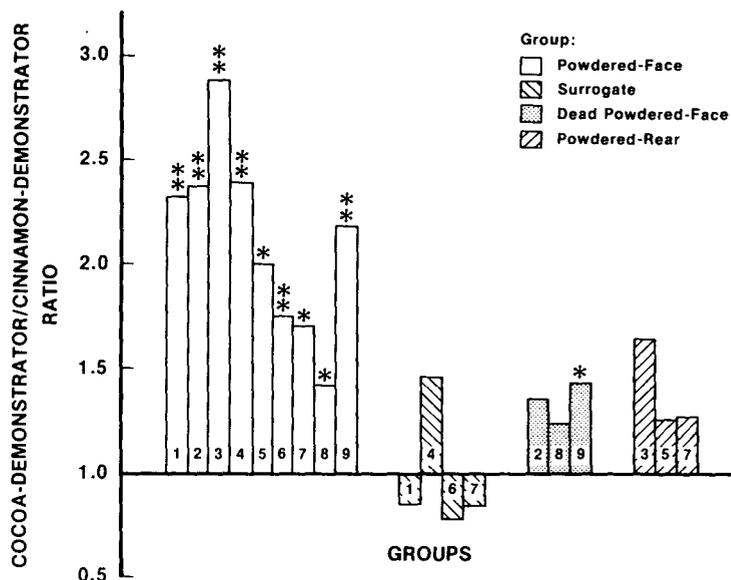


Fig. 14. Cocoa-demonstrator/Cinnamon demonstrator ratios of groups of observers interacting with demonstrators and surrogates in the apparatus illustrated in Figure 12. Observers were randomly assigned across groups labeled with the same integer. \* =  $p < .05$ , \*\* =  $p < .01$ . (Galef and Stein, 1985. Copyright 1985 by the Psychonomic Society, Inc. Reprinted by permission of the authors and publisher.)

the Powdered-face Group consistently exhibited a significant tendency to choose for ingestion the diet applied to their respective demonstrators. (2) Observers in the Surrogate Group exhibited no tendency to select the same diet for ingestion that their respective demonstrators had been fed. (3) Observers in the Dead-powdered-face and Powdered-rear Groups were both significantly less affected in their diet selection by demonstrators than were observers in the Powdered-face Group, and significantly more affected by demonstrators than were observers in the Surrogate Group. Taken together these findings suggest: (1) that simple exposure of an observer rat to the smell of a diet is not sufficient to enhance observer preference for that diet, and (2) that the contextual cues emitted by demonstrator rats, producing preference for a diet in their observers, are both widely distributed and most concentrated at the anterior end of live rats. These findings do not, of course, satisfactorily resolve the issue of the nature or origins of the effective contextual cues emitted by demonstrator rats. Determination of the active chemicals involved in potentiating observer preference for demonstrators' diets must await biochemical analyses. We will attempt such analyses in the future, but I suspect that identification of the critical agent or agents will prove as difficult in the present case as it has in other attempts to chemically define mammalian pheromones.

#### SUMMARY AND CONCLUSIONS

The series of studies described above provide compelling evidence that naive rats have the capacity to extract information from recently-fed conspecifics, permitting identification of the food those fed individuals

have eaten. Recipients of such information are biased in their subsequent food selection by the diet-related cues they encounter during interaction with a fed individual, and, in a restricted set of circumstances, can use the information acquired during social interaction to orient subsequent foraging activities.

Our data further indicate that information concerning distant diets is contained in olfactory signals passing from recently-fed rats to naive ones. These olfactory cues both permit recipient identification of the diet eaten by a conspecific and provide an as yet undefined social context that results in subsequent enhanced preference for diets eaten by informants.

It does not seem appropriate to conceive of the signals passing from a recently-fed rat to its fellows as ritualized or formalized over evolutionary time for a communicative function; anesthetized rats lacking the capacity to initiate or execute skeletal responses are as effective in signaling as are intact individuals. It seems to be the case that in rats the life-sustaining processes of ingestion, digestion, and respiration produce as by-products olfactory diet-identifying signals and contextual cues that are exploited by recipients to guide their future behavior. Thus, the results of the present experiments, in addition to demonstrating the possibility of communication of information concerning distant diets by rats, call attention to the potential importance in vertebrate communication of information extraction as a complement to formalized signaling. Life sustaining activities, such as feeding, not only promote the fitness of their initiators, but also provide a source of potential survival-enhancing information to others capable of extracting relevant information from their social environments.

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