

## TRANSFER OF INFORMATION CONCERNING DISTANT FOODS: A LABORATORY INVESTIGATION OF THE 'INFORMATION-CENTRE' HYPOTHESIS

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**Abstract.** When choosing between two novel diets, an 'observer' rat (*Rattus norvegicus*) prefers that diet previously eaten by a 'demonstrator' conspecific with whom the observer has interacted prior to making its choice between diets. Demonstrator influence on observer diet selection is maintained even if, during the period of demonstrator-observer interaction, the demonstrator is anaesthetized and a wire-mesh barrier prevents the demonstrator from physically contacting the observer. Demonstrator influence on observer diet choice is blocked by either rendering the observer anosmic or placing a transparent Plexiglas barrier between demonstrator and observer during their period of interaction. We conclude that olfactory cues passing from demonstrator to observer provide observers with information concerning demonstrators' diets and that these olfactory cues are sufficient to bias diet selection by observers. Further, observer rats that have learned the locations at which each of three diets are intermittently available can use information provided by demonstrators to increase foraging efficiency. We discuss the implications of the results both for the 'information-centre' hypothesis of the function of mammalian aggregations and for previous studies of social transmission of diet preference in rats.

Wild Norway rats (*R. norvegicus*) are social, central-place foragers. Each rat lives as a member of a colony inhabiting a fixed system of burrows from which colony members emerge to forage and to which they subsequently return (Calhoun 1962; Telle 1966).

It has been suggested that in environments characterized by an unpredictable and patchy distribution of food, social birds or mammals which forage from a central place could benefit from exchange of information with conspecifics at the central site concerning the availability of food in the larger environment (Ward & Zahavi 1973; Erwin 1977; Bertram 1978; Waltz 1982). This 'information-centre' hypothesis concerning the function of vertebrate aggregations carries the implication that members of vertebrate social groups can acquire information from others of their species concerning potential feeding sites or foods remote in both time and space from the locus of information transmission (Ward & Zahavi 1973; De Groot 1980).

Although the hypothesis that aggregation sites of birds and mammals may serve as information-centres is an attractive one, evidence sufficient to establish such a function of sociality in vertebrates has proven difficult to collect in field situations. Supporting evidence is largely circumstantial or comparative rather than direct (De Groot 1980). Further, there is little evidence from laboratory study of either mammals or birds of behavioural mechanisms

sufficient to support the transmission from one individual to another of information concerning distant food sources. In the literature, it is usually assumed that unsuccessful vertebrate foragers can use behavioural cues to identify successful foragers at a central site such as a burrow or roost, and will then follow a successful individual to food (Ward 1965; Ward & Zahavi 1973; De Groot 1980; Waltz 1982).

It is, of course, possible that information about distant foods can be transferred via behavioural mechanisms other than following to a food source (von Frisch 1967). For example, results of previous studies in our laboratory indicate that flavour cues contained in the milk of a lactating rat reflect the flavour of her diet. These flavours in mother's milk are sufficient to enable pups nursing from a dam to recognize her diet at weaning and to cause pups to seek their mother's diet when initiating feeding outside the nest (Galef & Clark 1972; Galef & Henderson 1972; Galef & Sherry 1973). Thus the nest-site serves as an information-centre for weanling rat pups where they acquire information about foods distant in both time and space. Such an information-centre is a restricted one in that the medium for information transfer (mother's milk) is available only to lactating females and the information contained in the medium can only be received by suckling young.

There is also evidence suggesting that adult rats might be able to exchange information

concerning distant foods. Strupp (1982) has shown that an observer rat, choosing between two diets available to a demonstrator on the opposite side of a wire-mesh barrier from the observer, will exhibit a strong preference for whichever diet the demonstrator is eating (see also Posadas-Andrews & Roper 1983). While Strupp's findings indicate that adult rats can exchange information concerning their diets, her paradigm allowed demonstrator and observer to interact in the presence of the foods about which information was being communicated. Extensive modifications in Strupp's procedure were, therefore, necessary to explore the possibility that rats can exchange information concerning foods distant from an ingestion site.

In the series of laboratory experiments described below, we first demonstrate that one Norway rat can communicate to another information concerning food it has eaten at a distant site. Second, we determine the mode of transmission of this information, and finally we demonstrate that the transmitted information is adequate to facilitate foraging by its recipient.

### Experiment 1

The first experiment was undertaken to determine whether one adult rat (a 'demonstrator') can communicate information to a second (an 'observer') concerning the food the demonstrator has eaten prior to interaction with the observer. Although we will refer to the rats in our experiments as demonstrators and observers to conform to current usage (Levitsky & Strupp 1981; Strupp 1982), we do not intend to imply that the behavioural process supporting information transfer is learning by observation. In fact, our experiments will demonstrate that observational learning is not involved.

### Methods

**Subjects.** Subjects were 32 Long-Evans rats born in the McMaster colony to breeding pairs descended from animals purchased from Blue Spruce Farms (Altamont, N.Y.). Prior to initiation of the experiment all subjects were maintained ad libitum on Purina Laboratory chow and water in same-sex groups of 4 to 5 littermates.

Sixteen subjects, 42 days of age at the time of initiation of the experiment, served as observers. Sixteen 90-120-day-old subjects served as demonstrators. At the start of the

experiment, each observer was randomly paired with a demonstrator of the same sex.

**Apparatus.** During the experiment, subjects were housed and tested as demonstrator-observer pairs in  $42.5 \times 24 \times 27.5$ -cm wire-mesh hanging cages (Wahmann Co., Baltimore, Md). Each hanging cage was divided in two equal parts by a 1.25-cm ( $\frac{1}{2}$ -inch) wire-mesh partition ( $24 \times 27.5$  cm) attached at the mid-points of each cage's 42.5-cm sides. The same apparatus was also used in experiments 2-5.

**Procedure.** Our procedure was designed to mimic a situation in which a foraging rat ingests a food at some distance from the burrow, returns to the burrow, and interacts with a familiar burrow-mate. We were interested to know whether, as a result of such interaction, the burrow-mate could acquire information concerning the food the forager had eaten and would use this information in selecting a diet.

Treatment of subjects during the experiment was as follows (Fig. 1a): Step 1: demonstrator and observer were first maintained together with ad libitum access to Purina Laboratory Chow pellets for a 2-day familiarization period. Step 2: the demonstrator was moved to the opposite side of the wire-mesh partition from the observer and food-deprived for 24 h to ensure that the demonstrator fed when given the opportunity to do so. Step 3: chow was then removed from the observer's side of the cage (in preparation for testing) and the demonstrator was moved to an enclosure in a separate room and allowed to feed for 30 min on either powdered Purina Laboratory chow adulterated with 2% by weight Hershey's cocoa (cocoa-

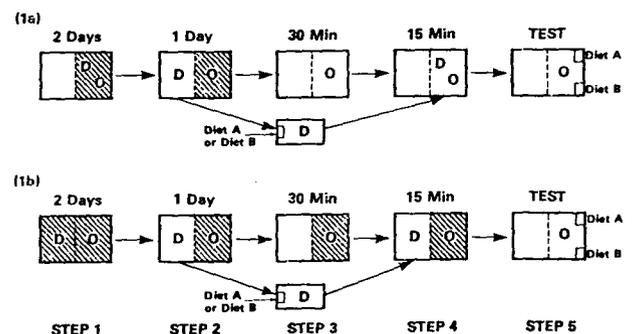


Fig. 1. Schematic diagram of the procedures of experiments 1 and 2 (Fig. 1a) and experiments 3, 4 and 5 (Fig. 1b). O = observer; D = demonstrator; hatching indicates that pellets of Purina Laboratory chow were present in the cage.

flavoured diet) or powdered Purina Laboratory chow adulterated with 1% by weight McCormick's pure ground cinnamon (cinnamon-flavoured diet). Step 4: the demonstrator was returned to the observer's 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, for 60 h, two weighed food-cups, one containing cinnamon-flavoured diet and one containing cocoa-flavoured diet. The food bowl containing the diet which a given observer's demonstrator had eaten was placed in the front of the cage of half the observers and in the back of the cage of the remainder of observers.

The experimenter weighed the two food cups once every 12 h throughout the 60-h test period.

### Results and Discussion

The results of experiment 1 are presented in Fig. 2, which shows the mean amount of cocoa-flavoured diet, as a percentage of total amount eaten, ingested by observers whose demonstrators had eaten cocoa-flavoured or cinnamon-flavoured diet during step 4 of the experiment (see Fig. 1a). Those observers whose demonstrators ate cocoa-flavoured diet ate a greater

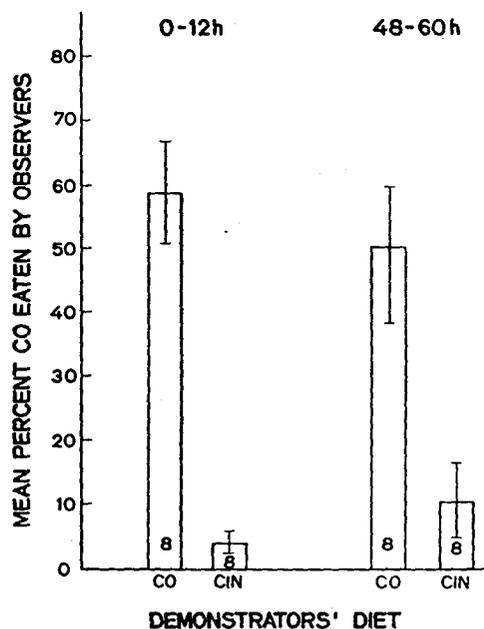


Fig. 2. Mean amount of cocoa-flavoured diet ingested, as a percentage of total amount eaten, by observers whose demonstrators had eaten either cocoa- or cinnamon-flavoured diet. CO = cocoa-flavoured diet; CIN = cinnamon-flavoured diet. Bars indicate  $\pm$  1SE.

percentage of cocoa-flavoured diet than did those observers whose demonstrators ate cinnamon-flavoured diet (0-12-h test, Mann-Whitney  $U = 0$ ,  $P < 0.001$ ). The effects of the diet eaten by the demonstrator on the diet preference of the observer were still observable 48-60 h after the interaction of observer and demonstrator in step 4 of Fig. 1a (Mann-Whitney  $U = 2$ ,  $P < 0.001$ ).

The results of experiment 1 clearly demonstrate that rats are able to communicate information concerning a diet they have eaten at a time and place distant from the locus of their interaction. The data also show that this information is sufficient to bias a recipient's subsequent choice of diet.

### Experiment 2

In experiment 1, an observer and demonstrator interacted immediately after the demonstrator had eaten a novel diet and the observer had the opportunity to choose between novel diets immediately following receipt of information from the demonstrator. Free-living rats must expend time in returning from a feeding site to their home burrow, and foragers departing from their home burrow must expend further time in reaching a feeding site. If the capacity of rats to transmit information concerning a food they have eaten at a distance from the nest site is to function as the basis for information transfer at the home-site in natural settings, transmission must occur even if there is a delay between a successful forager's ingestion of a food and its return to the burrow and a further delay between the interaction of a successful forager with other rats and the latter's arrival at a potential feeding site. The present experiment was undertaken to discover whether the information transfer demonstrated in experiment 1 could tolerate such delays.

### Methods

**Subjects.** Forty-eight 42-day-old experimentally-naive Long-Evans rats born in the McMaster colony served as observers, and 48 120-day-old Long-Evans rats as demonstrators. Observers and demonstrators were randomly assigned to one of three conditions: Control, 30-min-delay and 60-min-delay (described below).

**Apparatus.** The apparatus was that used in experiment 1.

**Procedure.** The eight demonstrator and eight observer rats assigned to the Control condition

were treated identically to observers and demonstrators in experiment 1 (see Fig. 1a). Demonstrators and observers assigned to 30-min-delay and 60-min-delay conditions were treated identically to those in the Control condition except in the following two respects. (1) After each demonstrator had eaten either cinnamon-flavoured or cocoa-flavoured diet for 30 min (step 3 of Fig. 1a), it was food-deprived for either 30 min (30-min-delay condition) or 60 min (60-min-delay condition) before being placed in the cage with its observer (step 4 in Fig. 1a). (2) After the observer and demonstrator had interacted for 15 min (step 4 in Fig. 1a), the observer was food-deprived for either 30 min (30-min-delay condition) or 60 min (60-min-delay condition) before being offered a choice of cinnamon- and cocoa-flavoured diets. A third departure from the procedure of experiment 1 was that the food cups offered to observers in the test phase (step 5) were weighed only once, 12 h after the initiation of testing.

### Results and Discussion

The main results of experiment 2 are presented in Fig. 3, which shows the mean percentage of cocoa-flavoured diet ingested by observers whose demonstrators had eaten either cinnamon- or cocoa-flavoured diet. Observers in both Control and 30-min-delay conditions exhibited marked effects of interaction with demonstrators on their food choice (Mann-

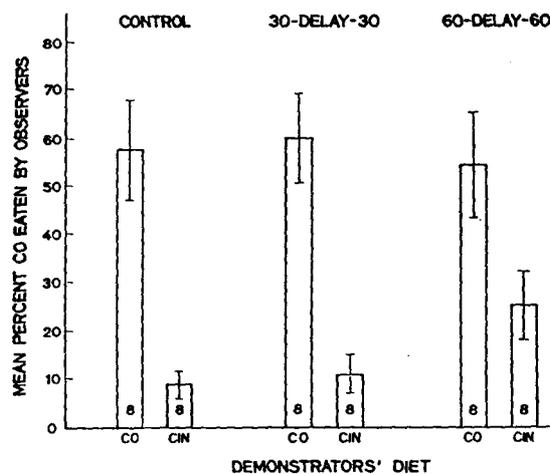


Fig. 3. Mean amount of cocoa-flavoured diet ingested, as a percentage of total amount eaten by observers in Control, 30-min-delay, and 60-min-delay groups when their demonstrators had eaten either cinnamon- or cocoa-flavoured diet. Bars indicate  $\pm 1$  SE.

Whitney  $U$ ; Control condition,  $U = 4$ ,  $P = 0.002$ , 30-min-delay condition,  $U = 3$ ,  $P = 0.002$ ). There was a marginal effect of demonstrator diet on the diet selection of observers in the 60-min-delay condition, but this failed to reach significance (Mann-Whitney  $U = 14$ ,  $P < 0.064$ ).

The results of the present experiment replicate the finding in experiment 1 of a transfer of information between adult rats concerning a diet distant in time and space. The results also indicate that this transfer is not disrupted by 30-min delays between a demonstrator's feeding and its interaction with an observer and an observer's interaction with a demonstrator and that observer's initiation of feeding. The data further suggest that similar 1-h delays interfere with the influence of demonstrators on the observers' diet choice. The present results do not provide sufficient information to determine whether this decrement is due to the first 1-h delay causing a deterioration of the signal passing from demonstrator to observer, or the second 1-h delay reducing the effect of the signal on the observer's behaviour. We shall address this issue elsewhere.

### Experiment 3

Experiments 3, 4, and 5 were undertaken to determine the medium of transmission of information from demonstrator to observer.

### Methods

**Subjects.** Thirty-two experimentally-naive 42-day-old Long-Evans rats born in the McMaster colony served as observers and 32 90-110-day-old Long-Evans rats served as demonstrators. Observers and demonstrators were randomly assigned to the two experimental groups described below.

**Apparatus.** The apparatus was the same as used in experiment 1.

**Procedure.** The procedure was similar to that described in Methods of experiment 1, except that during the period of interaction between demonstrator and observer in step 4 of Fig. 1a, demonstrator and observer were separated by a partition. For subjects in the 'Screen condition' this partition was constructed of 1.3-cm ( $\frac{1}{2}$ -inch) wire-mesh. For subjects in the 'Plexiglas condition' this partition was constructed of clear, 0.65-cm ( $\frac{1}{4}$ -inch) Plexiglas. Figure 1b presents a schematic diagram of the procedure of the present experiment. Minor differences between the procedure of experiment

1 and that of the present experiment may be noted in comparison of Fig. 1a and 1b. These differences are of no particular moment. They were introduced to ascertain whether the phenomenon under examination was sufficiently robust to withstand small modifications in procedure.

### Results and Discussion

The main results of experiment 3 are presented in Fig. 4, which shows the mean amount of cocoa-flavoured diet, as a percentage of total amount eaten, ingested by observers in Screen and Plexiglas conditions whose demonstrators had eaten either cocoa- or cinnamon-flavoured diet. Observers in the Screen condition exhibited an influence of their respective demonstrators on their diet choice, while subjects in the Plexiglas condition did not (Mann-Whitney  $U$ ; Screen condition,  $U = 0$ ,  $P = 0.001$ ; Plexiglas condition,  $U = 30$ ,  $P > 0.30$ ).

The results of the present experiment indicate that transfer of information from demon-

strator to observer can occur in the absence of free interaction between pair members. The data further indicate both that visual contact between observer and demonstrator is not sufficient and that some other form of contact (olfactory, gustatory, or tactile) is necessary for information transfer.

### Experiment 4

In this experiment we examined whether olfactory cues were sufficient to effect information transfer from demonstrator to observer.

### Methods

**Subjects.** Forty Long-Evans rats, 42 days of age at the initiation of the experiment, served as observers, and 40 100–120-day old rats of the same strain served as demonstrators. Half of the observers and half of the demonstrators were randomly assigned to Control and Anaesthetized conditions.

**Apparatus.** The apparatus was the same as used in experiment 1.

**Procedure.** Subjects in the Control group of the present experiment were treated identically to those in the 'Screen' condition of experiment 2 (see Methods of experiment 2 and Fig. 1b). Subjects in the Anaesthetized condition were treated like those in the Control group except that immediately after each demonstrator had eaten cinnamon- or cocoa-flavoured diet in step 3, it was anaesthetized by intraperitoneal injection of sodium pentobarbital, draped over an inverted Pyrex petri dish (100 cm diam  $\times$  50 cm), fastened to it with a piece of masking tape, and placed in the apparatus facing its observer with the end of its nose 2.5 cm from the wire-mesh partition separating demonstrator and observer. (Pilot studies had revealed that an anaesthetized demonstrator 2.5 cm from a hardware cloth partition could not be physically contacted by an observer on the far side of the barrier.) Each anaesthetized demonstrator was left on its side of the cage for 15 min (cf. step 4, Fig. 1b) and then removed. Each observer was then offered a choice of cinnamon- and cocoa-flavoured diets for 12 h.

### Results

The main results of experiment 4 are presented in Fig. 5, which shows the mean percentage of cocoa-flavoured diet ingested by observers in Anaesthetized and Control groups when their demonstrators had eaten either cinnamon- or cocoa-flavoured diet. Observers

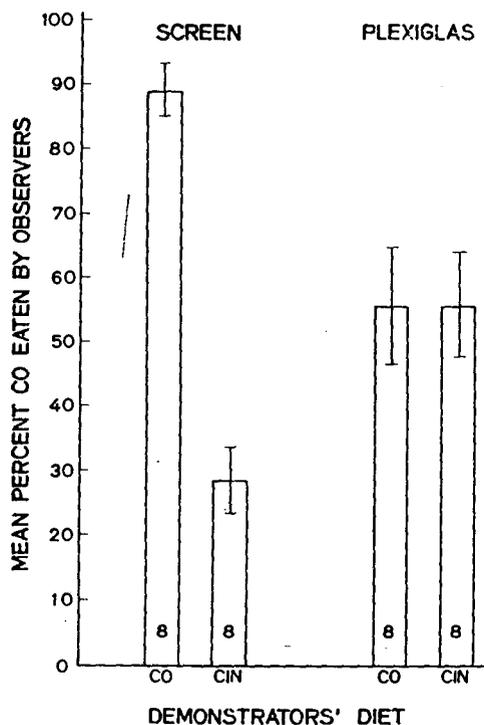


Fig. 4. Mean amount of cocoa-flavoured diet ingested, as a percentage of total amount eaten, by observers in Screen and Plexiglas conditions when their demonstrators had eaten either cinnamon- or cocoa-flavoured diet. Bars indicate  $\pm 1$  SE.

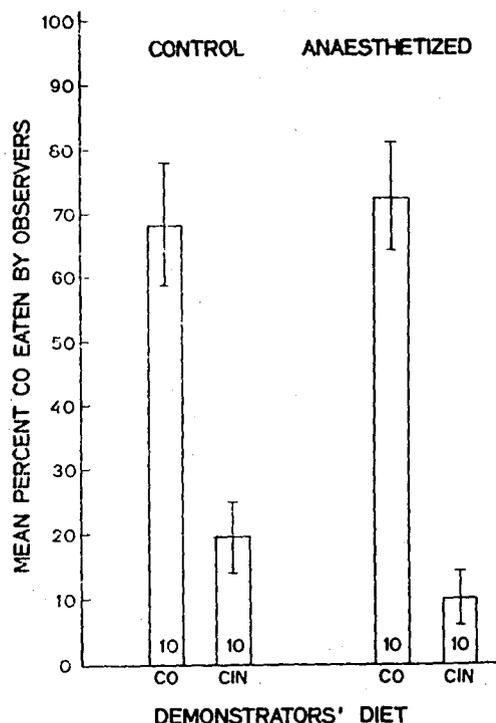


Fig. 5. Mean amount of cocoa-flavoured diet ingested, as a percentage of total amount eaten, by observers in Anaesthetized and Control groups when their demonstrators had eaten either cinnamon- or cocoa-flavoured diet. Bars indicate  $\pm 1$  SE.

in both Anaesthetized and Control groups exhibited marked effects of interaction with demonstrators on their food choice (Mann-Whitney  $U$ ; Anaesthetized group,  $U = 8$ ,  $P < 0.002$ ; Control group,  $U = 13$ ,  $P < 0.02$ ).

### Discussion

Because transfer of information between demonstrator and observer occurred in the absence of physical contact between them, it can be concluded that gustatory cues passing from demonstrator to receiver (for example the taste of the demonstrator's saliva or of food particles clinging to the demonstrator's coat) are not necessary for information transfer to occur. The finding that demonstrators kept 2.5 cm distant from their observers can transmit the necessary signal suggests that olfactory cues passing from demonstrator to observer are sufficient to support the transmission process.

Because anaesthetized demonstrators are as effective in transmitting information as intact demonstrators, it would appear that signal emission by the demonstrator is a passive rather

than active process, and that the necessary signal is emitted by the demonstrator rather than elicited by the observer.

### Experiment 5

Given that physical contact between demonstrator and observer is not necessary for information transfer from the former to the latter, it seems probable that olfactory cues sent by the demonstrator and received by the observer are sufficient for communication to occur. If so, anosmic observers should not exhibit an influence of interaction with an observer on their diet choice.

### Methods

**Subjects.** Thirty-six 42-day-old Long-Evans rats served as observers and 36 90-day-old rats of the same strain served as demonstrators. Half the observers were randomly assigned to an Anosmic group and half to a Control group.

**Apparatus.** The apparatus was the same as used in experiment 1.

**Procedure.** The procedure was that of experiment 2 (see Fig. 1b) except in two respects. (1) Twenty-four hours following initiation of the experiment, at the start of the last day of familiarization, observers assigned to the Anosmic group were rendered anosmic by intranasal lavage with zinc sulphate solution (Alberts & Galef 1971). Observers in the Control group were treated with isotonic saline solution at the time subjects in the Anosmic group were treated with Zinc Sulphate. (2) For 30 min during step 3 of Fig. 1b, demonstrator rats were fed either unadulterated powdered Purina Laboratory Chow (Pu Diet) or Normal Protein Test Diet (NPT Diet) (Teklad Test Diets, Madison, Wisc.). NPT Diet is a powdered mixture of the following ingredients (values in g/kg): vitamin-free test casein, 260.06; corn starch, 598.24; hydrogenated vegetable oil, 80.00; cod-liver oil, 20.00, USP XIV Mineral mix 40.00; vitamins, 1.70. (3) Observers were offered a choice between Pu Diet and NPT Diet for 12 h during the test period (step 5 of Fig. 1b).

The change in diets offered to demonstrators and observers in the present experiment was necessitated by pilot studies showing that anosmic rats could not discriminate cinnamon from cocoa-flavoured diet. (To test for the ability of anosmic subjects to discriminate between any pair of diets we compared the ability of anosmic and saline-lavaged subjects to exhibit a toxicosis-induced aversion to one of

those two diets when subsequently offered both simultaneously. The results of such tests were clear-cut. Anosmic subjects poisoned after they had eaten cocoa-flavoured diet ate as much cocoa- as cinnamon-flavoured diet in a 6-h test conducted 24 h after poisoning; control subjects poisoned after they had eaten cocoa-flavoured diet ate no cocoa-flavoured diet during the test. Both anosmic and control subjects poisoned after ingesting NPT Diet ate no NPT Diet when, 24 h after poisoning, they were offered a choice of NPT and Pu Diets for 6 h.) If anosmic observers were unable to discriminate between the two diets offered during testing (step 5 of Fig. 1b), then even if we were to observe a breakdown in demonstrator influence on diet selection in anosmic observers, we could not attribute this deficit to an anosmia-induced interference with communication between demonstrator and observer.

### Results and Discussion

The main results of experiment 5 are presented in Fig. 6, which shows the mean amount of

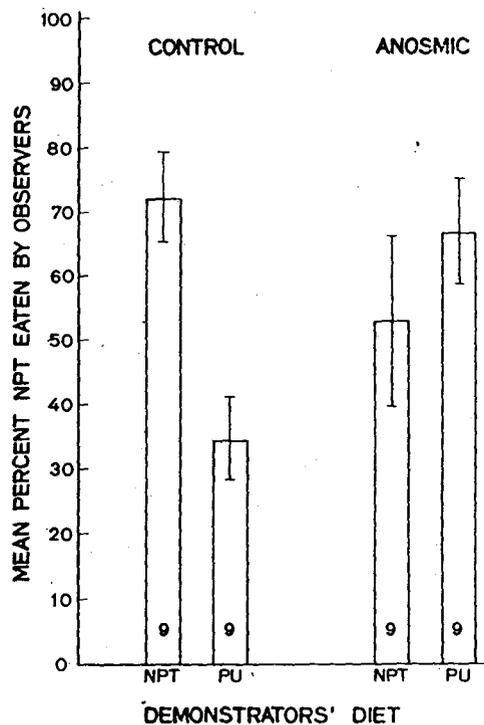


Fig. 6. Mean amount of NPT Diet, as a percentage of total amount eaten, ingested by observers in Anosmic and Control groups when their demonstrators had eaten either NPT Diet or Pu Diet. Pu = powdered Purina Laboratory Chow, NPT = Normal Protein Test Diet. Bars indicate  $\pm 1$  SE.

NPT Diet, as a percentage of total amount eaten, ingested by observers in Anosmic and Control groups whose demonstrators had eaten either NPT Diet or Pu Diet. Observers in the Control group whose demonstrators ate NPT Diet ate significantly more NPT Diet during testing than did observers in the Control group whose demonstrators ate Pu Diet (Mann-Whitney  $U = 4$ ,  $P < 0.002$ ). By contrast, the demonstrators' diet did not affect diet choice by anosmic observers during testing (Mann-Whitney  $U = 35$ ,  $P > 0.30$ ).

Given that NPT and Pu Diets are discriminable by anosmic subjects and that demonstrators can successfully transfer information concerning NPT and Pu Diets to intact observers, the failure of anosmic observers to use the information transmitted by their observers suggests that anosmia interfered with receipt of the necessary olfactory information. The results of both the present experiment and experiment 4 thus indicate that the cue passing from demonstrator to observer is olfactory in nature.

We have independent evidence of the presence of an olfactory cue carried on the breath of rats and reflecting the flavour of their diets, which could serve as the means of information transfer from demonstrator to observer. A human subject (C.M.), by sniffing rat breaths, successfully distinguished six rats fed cinnamon-flavoured diet from six rats fed cocoa-flavoured diet with better than 85% accuracy during two 18-trial sessions (binomial test, Session 1,  $x = 3$ ,  $P < 0.004$ , Session 2,  $x = 2$ ,  $P < 0.001$ ). While this does not prove that observer rats use information carried on the breath of demonstrators in selecting diets in our experiments, it does indicate that such information would be sufficient for communication from demonstrator to observer.

### Experiment 6

The results of the experiments described above demonstrate that rats can communicate information to their fellows about diets they have ingested far from the locus of information transfer. The data also indicate that such information can effect food preferences in a receiver, and that the signal passing from demonstrator to observer is olfactory in nature. They do not however provide evidence that such information can be used by a recipient to facilitate foraging in environments characterized by an unpredictable and patchy distribution of food.

In the present study we simulated an environment in which each of a variety of foods became available in fixed locations on an unpredictable schedule. Once our subjects had demonstrated that they knew the location in which each food was to be found, we provided each subject with the opportunity to interact with a conspecific which had eaten one of the foods. We then determined whether our subjects would use the information provided by the fed individual to direct their subsequent foraging.

### Methods

**Subjects.** Eight Long-Evans rats 42 days of age at the start of experimentation served as subjects and eight additional rats of the same age served as demonstrators. One subject and one demonstrator were excluded from the experiment when the subject learned to open the one-way doors described below from both sides.

**Apparatus.** The apparatus is illustrated in plan view in Fig. 7. It consisted of a three-arm maze attached to a cage holding four subject-

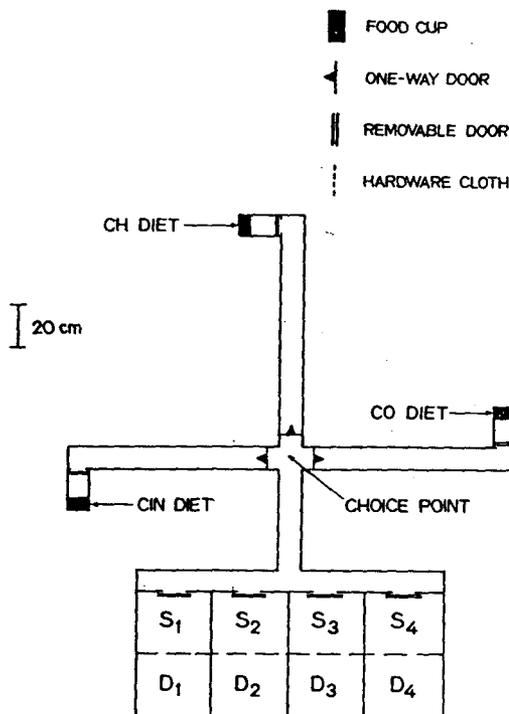


Fig. 7. Plan of apparatus used in experiment 6. CH = cheese-flavoured; CIN = cinnamon-flavoured; CO = cocoa-flavoured; S = Subject; D = Demonstrator.

demonstrator pairs. Each  $1 \times 0.09$ -m arm of the maze (constructed of plywood with a transparent Plexiglas cover) led via a removable guillotine door to a  $23 \times 15$ -cm goal box containing a food cup. At the choice point of the maze the subject was faced with a choice between three one-way doors.

Each subject was maintained in a  $30 \times 30 \times 15$ -cm plywood cage opening into an alley via a removable guillotine door. Each subject was housed adjacent to its demonstrator and separated from the latter by a  $30 \times 15$ -cm wire-mesh partition.

**Procedure.** To begin the experiment, subjects and demonstrators were tail-marked for individual recognition, introduced individually into their respective compartments, and placed on a 23 h/day food-deprivation schedule.

**Habituation.** Three days following initiation of the experiment, the guillotine doors were removed from the subjects' cages and from the goal boxes, the one-way doors were taped open, and subjects were allowed to explore around the apparatus for 2 h/day. Three different diets, cinnamon-flavoured powdered Purina Laboratory chow (Diet CIN), cocoa-flavoured powdered Purina Laboratory chow (Diet CO) and cheese-flavoured powdered Purina Laboratory chow (Diet CH, 2% by weight Kraft's romano cheese) were placed in the goal-boxes in the positions indicated in Fig. 7. These apparatus habituation sessions were continued for several days, with the experimenter gradually lowering the flaps on the one-way doors from one day to the next, until the one-way doors were completely closed and all subjects were passing through them without hesitation.

**Training.** On training days, each subject received four trials per day. To begin a series of trials the experimenter consulted a random number table to determine which of the three goal-boxes would be open to the first subject. That goal-box door was opened, the door to the first subject's living cage removed, and the subject was given 5 min to pass through a one-way door. If the subject chose the one-way door leading to food it was allowed to feed for 2 min and then returned to its living cage. If the subject chose one of the other two one-way doors, it was left in the arm it had chosen for 2.5 min and then returned to its living cage. If the subject failed to pass through a one-way door within 5 min, it was returned to its living cage.

Any subject choosing either of the incorrect doors was left in its living cage for 2 min and then allowed to choose again. The first trial was repeated until the subject chose the correct one-way door.

After the first subject's first trial of a day was completed, the second, third and fourth subjects' first trials of that day were run in an identical fashion to the first trial of the first subject, except that the goal-box door that was opened for each subject was different from that opened for the preceding subject.

Second, third and fourth trials on each day for each subject were run under conditions identical to those prevailing on that subject's first trial of the day. Because the location of the three diets remained fixed and the same goal-box was open on trials 1-4 of each day for each subject, perfect performance was possible on trials 2-4 (but not trial 1) of each day. After all subjects had completed their four trials, each was offered a food bowl containing unadulterated powdered Purina Laboratory chow for 1 h.

**Testing.** Once subjects were responding correctly on an average of two or more of the last three trials of each day for six consecutive days, that subject entered into the test phase of the experiment. During the test phase, each subject was run 4 trials/day, exactly as during training. However, during testing, 45 min prior to each subject's first trial of each day, that subject's demonstrator was removed from its living cage, and treated in the following fashion: (1) Each demonstrator was first placed in a cage in a separate room and allowed to feed for 30 min on the diet which was located in the arm of the maze to which that demonstrator's subject was to have access on that day. (2) The demonstrator was then returned to its living cage to interact through the wire-mesh partition with its subject for 15 min, and was then removed from its living cage until that day's testing of all subjects was completed. Each subject was tested (four trials/day) for 12 consecutive days.

### Results and Discussion

The main results of experiment 6 are presented in Fig. 8, which indicates the percentage correct responses made by each of the seven subjects on its daily first trials of the last 18 days of training and on its daily first trials during the 12 days of testing. Four of the seven subjects did significantly better than chance

during the testing phase of the experiment (Binomial test,  $H_0$  that  $p = \frac{1}{2}$ ; see Fig. 8 for significance levels). It is somewhat disappointing that not all subjects made use of the information provided by their respective demonstrators in selecting an arm of the maze for initial exploration. However, the fact that four subjects did use the information provided by their demonstrators indicates that the mode of information transfer examined in experiments 1-5 is adequate to facilitate foraging in circumstances in which a food is available intermittently at a fixed location.

### General Discussion

The results of the present experiments demonstrate that adult rats can exchange information concerning ingested foods at a time and place distant from the ingestion site. The results also demonstrate that the reception of olfactory information from conspecifics can profoundly bias diet choice in the recipient, and under appropriate circumstances, can facilitate the recipient's location of available nutrients. The present data thus provide indirect support for

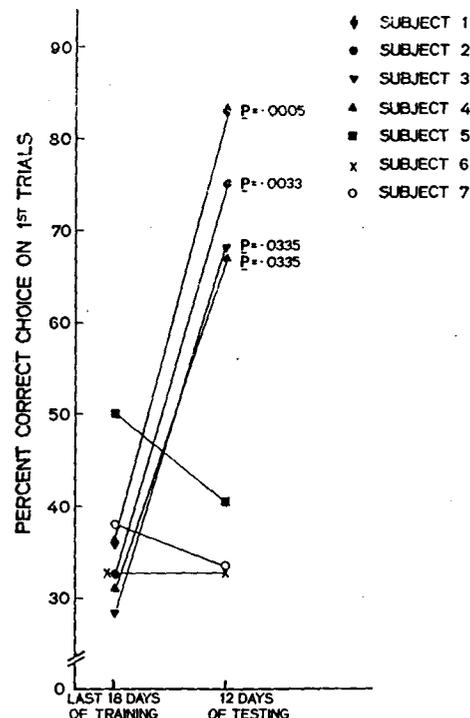


Fig. 8. Percentage of correct choices on first trials by individual subjects on the last 18 days of training and the 12 days of testing in experiment 6.

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