Journal of Comparative Psychology
1983, Vol. 97, No. 4, 364–371

Utilization by Norway Rats (*R. norvegicus*) of Multiple Messages Concerning Distant Foods

Bennett G. Galef, Jr.
McMaster University, Hamilton, Ontario, Canada

The results of this series of studies indicate that a naive rat interacting with a series of conspecifics, each of which has previously eaten a distinctive diet, (a) can extract information from each conspecific sufficient to permit identification of the diet that individual has eaten, (b) can distinctively encode that information, (c) can store it for at least 12 hr, and (d) can retrieve and use the stored information to orient its own feeding behavior. These results extend the findings of Galef and Wigmore (1983) of a capacity of rats to extract sufficient olfactory information from an individual conspecific to permit identification of the diet that individual has previously eaten.

Results of recent studies both in this laboratory and elsewhere have demonstrated that a naive rat can extract from a recently fed conspecific information sufficient to permit identification of the particular food the recently fed individual has eaten (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, in press-a, in press-b). Such information can be used by its recipient to orient and facilitate subsequent foraging behavior (Galef & Wigmore, 1983).

Previous research has focused on the extraction of information concerning a single food from a single individual. However, in natural circumstances rats live in social groups comprising many members (Telle, 1966). Although there is little direct information concerning social life in wild rat burrows, it seems reasonable to suppose that each colony member, prior to leaving its colony's burrow system to forage, may have the opportunity to acquire information from a number of different conspecifics about foods they have recently exploited.

In the present article, I explore the possibility that an individual rat remaining in its burrow and interacting with a succession of conspecifics returning from foraging trips could collect information concerning the range of foods the returning foragers have exploited. I further explore the possibility that the recipient of this wealth of information can use it to orient its own subsequent foraging activities.

For a subject to make use of information extracted sequentially from a number of conspecifics, it must have at least four capabilities. First, the subject must be able to acquire from each of the successful foragers with which it interacts sufficient information to permit subsequent identification of the food which that forager has eaten. Second, it must be able to distinctively encode the information gathered during a succession of encounters. Third, the subject must be able to store each encoded event until such time as it initiates foraging behavior. Last, it must retrieve and process the stored information. Previous studies in this laboratory clearly indicate that rats have the first capacity. The present series of studies was undertaken to determine whether they have the latter three.

Experiment 1

If rats remaining in their burrow are to make use of information received from a succession of their foraging colony mates, they must be able to distinctively encode and store the information they extract from each informant. In the present experiment, animals remaining in their home cages (observers) were exposed to a series of four recently fed, unfamiliar conspecifics (demonstrators) each of which had eaten a dif-

The research reported here was supported by Natural Sciences and Engineering Research Council of Canada Grant A-0307 and McMaster University Research Board grants to B. G. Galef, Jr. I thank Deborah Kennett, Maryanne Hawes, Doug Symons, and Cathy Maskell for technical assistance.

Requests for reprints should be sent to Bennett G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, Ontario, Canada L8S 4K1.

ferent diet. Each observer was then offered a choice between a pair of diets, one of which had been eaten by one of that observer's four demonstrators and one of which was totally unfamiliar. Consistent observer preference for the diet eaten by demonstrators would indicate an ability of observers to distinctively encode information acquired from a sequence of demonstrators.

Method

Subjects. Thirty-two experimentally naive 42-day-old Long-Evans rats, born in the McMaster colony to breeding stock acquired from Blue Spruce Farms (Altamont, New York) served as observers. Observers had been weaned at 21 days of age and maintained in same-sex groups of four on ad lib Purina Laboratory Rodent Chow and water until initiation of the experiment.

An additional 128 rats 92 days old served as demonstrators. Many of these rats had been observers in previous studies. During the 2 wk prior to the initiation of the present experiment, demonstrators were housed in individual cages in a room separate from observers and maintained on ad lib Purina Laboratory Rodent Chow and water.

Half of the demonstrators and observers were randomly assigned to the Diet Set 1 condition and half to the Diet Set 2 condition described in Procedure.

Apparatus. During the experiment, all observers were housed and tested in 21.5 × 24 × 27.5 cm wire mesh hanging cages (Wahmann Co., Baltimore, Maryland).

Procedure. Treatment of observers and demonstrators during the experiment was as follows (see Figures 1a and 1b): In order to permit familiarization with the apparatus, each observer was left undisturbed in the apparatus for 2 days. At the end of this habituation period, observers were exposed to a series of four demonstrators each of which had been food deprived for 24 hr and then fed one of the five diets described below for the 30 min immediately preceding its introduction into an observer's cage.

1. Cinnamon-flavored diet (CIN diet). Powdered Purina Laboratory Rodent Chow was adulterated 1% by weight with McCormick's Fancy Ground Cinnamon (Club House Foods Inc., London, Ontario).
2. Cocoa-flavored diet (COC diet). Powdered Purina Laboratory Rodent Chow was adulterated 2% by weight with Hershey's Pure Cocoa (Hershey Canada, Smiths Falls, Ontario).
3. Coffee-flavored diet (COF diet). Twenty-one grams of Sanka decaffeinated instant coffee (General Foods Inc., Toronto) were dissolved in 1,000 ml of tap water. Two-hundred grams of Five Roses enriched flour (Lake of the Woods Mills Ltd., Montreal) were mixed with 235 ml of the coffee solution.

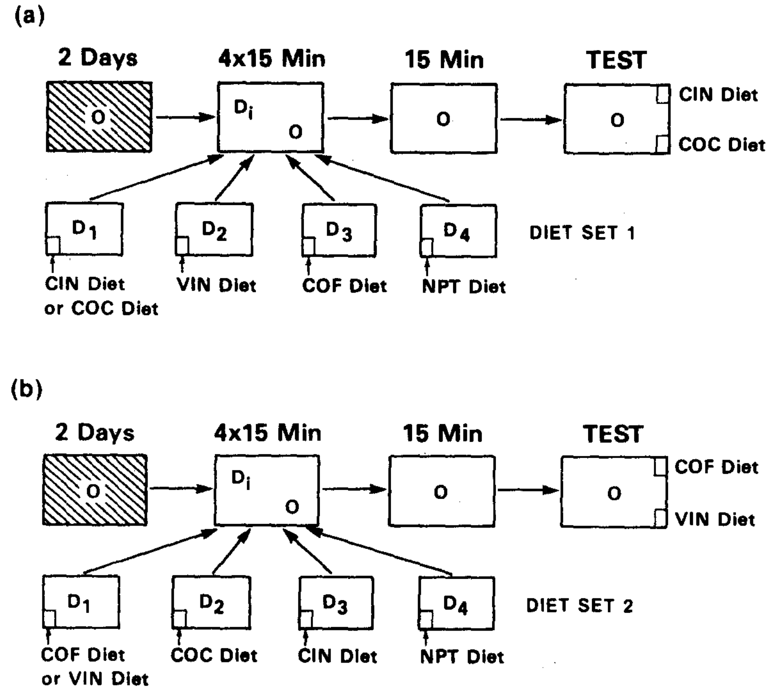

Figure 1. Schematic diagram of the procedure of Experiment 1. (O = observer; D = demonstrator; hatching indicates pellets of Purina Laboratory Rodent Chow were present in cage. The diets were flavored with cinnamon [CIN], cocoa [COC], vinegar [VIN], or coffee [COF]; NPT = normal protein test.)

4. Vinegar-flavored diet (VIN diet). Thirty-two milliliters of Allen's Pure Apple Cider Vinegar (CanVin Products Ltd., Toronto) were added to 1,000 ml of tap water. Two hundred grams of Five Roses enriched flour (Lake of the Woods Mills Ltd., Montreal) were mixed with 235 ml of the vinegar solution.

5. Normal protein test diet (NPT diet). This is a nutritionally adequate diet, consisting (in grams per kilogram) of vitamin-free test casein (260.06), corn starch (598.24), vegetable oil (80.0), cod liver oil (20.0), USP XIV mineral mix (40.0) plus necessary vitamins, purchased from Teklad Test Diets (Madison, Wis.).

Half of the observers interacted with four demonstrators each fed one of the four diets labeled Diet Set 1 in Figure 1a (VIN diet, COF diet, NPT diet, and either CIN diet or COC diet), and half interacted with four demonstrators each fed one of the four diets labeled Diet Set 2 in Figure 1b (NPT diet, CIN diet, COC diet, and either COF diet or VIN diet). Half of the observers in the Diet Set 1 condition interacted with a demonstrator that had ingested CIN diet, and half with a demonstrator that had ingested COC diet. Half of the observers in the Diet Set 2 condition interacted with a demonstrator that had ingested COF diet, and half with one that had ingested VIN diet.

Order of presentation of demonstrators eating each diet was counterbalanced within each diet set so that demonstrators eating each diet were presented equally often in first, second, third, and fourth positions.

After the hour of interaction with demonstrators, each observer was left undisturbed for 15 min and then offered for 16 hr a choice between two diets. The 16 observers whose demonstrators had eaten Diet Set 1 were offered for 16 hr a choice between weighed samples of CIN diet and COC diet; those 16 observers whose demonstrators had eaten Diet Set 2 were offered for 16 hr a choice between weighed samples of COF diet and VIN diet.

As a control for evaporation of the wet mashes (COF and VIN diets) offered to observers in the Diet Set 2 condition, six control feeding dishes, three containing COF diet and three containing VIN diet, were placed in empty cages in the experimental room during the testing of subjects assigned to Diet Set 2. At the end of 16 hr of testing, the mean water loss of the six control dishes was calculated, and this amount was added to the weight of food cups taken from observers offered the choice of COF and VIN diets before calculation of their diet intake.

Results and Discussion

The main results of Experiment 1 are presented in Figure 2 which shows (left panel) the amount of COC diet, as a percentage of total amount eaten, ingested by observers in the Diet Set 1 condition and (right panel) the amount of COF diet, as a percentage of total amount eaten, ingested by observers in the Diet Set 2 condition.

As is clear from examination of the figures and as statistical tests confirmed (Mann-Whitney U tests, see Figure 2 for p values), (a) observers in the Diet Set 1 condition one of whose four demonstrators ate COC diet showed a preference for COC diet during testing, while observers in the same condition one of whose demonstrators ate CIN diet exhibited a preference for that diet. (b) Observers in the Diet Set 2 condition one of whose four demonstrators ate COF diet showed a preference for COF diet,

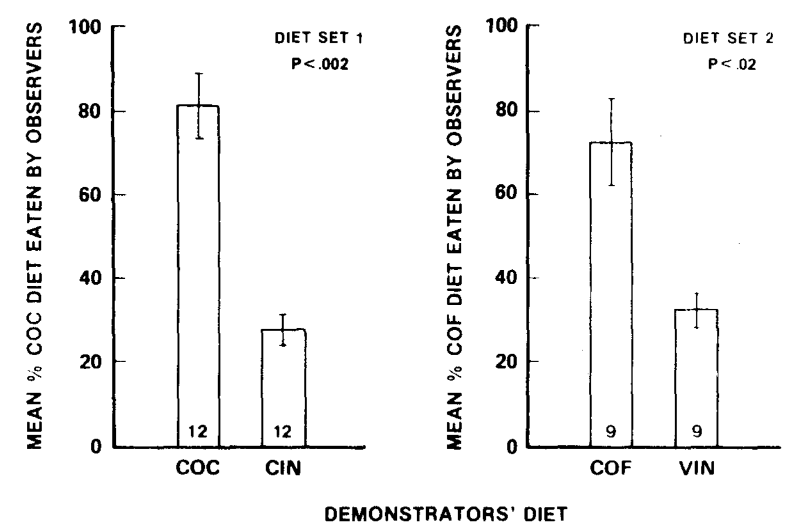

Figure 2. Mean amount of COC diet (left panel) or COF diet (right panel) ingested, as a percentage of total amount eaten, by observers in Diet Set 1 (left panel) and Diet Set 2 (right panel) conditions. (Bars indicate ±1 *SE*. See caption to Figure 1 for identification of diets.)

while observers in the same condition one of whose demonstrators ate VIN diet showed a preference for that diet.

This preference for a diet eaten by one of four demonstrators in the presence of three masking events indicates that observers are capable of distinctively encoding a number of signals received sequentially from demonstrators.

Experiment 2

In natural circumstances a rat remaining in its burrow and collecting information from a series of returning foragers is unlikely to have the opportunity to utilize information extracted from any one forager for some time after receiving it. Thus, if rats are to utilize information acquired from a number of conspecifics, it is important that they be able to store that information for many minutes or hours.

In the present experiment, each observer was allowed to interact with a demonstrator and was tested 0 to 48 hr later for its preference for the diet its demonstrator had eaten.

Method

Subjects. Ninety 42-day-old Long-Evans rats from the McMaster colony served as observers. A further 90 rats, 2–3 wk older than the observers, served as demonstrators.

Apparatus. Subjects were housed and tested in same-sex demonstrator–observer pairs in 42.5 × 24 × 27.5 cm wire mesh hanging cages (Wahmann Co., Baltimore, Maryland). Each cage was divided into two equal parts by a ½-in. (1.25-cm) hardware-cloth screen attached to the midpoint of each 42.5-cm side.

Procedure. Treatment of subjects during the experiment was as follows (see Figure 3):

In order to permit familiarization with both apparatus and pair-mate, demonstrator and observer were maintained together with ad lib access to Purina Laboratory Rodent Chow pellets (their normal maintenance diet) and left undisturbed for 2 days.

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

Next, chow was removed from each observer's side of the apparatus (in preparation for testing of the observer), and each demonstrator was moved to an individual enclosure in a room separate from that housing observers and fed for 30 min. Half of the demonstrators were fed COC diet (powdered Purina Laboratory Rodent Chow adulterated 2% by weight with sifted Hershey's Pure Cocoa), and half were fed CIN diet (powdered Purina Laboratory Rodent Chow adulterated 1% by weight with McCormick's Fancy Ground Cinnamon).

Immediately following the end of the 30-min feeding period, each demonstrator was returned to its observer's cage. Demonstrator and observer were then allowed to interact freely for 15 min. At the end of the 15-min period of interaction, all demonstrators were discarded, and observers were randomly assigned to one of five independent groups differing in the delay imposed before the initiation of testing. Eight observers whose demonstrators had eaten COC diet and eight observers whose demonstrators had eaten CIN diet were tested starting 0, 6, 12, 24, or 48 hr after the end of the 15-min period of demonstrator–observer interaction.

To initiate testing, the experimenter placed two weighed food cups, one containing CIN diet and one containing COC diet, in each observer's cage. Intake was determined 16 hr later by weighing both food cups.

Results and Discussion

The main results of Experiment 2 are presented in Figure 4 which indicates the amount of COC diet, as a percentage of total amount eaten, ingested by observers whose demonstrators ate COC or CIN diet. Observers in the 0-, 6-, and 12-hr delay conditions whose demonstrators ate COC diet ate a greater percentage of COC diet than did observers whose demonstrators ate CIN diet (Mann-Whitney U tests, all $ps < .02$). There were no significant differ-

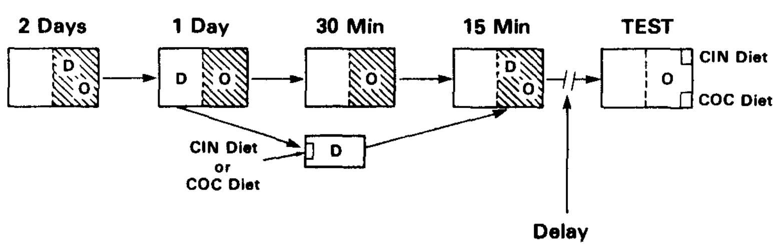

Figure 3. Schematic diagram of the procedure of Experiment 2. (O = observer; D = demonstrator; hatching indicates pellets of Purina Laboratory Rodent Chow were present in cage. CIN = cinnamon flavored; COC = cocoa flavored.)

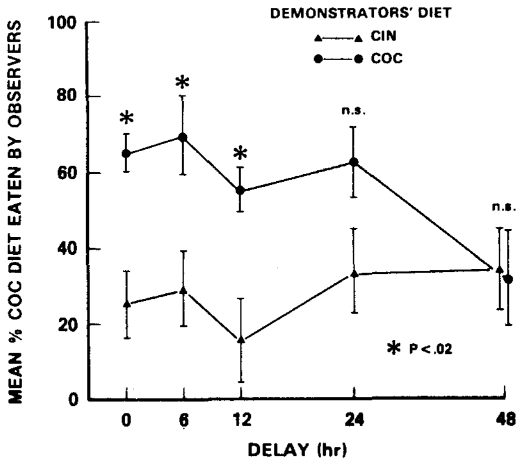

Figure 4. Mean amount of COC diet ingested, as a percentage of total amount eaten, by observers as a function of demonstrators' diets and the delay between interaction of demonstrator and observer and the initiation of testing. (Bars indicate ±1 *SE*. CIN = cinnamon flavored; COC = cocoa flavored.)

ences in observer diet preference as a function of demonstrators' diet to be seen in observers in the 24- and 48-hr delay conditions.

These data indicate that observer rats can store information extracted from demonstrators concerning the diet those demonstrators have eaten and retrieve it at least 12 hr later. It is, of course, possible that information obtained from demonstrators is stored by observers for longer than 12 hr but that the test we used was not sufficiently sensitive to detect it. In any case, 12-hr storage of information received from demonstrators is more than adequate to permit utilization of information received from a series of demonstrators in a wide range of potential natural situations.

Experiment 3

The results of Galef and Wigmore (1983) and of Experiments 1 and 2 of the present study demonstrate that rats can extract, distinctively encode, store, and retrieve information extracted from conspecifics concerning diets they have recently eaten. In the present experiment, I asked whether information extracted from a series of demonstrators could be used some hours later to facilitate foraging by its recipient. I simulated an environment in which each of three foods is available in fixed locations on an unpredictable schedule. Once the subjects had demonstrated that they knew the location at which each food was to be found, each subject was provided the opportunity to interact with a series of conspecifics one of which had eaten one of the three foods. I then determined whether, after a delay of several hours, the subjects would use the information provided by the relevant conspecific to direct their subsequent foraging.

Method

Subjects. Four female Long-Evans rats, 42 days of age at the start of experimentation, served as subjects, and 16 female littermates of the subjects served as demonstrators.

Apparatus. The apparatus is illustrated in plan view in Figure 5. It consisted of a three-arm maze attached to four 30 × 30 cm cages, each holding a single subject and each opening via a guillotine door onto a 9-cm-wide alley leading to the maze entrance. Each 1 m × 9 cm arm of the maze led via a removable guillotine door to a 23 × 15 cm goal box containing a food cup. At the choice point of the maze, a subject was faced with a choice among three one-way doors.

Procedure. To begin the experiment, the experimenter tail marked subjects to facilitate individual recognition, introduced them singly into their respective compartments, and placed them on a 23-hr/day food deprivation schedule.

Habituation: Three days following initiation of the experiment, three different diets, Diets CIN, COC (see procedure of Experiment 1), and CH (powdered Purina Laboratory Rodent Chow adulterated 2% by weight with Kraft's Grated Romano Cheese) were placed in the goal boxes of the maze in the positions indicated in Figure 5. Then the guillotine doors were removed from subjects' cages and goal boxes, the one-way doors were taped open, and subjects were allowed to explore the apparatus for 2 hr/day. These habituation sessions were continued for 2–3 wk, 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 each subject was passing through them without hesitation.

Training: On each day of training each subject received four trials in the apparatus. 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 cage was removed, and the first 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 cage. If the subject chose one of the two other one-way doors, it was left in the arm it had chosen for 2.5 min and then returned to its

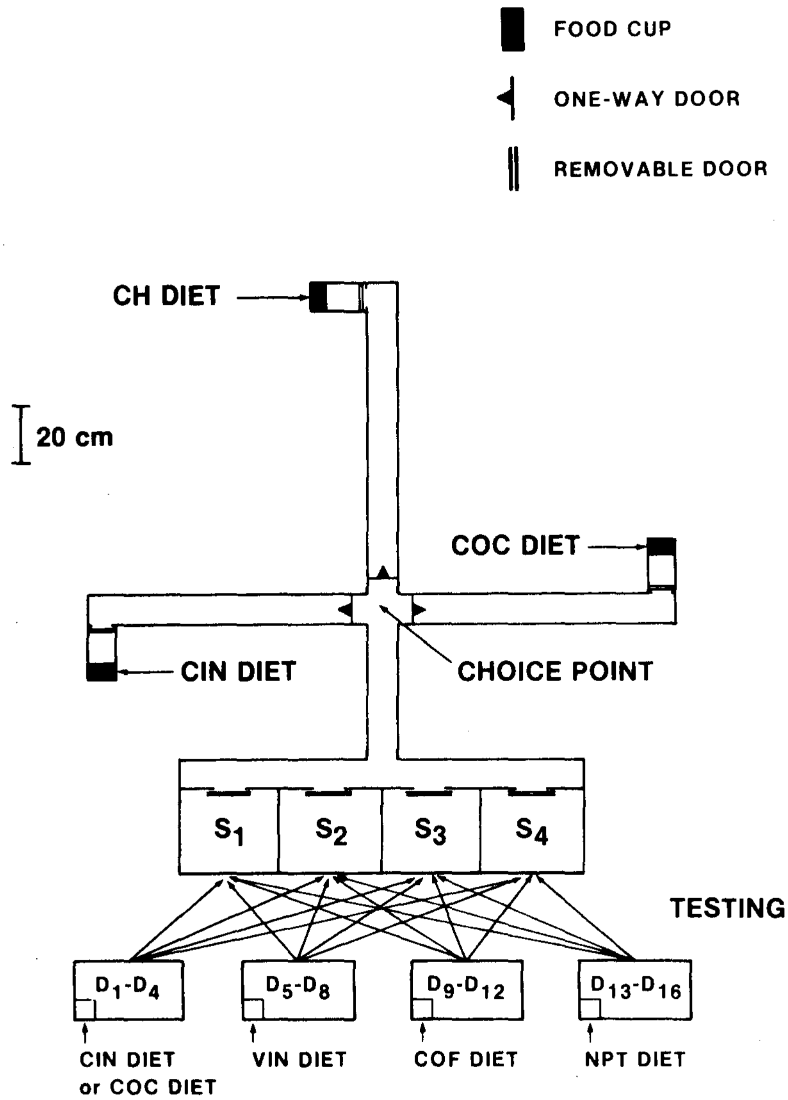

Figure 5. Plan of apparatus used in Experiment 3. (CH = cheese flavored. See caption to Figure 1 for identification of other diets.)

living cage. If the subject failed to pass through a one-way door within 5 min (a very infrequent event after the first 2 wk of training), it was returned to its living cage.

A 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 opened for each subject was different from that opened for the preceding subject.

Second, third, and fourth trials of each day for each subject were run under conditions identical to those prevailing on that subject's first trial of that 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 (and improbable on Trial 1) of each day.

Thirty minutes after all subjects had completed their four trials, each was offered a food bowl containing unadulterated powdered Purina Laboratory Rodent Chow for 1 hr.

Testing: Once a subject had responded correctly on two or more of the last three trials of each day for 6 consecutive days (M = 48 days following initiation of habituation training), that subject entered the test phase of the experiment. During testing, each subject was run four trials/day, exactly as during training. However during testing, 5 hr prior to each subject's first trial of each day, it was allowed to interact for 15 min with each of a series of four demonstrators, each of which had been 24 hr food deprived and then offered for 30 min one of the five diets (Diets COF, VIN, NPT, and either COC or CIN) described in Diet Set 1 of Procedure of Experiment 2. On each of 6 consecutive days of testing, two of the four subjects encountered a demonstrator that had eaten CIN diet and two encountered a demonstrator that had eaten COC diet. The goal box open to a subject on each test day corresponded to the diet eaten by one of its demonstrators. Thus, if one of a given subject's four demonstrators had eaten COC diet on a particular test day, then on that test day the goal box leading to COC diet was opened.

Order of presentation of demonstrators was counterbalanced across subjects and test days so that demonstrators conveying the critical information were presented equally often in first–fourth positions.

After a subject had completed interaction with its fourth demonstrator, it was left undisturbed for 3–4 hr and then tested for four trials.

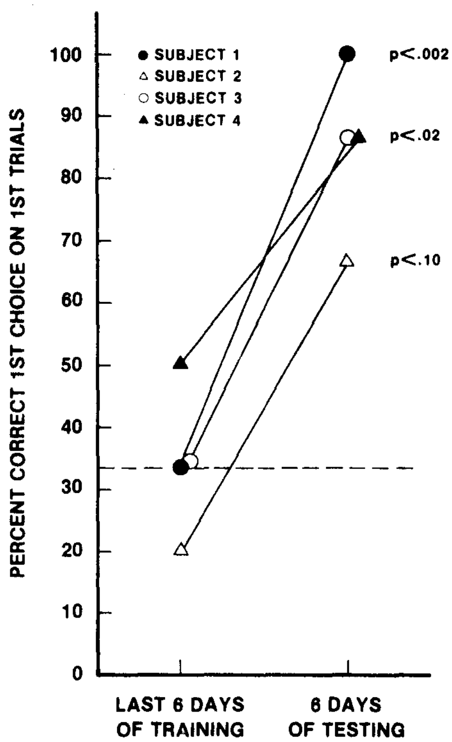

Figure 6. Percentage of correct first choices on first trials by individual subjects on the last 6 days of training and 6 days of testing in Experiment 3.

Results and Discussion

The main results of Experiment 3 are presented in Figure 6 which indicates the percentage correct choices made by each of the four subjects on its first choice of its first trial on the last 6 days of training (when no information was available from conspecifics) and on the 6 days of testing (when information was available from conspecifics). All four subjects performed at a greater than chance level during the testing phase of the experiment, three of them significantly so (binomial test, $H_0 = 1/3$; see Figure 6 for significance levels). The results of the present experiment indicate not only that rats can distinctively encode, store, and retrieve information extracted from a number of conspecifics but also that they can use such information to facilitate foraging in circumstances in which food is available intermittently at a fixed location.

General Discussion

The results of the present series of studies extend those of Galef and Wigmore (1983) by demonstrating that rats can encode, store, retrieve, and utilize information concerning distant diets received from a number of conspecifics. The individual rat remaining in its burrow and interacting with a number of others returning from foraging trips can both extract information permitting identification of the range of foods its colony mates are exploiting and use extracted information to organize its own foraging activities. Whether rats use all of these capacities in their natural habitats to increase the efficiency of their foraging may in practice be impossible to determine directly. However, evidence uncovered during the past decade both in this laboratory and elsewhere of multiple independent mechanisms allowing the social facilitation of foraging (see Galef, 1977, 1982, for reviews) in itself strongly suggests that life in social groups is an important factor in increasing the feeding efficiency of Norway rats in natural conditions.

References

Galef, B. G., Jr. Mechanisms for the social transmission of food preferences from adult to weanling rats.

In L. M. Barker, M. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection.* Waco, Tex.: Baylor University Press, 1977.

Galef, B. G., Jr. Studies of social learning in Norway rats: A brief review. *Developmental Psychobiology,* 1982, *15,* 279-295.

Galef, B. G., Jr., & Wigmore, S. W. Transfer of information concerning distant foods: A laboratory investigation of the "information-centre" hypothesis. *Animal Behaviour,* 1983, *31,* 748-758.

Posadas-Andrews, A., & Roper, T. J. Social transmission of food preferences in adult rats. *Animal Behaviour,* 1983, *31,* 265-271.

Strupp, B. J., & Levitsky, D. A. Early brain insult and cognition: A comparison of malnutrition and hypothyroidism. *Developmental Psychobiology,* in press-a.

Strupp, B. J., & Levitsky, D. A. PKU, learning, and models of mental retardation. *Developmental Psychobiology,* in press-b.

Telle, H. J. Beitrag zur Kenntnis der Verhaltensweise von Ratten, vergleichand dargestellt bei *Rattus norvegicus* und *Rattus rattus. Zeitschrift fur angewandte Zoologie,* 1966, *53,* 129-196.

Received April 2, 1983
Revision received June 16, 1983 ■