OLFACTORY COMMUNICATION IN RATS:

A MECHANISM FOR INFORMATION CENTRE FUNCTIONING

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A MECHANISM FOR INFORMATION CENTRE FUNCTIONING

by

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ABSTRACT

The present research investigates whether information concerning distant foods can be exchanged by domestic rats at a central site. Experiments were designed to model a natural situation in which a successful forager ("demonstrator" rat) returns to the burrow (home cage) and interacts briefly with a fellow colony member ("observer" rat). Information transfer was demonstrated, as observers exhibited a marked preference for the food that their demonstrators had eaten.

A series of experiments designed to analyze the means of information exchange demonstrated that communication was mediated by olfactory cues. Active communication regarding the demonstrator's feeding success proved unnecessary for effective information transfer between demonstrators and observers.

Finally, observers exposed to poisoned demonstrators during the interaction period, nevertheless exhibited a preference for the food that their demonstrators had eaten. This result suggested that observers had failed to associate olfactory cues regarding the food with their demonstrators' illness.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Dr. Jeff Galef for his continual expert guidance, assistance and encouragement throught the course of this research. Dr. Martin Daly has also provided critical discussion and for this I am grateful.

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INTRODUCTION

A number of behavioral ecologists have suggested that birds and mammals can exchange information regarding the location of distant food sources (Bertram, 1968; Erwin, 1977; Horn, 1968; Waltz, 1982; Ward and Zahavi, 1973). By sharing knowledge of good feeding sites each member of a group of animals could enhance its efficiency in exploiting unpredictably distributed supplies of food (Waltz, 1982).

Ward and Zahavi (1973) have argued that members of several bird species use communal roosts as centres for information exchange. They suggest that unsuccessful foragers recognize successful roost-mates by their behaviour and that the former could follow knowledgable birds to feeding grounds. DeGroot (1980) has provided inferential experimental support for this "information centre" hypothesis in vertebrates, however no direct evidence has been reported.

The most compelling evidence of an information centre is provided by the classic experiments of vonFrisch (1954). VonFrish noticed that soon after a successful forager arrived in a honey bee hive, large numbers of bees appeared at the location the initial forager had been exploiting. Through careful observation he established a correlation between elements of a "dance" executed by successful foragers at the hive, and the physical location of a food source in the field.

There is controversy as to whether the proposed "dance language" is the principal mechanism involved in bee recruitment (Wenner, 1967;

Gould, 1976). Olfactory cues absorbed by bees bodies such as food odours and characteristic odours of particular locations have been suggested as sufficient for honey bee recruitment (Wenner, 1967). In either case, bees exchange information at the hive regarding the location of distant food sources (Gould, 1976; Wenner, 1971).

If information centres were employed by groups of mammals, individuals benefiting most would be those belonging to species whose members gathered and dispersed frequently in search of unpredictably distributed food (Bertram, 1978). Although there is little evidence of information centres in mammalian groups (Bertram, 1978; Waltz, 1982), information exchange at the nest site regarding the flavour of food removed in both space and time has been demonstrated in rats, albeit restricted to interaction between a mother and her litter. The milk of a lactating female rat contains cues directly reflecting the flavour of her diet and pups at weaning will exhibit a preference for the diet that their mother was eating during lactation (Galef and Henderson, 1972; Galef and Sherry, 1973).

The adaptive value of social transmission of food preferences seems clear. Aquiring information about foods that are safe to ingest from experienced conspecifics facilitates pups' transfer of feeding from milk to solid food by reducing the amount of time and energy they would require to locate foods in the environment. The young animal's likelihood of ingesting potentially toxic or lethal substances is also lessened.

Conveivably, adult rats living in an unstable environment could also benefit from information exchange at the burrow regarding fellow colony members' food choices. This process could serve both to facilitate less exploratory conspecifics' initial acceptance of safe novel foods, and signal replenishment of a previously available food source. The present research, therefore, investigated whether information concerning distant foods could be exchanged by domestic rats at a central site.

I THE STRUPP EFFECT

Strupp and Levitsky (1981) have demonstrated that an adult rat can influence that food choice of a six week old conspecific. Animals were housed in pairs on opposite sides of cages divided by a hardware-cloth screen and for seven days the younger rat observed its older pair-mate feed exclusively on one of two available diets. The older rat ate only one diet because the other was adulterated with bitter-tasting quinine sulfate. Subsequently, the "observer" rats were offered a choice between the same two foods that their older pair-mates had had available. Observers exhibited a marked preference for the diet that their respective "demonstrator" had been eating, even though prior to preference testing, observers had never ingested either of the diets available to demonstrators.

The present research began by replicating the effect demonstrated by Strupp and Levitsky (1981), as their results suggested the possibility of information exchange between adult rats.

EXPERIMENT I

Experiment 1 was undertaken to replicate the effect demonstrated by Strupp and Levitsky (1981). A control group was added to examine the possibility that observers' preferences were for the position of the food cup utilized by their demonstrators, rather than for the diet it contained.

Method

Subjects

Subjects were 24 pairs of male Long-Evans rats born in the McMaster colony to dams obtained from Canadian Breeding Farms, St. Constant, Quebec. Twelve pairs were assigned to the Control Group and twelve to the Experimental Group described below. Subjects were assigned to each of the two groups in a random fashion to control for litter effects.

Apparatus

The apparatus consisted of fifteen hanging cages (42 x 18 x 24 cm). Each cage was divided in half by 1.2 cm (1/2 in.) hardware-cloth screen.

Procedure

Experimental Group. One side of each cage was occupied by a 10 week old "demonstrator" rat that had access to two differently flavoured foods: cocoa - (2 percent by weight Hershey's Pure Cocoa) and cinnamon - (2 percent by weight McCormick Cinnamon) flavoured powdered Purina Laboratory Chow. One of the two foods offered to each demonstrator was adulterated with bitter tasting quinine sulfate (.75 percent by weight) so that demonstrators fed exclusively on the unadulterated flavoured chow. For half of the demonstrators, cocoa-flavoured chow was adulterated with quinine sulfate and for the other half, quinine sulfate was added to the cinnamon-flavoured chow. The position of the food cups offered to demonstrators in the Experimental Group was counterbalanced so that quinine sulfate-adulterated flavoured chow occurred equally often in the front and rear of the cages, as did cinnamon-and cocoa-flavoured chow.

Individual six week old "observer" rats were placed on the side of the divided cages opposite to their respective demonstrator. Each observer and demonstrator pair lived side by side for seven days during which time observers had Purina Laboratory Chow pellets and water available ad lib (Figure 1, Step A).

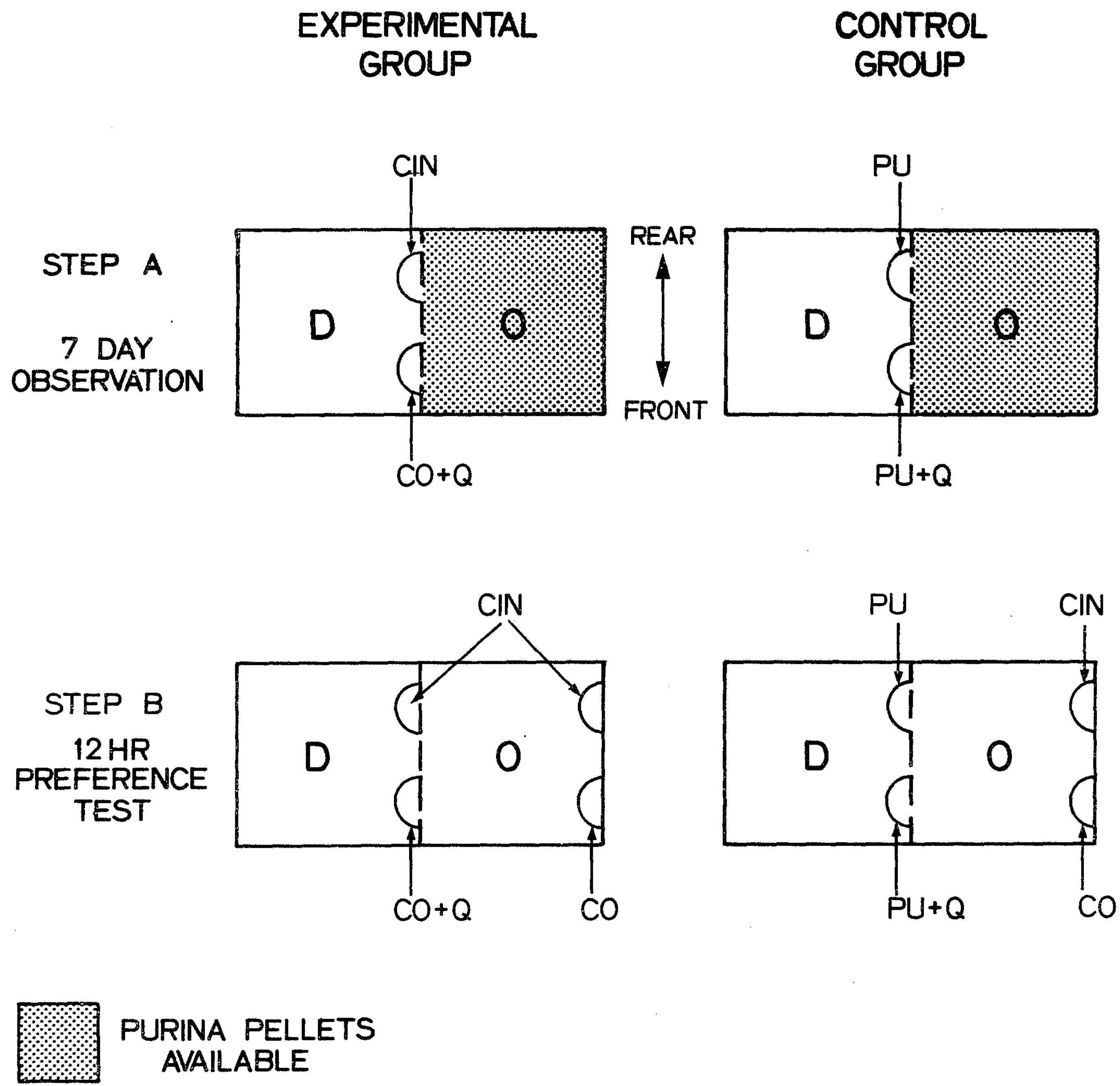
Control Group. Demonstrators in the Control Group had access to two food cups, one containing powdered Purina Laboratory Chow and the other containing powdered Purina Laboratory Chow adulterated with quinine sulfate (.75 percent by weight). The position of the food cups offered to demonstrators in the Control Group was counterbalanced so that quinine sulfate - adulterated chow occurred equally often in the front and rear of the cages. Pairs of demonstrators and observers in the Control Group were otherwise treated identically to those in the Experimental Group.

Each pair of subjects in the Control Group was yoked to a pair of subjects in the Experimental Group in the manner illustrated in Figure 1, Step A. The position of the quinine sulfate-adulterated food offered to a demonstrator in the Experimental Group corresponded to the position of the quinine sulfate-adulterated food offered to its yoked demonstrator in the Control Group. Consequently, for each yoked pair, the demonstrators ate from the same food cup position.

Testing. On the evening of the seventh day of the experiment, food pellets were removed from the cages of observers in both Experimental and Control Groups and replaced by two weighed food cups containing unadulterated cinnamon-and cocoa-flavoured chow. After remaining in

Figure 1

A schematic of the procedure of Experiment 1 showing a top view of the divided cages. D = Demonstrator, O = Observer, Cin = Cinnamon - flavoured chow, Co = Cocoa - flavoured chow, Pu = Powdered Purina Laboratory Chow, +Q = plus quinine sulfate.


EXPERIMENTAL GROUP
CONTROL GROUP
STEP A
7 DAY OBSERVATION
CIN
CO+Q
D
O
REAR
FRONT
PU
PU+Q
STEP B
12 HR PREFERENCE TEST
CIN
CO+Q
CO
PU
CIN
PU+Q
CO
PURINA PELLETS AVAILABLE

observer's cages for 12 hr. the food cups were removed and weighed to determine the amount of each food each observer had consumed.

The position of observers' food cups during preference testing was determined as illustrated in Figure 1, Step B. The position of the food cups of an observer in the Experimental Group corresponded to the position of its demonstrator's food cups. If, for example, a demonstrator in the Experimental Group had cocoa-flavoured chow located in the front of its cage and cinnamon-flavoured chow in the rear, then its observer's cocoa-and cinammon-flavoured chow were placed in the front and rear positions respectively.

The position of the food cups of an observer in the Control Group corresponded to the position of the food cups of its yoked observer in the Experimental Group.

In the example illustrated in Figure 1, Step B, one would expect, on the basis of Strupp and Levitsky's (1981) results, that the observer in the Experimental Group would preferentially ingest cinnamon-flavoured chow. If an observer's preference was for the position of the food cup utilized by its demonstrator rather than the diet it contained, one would also expect the yoked observer in the Control Group to prefer cinnamon-flavoured chow.

Date Treatment

For each observer in the Experimental Group, I calculated the percentage of its total food intake during the preference test that was the same flavour as the food its demonstrator had been eating (referred to below as "percent demonstrators' diet eaten"). If the food choice of a demonstrator in the Experimental Group had no effect on its observer's food choice, given an equal number of demonstrators in both flavour conditions, the mean "percent demonstrators' diet eaten" would not differ significantly from 50 percent. If observers preferentially ingested the same flavoured food as their respective demonstrators, mean "percent demonstrators' diet eaten" would be significantly greater than 50 percent.

Observers in the Experimental condition were also divided into two groups: those paired with demonstrators that ate cocoa-flavoured chow and those paired with demonstrators that ate cinnamon-flavoured chow. Percent preference for cocoa-flavoured chow was calculated for each observer in both groups by dividing the amount of cocoa-flavoured chow consumed during the preference test by the total amount of both foods consumed. Mean percent preference for cocoa-flavoured chow was then calculated for both groups and the two means were compared to determine whether observers whose demonstrators ate cocoa-flavoured chow ate significantly more cocoa-flavoured chow than did observers whose demonstrators ate cinammon-flavoured chow. Note that deciding to present the data in the form of percent preference for cocoa-flavoured chow is arbitrary, because the percent preference for cocoa-flavoured chow is always 100 minus the percent preference for cinnamon-flavoured chow.

For each observer in the Control Group, I calculated the percentage of its total food intake during the preference test that was from the food cup corresponding to the position of the food cup utilized by its demonstrator (referred to below as "percent eaten at demonstrators' position"). If an observer's preference was for the position of the food cup utilized by its demonstrator instead of the diet it contained, one would expect the mean "percent eaten at demonstrators' position" to be significantly greater than 50 percent.

Observers in the Control condition were also divided into two groups: those paired with demonstrators that ate from the food cup in the front of the cage ("front food cup") and those paired with demonstrators that ate from the food cup in the rear of the cage ("rear food cup"). Percent eaten from the "front food cup" was calculated for each observer in both groups by dividing the amount of food consumed from the "front food cup" by the total amount of both foods consumed. Mean percent eaten from the "front food cup" was then calculated for each group and the two means were compared to determine whether observers whose demonstrators ate from the "front food cup" consumed significantly more flavoured chow from the "front food cup" than did observers whose demonstrators ate from the "rear food cup".

All $\underline{p}$ values reported in Experiment 1, and throughout the remainder of this study, are two-tailed.

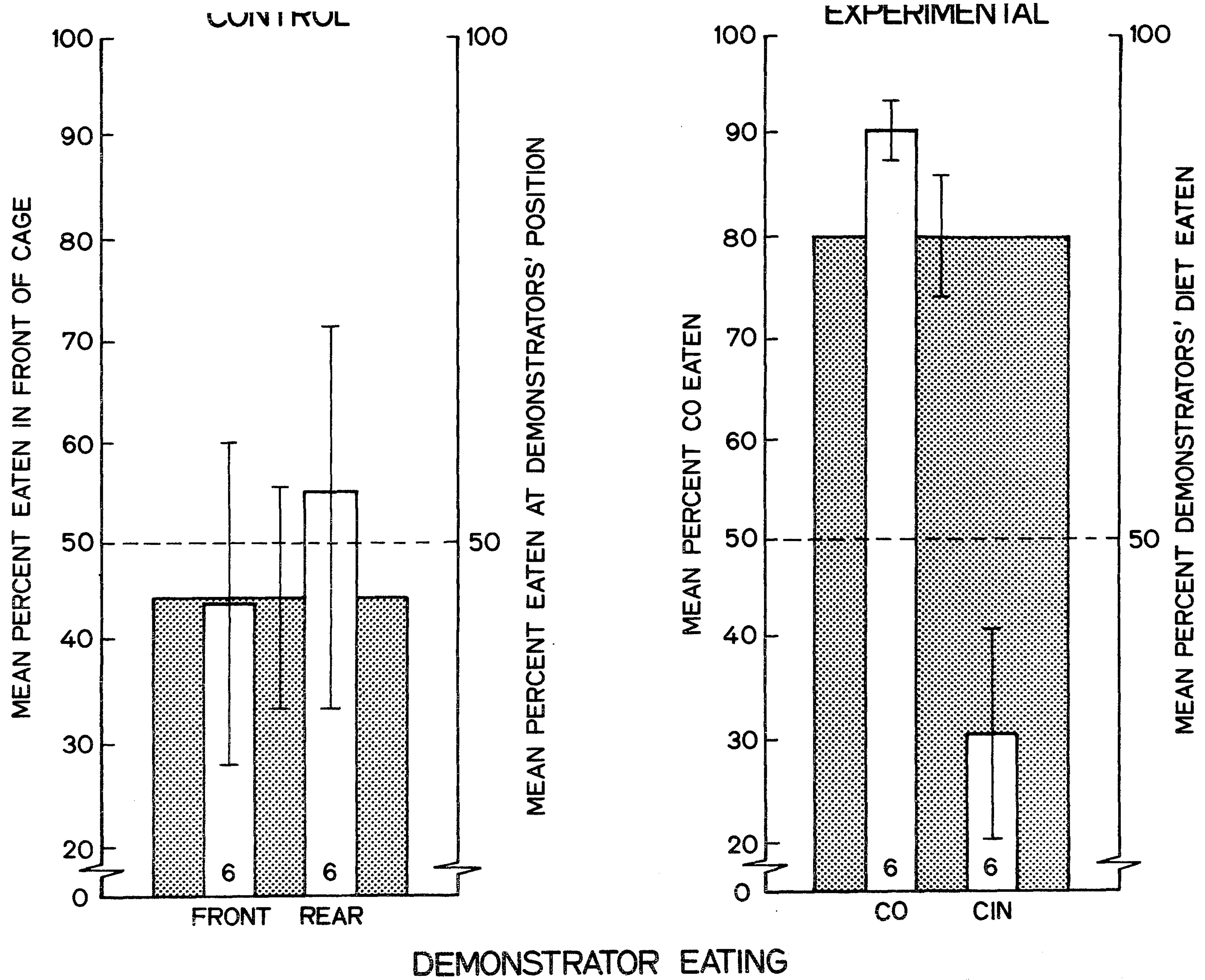
Results and Discussion

The results of Experiment I are presented in Figure 2. Observers in the Experimental Group whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers in the Experimental Group whose demonstrators ate

Figure 2: Experiment 1

Control Group: The stippled bar indicates the mean percentage of observers' total food intake that was from the food cup corresponding to the position of the food cup utilized by their demonstrators. Open bars indicate the mean percentage of observers' total food intake that was from the food cup in the front of the cage, for observers whose demonstrators ate from either the food cup in the front, or rear of the cage. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.

Experimental Group: The stippled bar indicates the mean percentage of observers' total food intake that was the same flavour as the food that their demonstrators ate. Open bars indicate the mean percentage of observers' total food intake that comprised cocoa-flavoured chow, for observers whose demonstrators ate either cocoa-or cinnamon-flavoured chow. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.


CONTROL
EXPERIMENTAL
MEAN PERCENT EATEN IN FRONT OF CAGE
MEAN PERCENT EATEN AT DEMONSTRATORS' POSITION
MEAN PERCENT CO EATEN
MEAN PERCENT DEMONSTRATORS' DIET EATEN
100
90
80
70
60
50
40
30
20
0
6
6
FRONT
REAR
CO
CIN
DEMONSTRATOR EATING

cinnamon-flavoured chow (Mann Whitney U Test, U = 1, p = .002). Mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, x = 1, p = .006). These data indicate that the food choices of observers in the Experimental Group were markedly affected by the food preference of their demonstrators.

Observers in the Control Group whose demonstrators ate from the "front food cup" did not consume significantly more flavoured chow from the "front food cup" than did observers in the Control Group whose demonstrators ate from the "rear food cup" (Mann Whitney U Test, U = 17, p = .628). Mean "percent eaten at demonstrators' position" was not significantly different from 50 percent (Sign Test, x = 6, $p > .40$). One can conclude from these data that the food choices of observers in the Experimental Group were affected by cues other than the position of the food cup utilized by their demonstrators.

II SOCIAL TRANSMISSION IN CENTRAL PLACE FORAGERS

Although the Strupp effect is interesting, it is difficult to imagine an analogous set of circumstances occurring in nature. It is unlikely that a rat would have opportunity to continuously observe a fellow colony member eating one particular food for seven days.

One might, however, conceive of a biologically more relevant situation in which the burrow acted as an information centre. A successful forager, upon returning to the burrow, might transmit information to other colony members regarding the stimulus properties of the food it had been eating. This process could serve both to facilitate less exploratory conspecifics' initial acceptance of safe novel foods and, in an unstable environment, signal replenishment of a previously available food source. The following experiment was designed to model this hypothesized natural situation.

EXPERIMENT 2

Experiment 2 was designed to determine whether rats would exhibit a preference for a food they had never encountered following brief exposure to a familiar conspecific that had recently ingested this food outside the home cage.

Method

Subjects

Subjects were 16 same-sex pairs of Long-Evans rats born in the McMaster colony to dams obtained from Canadian Breeding Farms, St. Constant, Quebec. One member of each pair was designated as an "observer" and tail painted to facilitate recognition. Observers' pair-mates were designated as "demonstrators" and were 65 days of age at the beginning of experimentation. Observers were six weeks old.

Apparatus

The apparatus described in Experiment 1 was also used in Experiment 2.

Procedure

A schematic of the procedure of Experiment 2 is presented in Figure 3. Each pair of demonstrators and observers shared one side of a divided cage for three days and during this time both received ad lib access to Purina Laboratory Chow pellets and water (Step A). On the following morning each demonstrator was placed on the opposite side of the divider from its observer and deprived of food for 12 hr. (Step B). Demonstrators were subsequently removed from the apparatus and allowed 1/2 hr. access to either cocoa-(2 percent by weight Hershey's Pure Cocoa) or cinnamon[1] -(1 percent by weight McCormick Cinnamon plus 2 percent by weight granulated sugar) flavoured powdered

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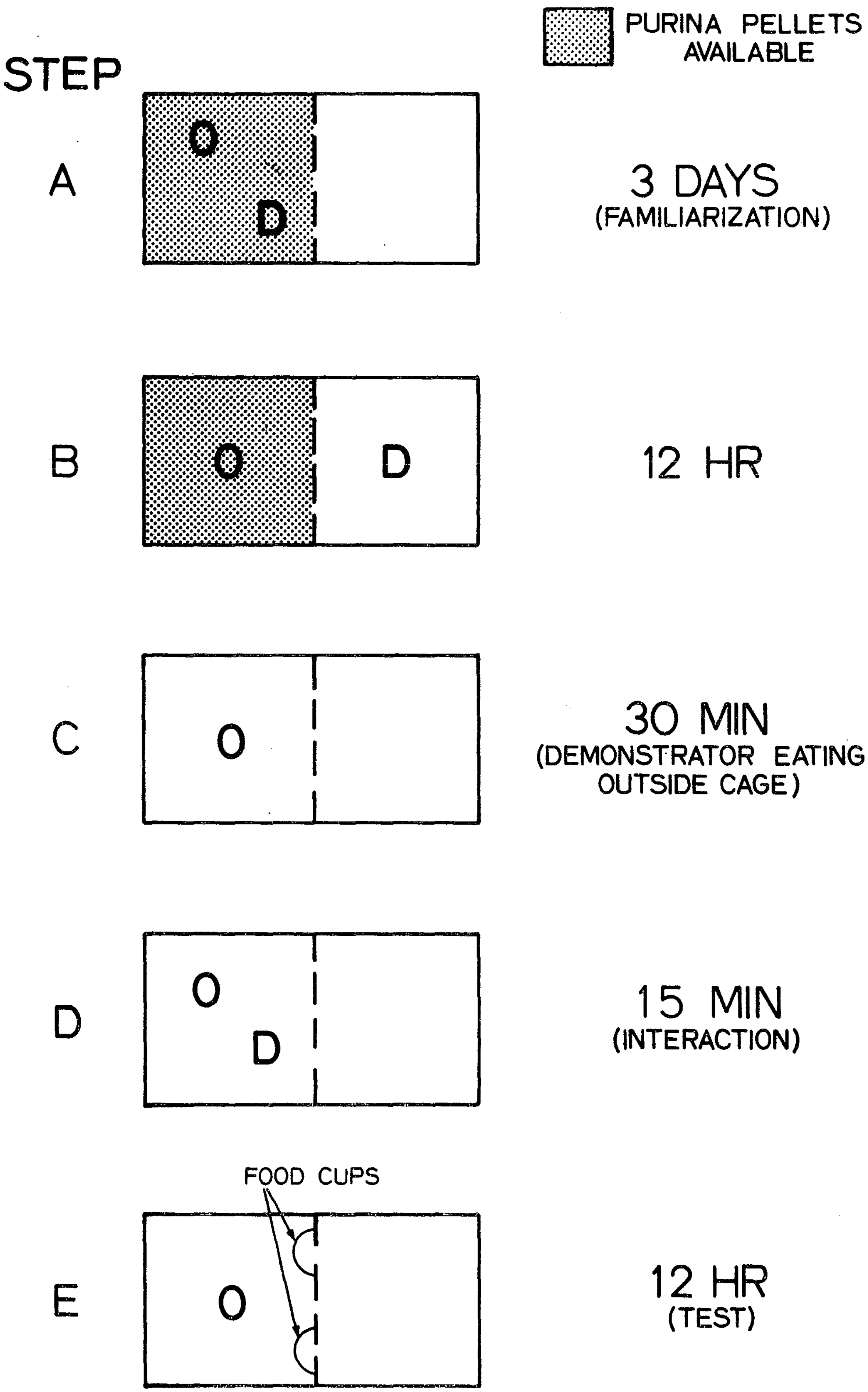
[1] It is important that the two diets offered to observers during the preference test are roughly equipalatable, since any effect of information transfer might be masked by a strong preference for one diet over the other. The relative palatability of pairs of diets was monitored throughout the present by offering rats 12 hr. choice tests. If there was a marked discrepancy between the relative palatability of the diets, a small amount of sugar was added to the less preferred diet.

Figure 3

A schematic of the procedure
of Experiment 2 showing a
top view of the divided cages.


PURINA PELLETS AVAILABLE
STEP
A
O
D
3 DAYS
(FAMILIARIZATION)
B
O
D
12 HR
C
O
30 MIN
(DEMONSTRATOR EATING OUTSIDE CAGE)
D
O
D
15 MIN
(INTERACTION)
FOOD CUPS
E
O
12 HR
(TEST)

Purina Laboratory Chow in individual transparent plastic cages (35 x 30 x 15 cm) located in a room separate from the test room (Step C). This step in the experiment was intended to represent a forager leaving the burrow in search of food. Demonstrators were observed during this feeding period and those that did not eat were excluded from the experiment. Observers' food pellets were removed during the demonstrators' absence.

After feeding, each demonstrator was returned to the side of the cage containing its observer and each pair was allowed to interact for 15 min. (Step 4). This step represented the opportunity for information exchange at a central site (home cage) regarding the food a successful forager (demonstrator) had consumed at a distant location. Following Step 4, demonstrators were removed from the apparatus and two weighed food cups containing cocoa-and cinammon-flavoured chow were placed in each observer's cage for 12 hr. (Step 5). Across subjects, each flavour occurred equally often in the front and rear of the cages.

The following morning food cups were removed from the cages and weighed to determine the amount of each food each observer had consumed.

Data Treatment

For each observer, "percent demonstrators' diet eaten" was calculated by dividing the amount of food the observer consumed that was the same flavour as its demonstrator had eaten by the total amount of both foods consumed. I then determined whether the mean "percent demonstrators' diet eaten" was significantly different from 50 percent.

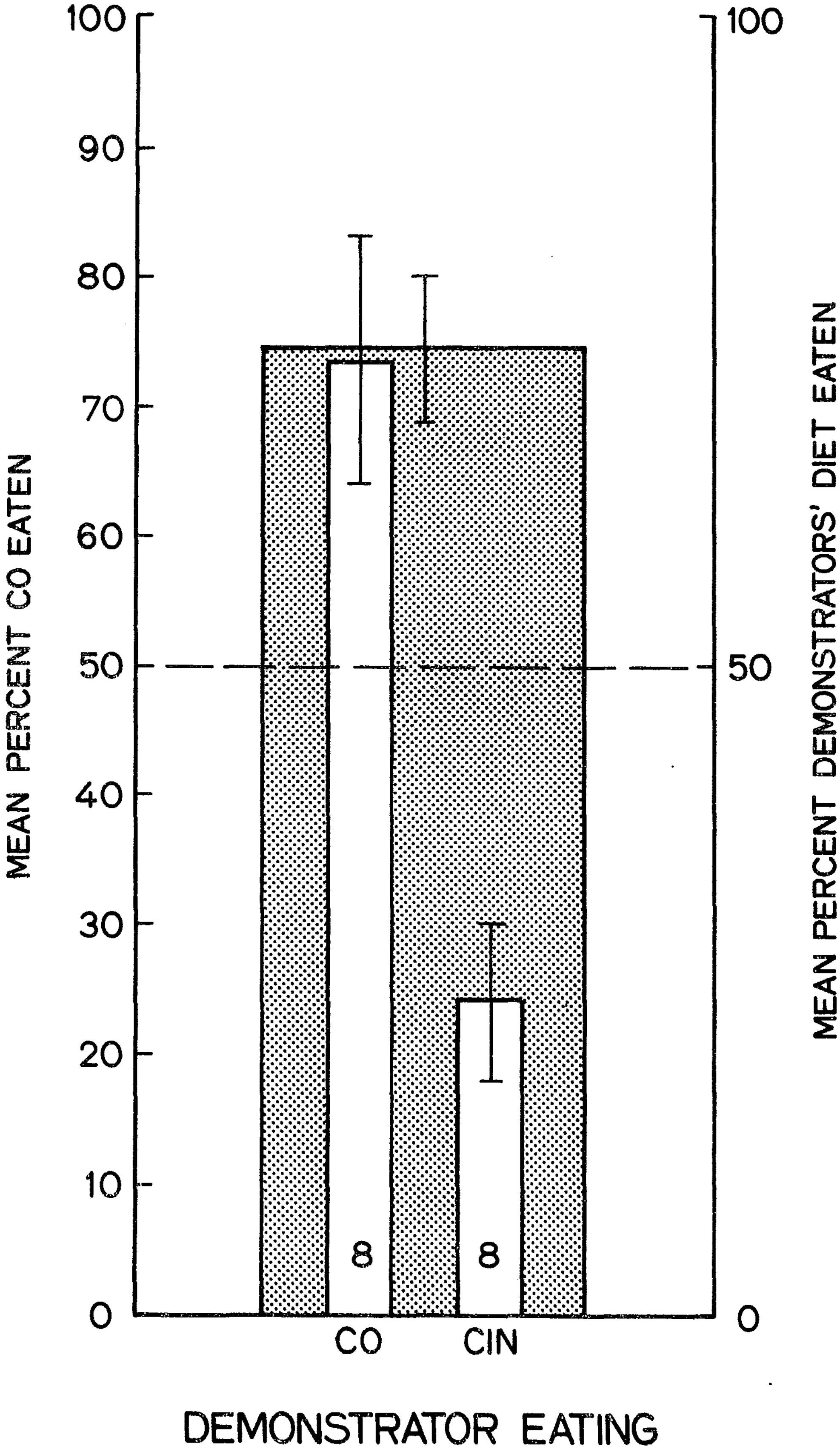
Observers were also divided into two groups: those paired with demonstrators that ate cocoa-flavoured chow and those paired with demonstrators that ate cinnamon-flavoured chow. Mean percent preference for cocoa-flavoured chow was calculated for both groups and the two means were compared to determine whether observers whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers whose demonstrators ate cinnamon-flavoured chow.

Results and Discussion

The results of Experiment 2 are presented in Figure 4. Observers whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers whose demonstrators ate cinnamon-flavoured chow (Mann Whitney U Test, $U = 4$, $p = .002$). Mean "percent demonstrators' diet eaten" was also significantly greater than 50 percent (Sign Test, $x = 3$, $p = .002$). Interaction at the home cage with a familiar demonstrator that had recently ingested a distant novel food, facilitated its observer's acceptance of that food. Information transmitted by demonstrators during Step D, was sufficient to permit their respective observers to exhibit a preference for the food that their demonstrators had eaten during Step C.

Figure 4: Experiment 2

The stippled bar indicates the mean percentage of observers' total food intake that was the same flavour as the food that their demonstrators ate. Open bars indicate the mean percentage of observers' total food intake that comprised cocoa-flavoured chow, for observers whose demonstrators ate either cocoa-or cinnamon-flavoured chow. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.



100
90
80
70
60
50
40
30
20
10
0
MEAN PERCENT CO EATEN
100
50
0
MEAN PERCENT DEMONSTRATORS' DIET EATEN
8
8
CO
CIN
DEMONSTRATOR EATING

III PARADIGM MODIFICATION AND GENERALITY OF EFFECT

To analyze the means of information exchange, it was necessary to control the degree of interaction between observers and demonstrators in Step 4.

The modified paradigm allowing for control over the degree of interaction between demonstrators and observers is described below in General Procedure. The critial modification consisted of separating demonstrators and observers by screen dividers during the brief interaction period (Step 5, Figure 3). Although subject pairs could not interact fully across the dividers, spaces in the screen did allow for restricted physical contact.

Experiment 2 was replicated under the new paradigm using three different pairs of diets to determine whether information exchange was restricted to cocoa-and cinnamon-flavoured chow. If the burrow acts as a centre for information exchange regarding the stimulus properties of foods available in the environment, one would expect that rats could receive information regarding a wide range of different diets.

General Method

Subjects

Subjects were same-sex pairs of Long-Evans rats born in the McMaster colony to dams obtained from Canadian Breeding Farms, St. Constant, Quebec. Those designated as "observers" were six weeks old at the beginning of experimentation, and "demonstrators" ranged in age from six to twelve weeks. To control for litter effects, subjects were assigned to groups in a random fashion.

Apparatus

The apparatus described in Experiment 1 was used in the remainder of this study. Each cage was partitioned in half by 1.2 cm (1/2 in.) hardware-cloth screen, except where otherwise indicated.

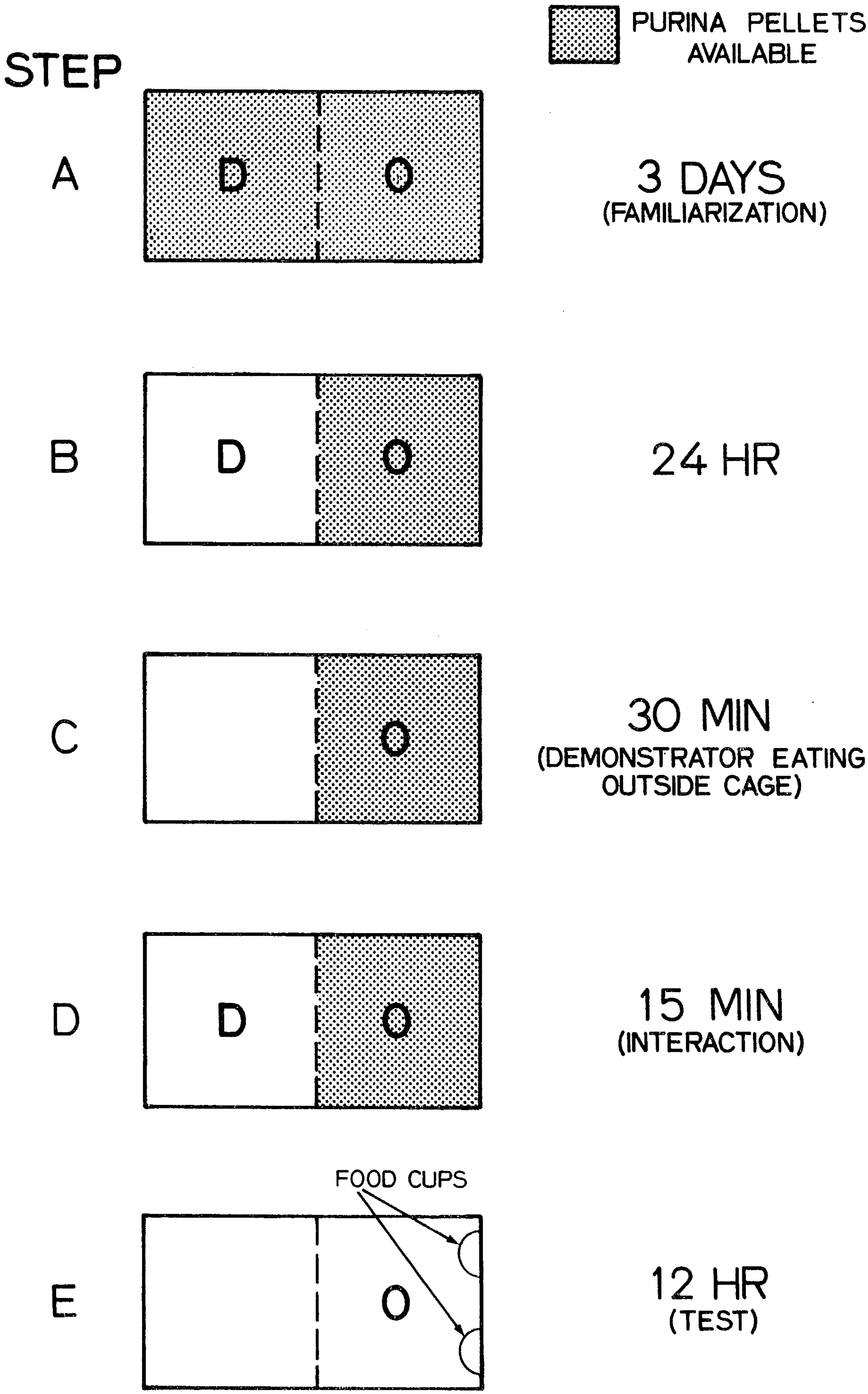
Procedure

Figure 5 provides a schematic of the General Procedure. Pairs of demonstrators and observers occupied opposite sides of each divided cage for three days. During this time both received *ad lib* access to Purina Laboratory Chow pellets and water (Step A). Food pellets were removed from demonstrators' cages on the evening of the third day (Step B). Twenty-four hr. later, demonstrators were allowed 1/2 hr. access to a novel diet in individual transparent plastic cages (35 x 30 x 15 cm) located in a room separate from the test room (Step C). Demonstrators were observed during the access period and those that did not eat were excluded from the experiment.

After feeding, each demonstrator was returned to the side of the divided cage opposite to its observer and each pair was allowed to interact for 15 min. (Step D). Demonstrators and food pellets were then removed from the cages and two weighed food cups, one containing the novel diet the demonstrator had consumed and the other containing

Figure 5

A schematic of the General
Procedure showing a top view
of the divided cages.


PURINA PELLETS AVAILABLE
STEP
A
D
O
3 DAYS
(FAMILIARIZATION)
B
D
O
24 HR
C
O
30 MIN
(DEMONSTRATOR EATING OUTSIDE CAGE)
D
D
O
15 MIN
(INTERACTION)
FOOD CUPS
E
O
12 HR
(TEST)

a second novel diet, were placed in observers' cages for 12 hr. (step E). The next morning the food cups were removed from the cages and weighed to determine the amount of each food each observer had consumed.

Data Treatment

The data were treated in the same fashion as in Experiment 2. "Percent demonstrators' diet eaten" was calculated by dividing the amount of food that each observer had consumed that was the same flavour as the food its demonstrator had eaten by the total amount of both foods consumed.

Within each experiment, observers were divided into two groups: those paired with demonstrators that ate Diet A (for example) and those paired with demonstrators that ate Diet B (for example). Mean percent preference for Diet A was calculated for both groups and the two means were compared to determine whether observers whose demonstrators ate Diet A consumed significantly more Diet A than did observers whose demonstrators ate Diet B.

EXPERIMENT 3

Experiment 3 consisted of three separate studies all of which followed the General Procedure. Each study examined observers' ability to receive information concerning two different diets.

Method

Study A

Subjects

Subjects were 16 pairs of Long-Evans rats.

Procedure

Half of the demonstrators in Study A ate cocoa-flavoured chow during Step C of the General Procedure (Figure 5) and the other half ate cinnamon-flavoured chow. Note that these two diets consisted of a familiar food with added novel flavouring. Observers were offered a choice between cocoa- and cinnamon-flavoured chow in Step E.

Study B

Subjects

Subjects were 18 pairs of Long-Evans rats.

Procedure

Half of the demonstrators in Study B ate powdered Purina Laboratory Chow, a familiar food, during Step C of the General Procedure. The remaining demonstrators ate Normal Protein Test Diet (Teklad Mills, Madison Wisconsin) plus four percent granulated sugar (referred to below as Diet NPT), a novel food. Observers were offered a choice between these two foods in Step E.

Study C

Subjects

Subjects were 16 pairs of Long-Evans rats.

Procedure

All demonstrators in Study C were both food and water deprived during Step B of the General Procedure. During Step C, half of the demonstrators had access to a coffee-flavoured solution (2.1 percent by weight Sanka Decaffeinated Instant Coffee) and the other half had access to a vinegar-flavoured solution (3.2 percent by volume Allen's Pure Apple Cider Vinegar).

Observers were offered a choice between a coffee-flavoured mash (235 ml. tap water plus 4 percent by weight Sanka Decaffeinated Instant Coffee mixed with 200g of Five Roses White Enriched Flour) and a vinegar-flavoured mash (235 ml. tap water plus 6 percent by volume Allen's Pure Apple Cider Vinegar mixed with 200g of Five Roses White Enriched Flour) which were prepared immediately prior to Step C of the General Procedure. Note that these two mashes were both totally novel foods.

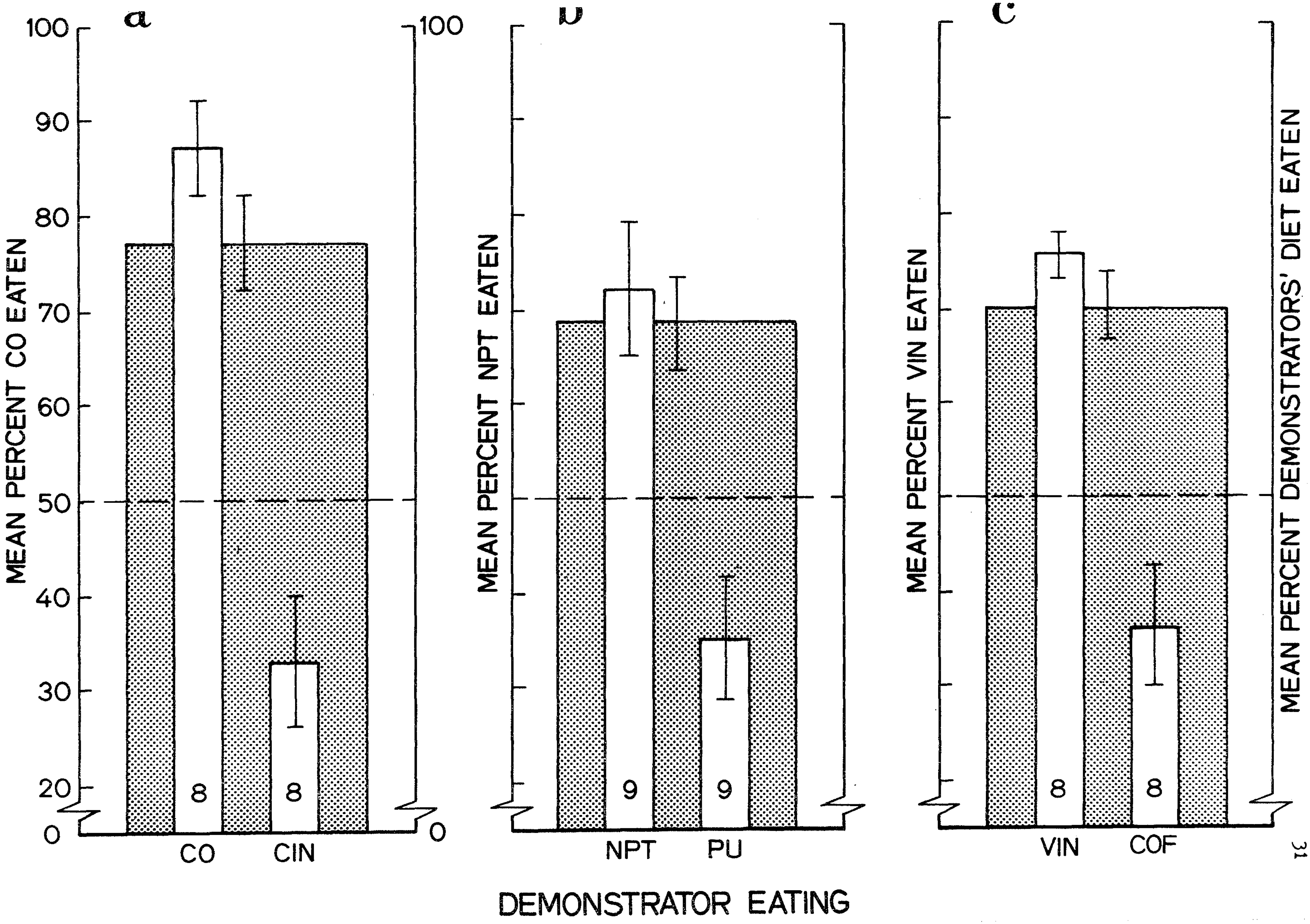
To control for evaporation of these mashes during Step E of the General Procedure, six weighed food cups, half containing coffee-flavoured mash and half containing vinegar-flavoured mash, were placed in empty cages located in the same room as the apparatus. These food cups, used to control for evaporation, were weighed 12 hr. later and the mean amount of evaporation was calculated. This quantity was subtracted from the amount of each food each observer had consumed.

Results and Discussion

The results of Experiment 3 are presented in Figure 6. Observers in Study A whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers

Figure 6: Experiment 3

Stippled bars indicate the mean percentage of observers' total food intake that was the same flavour as the food (or solution) that their demonstrators consumed. Open bars indicate the mean percentage of observers' total food intake that comprised a) Co = cocoa-flavoured chow, b) NPT = Normal Protein Test Diet (Teklad Mills, Wisconsin) plus four percent granulated sugar, c) Vin = vinegar-flavoured mash, for observers whose demonstrators consumed a) Co or Cin = cinnamon-flavoured chow, b) NPT or Pu = powdered Purina Laboratory Chow, c) Vin = vinegar-flavoured solution or Cof = coffee-flavoured solution. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.


a
b
c
MEAN PERCENT CO EATEN
MEAN PERCENT NPT EATEN
MEAN PERCENT VIN EATEN
MEAN PERCENT DEMONSTRATORS' DIET EATEN
100
90
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70
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20
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8
9
CO
CIN
NPT
PU
VIN
COF
DEMONSTRATOR EATING

whose demonstrators ate cinnamon-flavoured chow (Mann Whitney U Test, $U = p < .001$) and mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, $x = 2$, $p = .004$). These data indicate that separation of observers and demonstrators by hardware-cloth screen during Step D does not interfere with information exchange.

Observers in Study B whose demonstrators ate Diet NPT consumed significantly more Diet NPT than did observers whose demonstrators ate powdered Purina Laboratory Chow (Mann Whitney U Test, $U = 4$, $p < .002$) and mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, $x = 3$, $p = .008$). Therefore, interaction with demonstrators that had recently consumed Diet NPT facilitated observers' acceptance of this novel food.

Observers in Study C whose demonstrators drank vinegar-flavoured solution consumed significantly more vinegar-flavoured mash than did observers whose demonstrators drank coffee-flavoured solution (Mann Whitney U Test, $U = 0$, $p < .001$) and mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, $x = 2$, $p = .004$). Even though these demonstrators did not consume exactly the same substances as were offered to their observers in Step E, the observers exhibited a preference for the food similar in odour and flavour to the solution that their demonstrators drank.

The results of Experiment 3 demonstrate that observer rats are able to receive information regarding a range of different diets including familiar dry food with added novel flavouring, novel dry food and novel food in paste form. Furthermore, separation of observers and demonstrators by hardware-cloth screen during Step D did not interfere with information exchange. The following series of experiments was designed to analyze the means by which information is transferred between demonstrators and observers.

IV ANALYSIS

To analyze the mode of information exchange, the following series of experiments was designed in which the degree of interaction between demonstrators and observers was degraded during Step D of the General Procedure (Figure 5).

It was suspected that information transfer is mediated by either olfactory or gustatory cues, because observers in Experiment 3 (Study C) preferentially ingested the food similar in odour and flavour to the solution consumed by their demonstrators. However, it is also possible that information exchange is mediated by visual cues. Experiment 4 investigated this possibility.

EXPERIMENT 4

Experiment 4 addressed the possibility that information exchange was mediated by visual cues. Pairs of observers and demonstrators could see each other, but the opportunity for communication regarding the smell and taste of the food demonstrators had consumed during Step C (Figure 5) was blocked. If observers nevertheless exhibited a preference for the food that their demonstrators ate, one could infer that information exchange might me mediated by visual cues.

Method

Subjects

Subjects were Long-Evans rats randomly assigned to one of two groups of 16 pairs each. Subjects assigned to Group S occupied cages divided in half by hardware-cloth screens. Subjects assigned to Group P occupied cages divided in half by transparent plastic (Plexiglas).

Apparatus

The apparatus described under General Method was used, except that transparent plastic (Plexiglas) partitions were installed in half of the cages.

Procedure

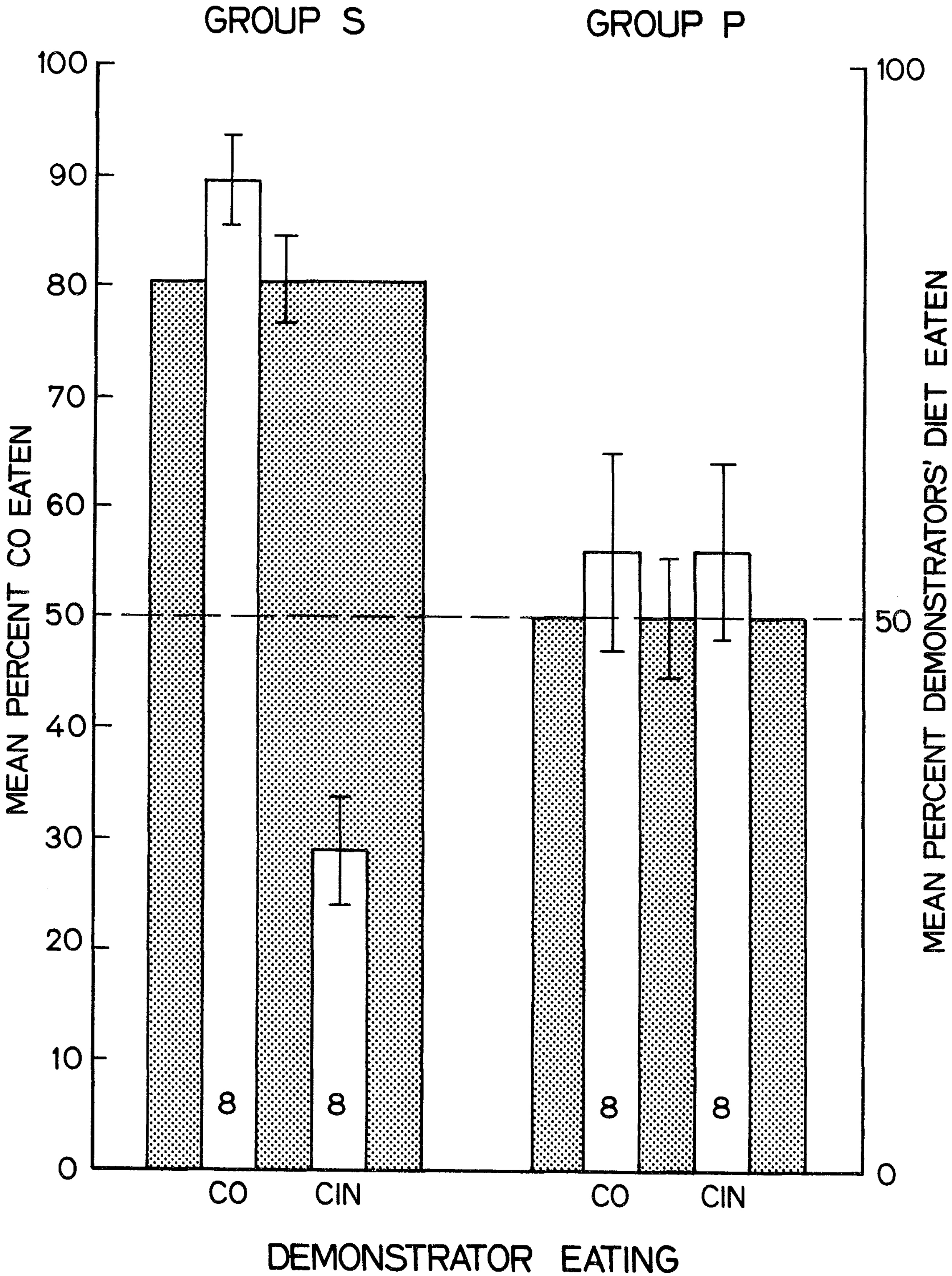
The General Procedure was followed for pairs of subjects assigned to Group S. Throughout the experiment, pairs of subjects assigned to Group P occupied cages divided in half by transparent plastic, but were otherwise treated identically to subjects in Group S. Half of the demonstrators in each group ate cinnamon-flavoured chow during Step C and the other half ate cocoa-flavoured chow.

Results and Discussion

The results of Experiment 4 are presented in Figure 7. Observers in Group S whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers in Group S whose demonstrators ate cinnamon-flavoured chow (Mann Whitney $\underline{U}$ Test, $\underline{U} = 0$, $\underline{p} < .001$). Mean "percent demonstrators' diet eaten" calculated for Group S was significantly greater than 50 percent (Sign Test, $\underline{x} = 1$, $\underline{p} < .001$). These data replicated the effect demonstrated in Experiment 3 and indicate that observers' food choices were affected by brief interaction with their demonstrators across screen cage-dividers.

Figure 7: Experiment 4

Stippled bars indicate the mean percentage of observers' total food intake that was the same flavour as the food that their demonstrators ate. Open bars indicate the mean percentage of observers' total food intake that comprised cocoa-flavoured chow, for observers whose demonstrators ate either cocoa- or cinnamon-flavoured chow. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.


GROUP S
GROUP P
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10
0
MEAN PERCENT CO EATEN
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MEAN PERCENT DEMONSTRATORS' DIET EATEN
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CO
CIN
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CIN
DEMONSTRATOR EATING

Observers in Group P whose demonstrators ate cocoa-flavoured chow did not consume significantly more cocoa-flavoured chow than did observers in Group P whose demonstrators ate cinnamon-flavoured chow (Mann Whitney U Test, $U = 30$, $p > 0.4$). Mean "percent demonstrators' diet eaten" calculated for Group P did not differ significantly from 50 percent (Sign Test, $x = 9$, $p > 0.7$). These data indicate that the food choices of observers in Group P were unaffected by interaction with their demonstrators during Step D. Transparent plastic cage-dividers served to block transmission of information regarding the food that demonstrators in Group P had consumed, indicating that information exchange was not mediated by visual cues.

EXPERIMENT 5

Physical contact between demonstrators and observers would be necessary if information exchange was mediated by gustatory cues in a demonstrator rat's saliva or on its fur. However, if information transfer was mediated by olfactory cues, one would expect observers to receive the relevant message even if physical contact with their respective demonstrators was blocked. Consequently, Experiment 5 was designed to prevent physical contact between observers and demonstrators during Step D of the General Procedure (Figure 5).

Method

Subjects

Subjects were Long-Evans rats randomly assigned to either

Experimental or Control Groups. Each group consisted of 20 pairs of subjects.

Apparatus

The apparatus described under General Method was used.

Procedure

The General Procedure was adhered to except for the following changes. Immediately after Step C, each demonstrator in the Experimental Group was anesthetized by intraperitoneal injection of Equithesin (2.2 ml/kg) and draped across the bottom of an inverted 100 x 50mm glass dish (Pyrex) to which it was attached with a single strip of masking tape that ran across the rat's dorsal surface. During Step D, each demonstrator in the Experimental Group was positioned so that its nose was 1.5 cm from the screen cage-divider on the side opposite to its observer. Therefore, observers could sniff at their respective demonstrators, but could not make physical contact with them.

Each demonstrator assigned to the Control Group was administered an intraperitoneal injection of physiological saline (2.2 ml/kg) immediately following Step C to control for any effects of injection on the reaction of an observer in the Experimental Group to its demonstrator.

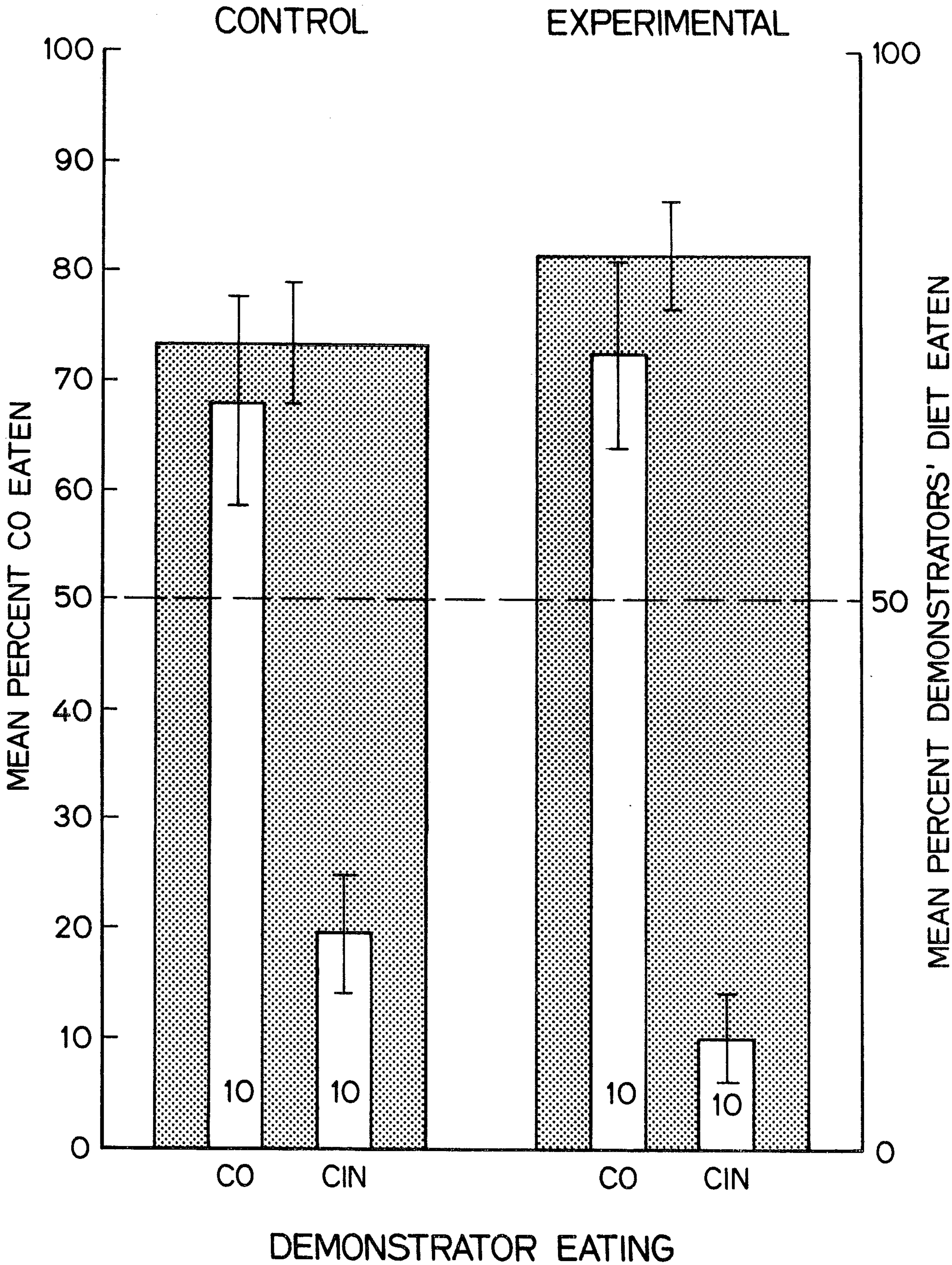
Half of the demonstrators in both the Experimental and Control Groups ate cocoa-flavoured chow during Step C, and the other half ate cinnamon-flavoured chow.

Results and Discussion

The results of Experiment 5 are presented in Figure 8.

Figure 8: Experiment 5

Stippled bars indicate the mean percentage of observers' total food intake that was the same flavour as the food that their demonstrators ate. Open bars indicate the mean percentage of observers' total food intake that comprised cocoa-flavoured chow, for observers whose demonstrators ate either cocoa- or cinnamon-flavoured chow. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.


CONTROL
EXPERIMENTAL
100
90
80
70
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50
40
30
20
10
0
MEAN PERCENT CO EATEN
MEAN PERCENT DEMONSTRATORS' DIET EATEN
100
50
0
10
10
10
10
CO
CIN
CO
CIN
DEMONSTRATOR EATING

Observers in the Control Group whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers in the Control Group whose demonstrators ate cinnamon-flavoured chow (Mann Whitney U Test, $U = 13$, $p < .02$). Mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, $x = 2$, $p < .001$). Therefore, saline injections administered to demonstrators in the Control Group did not disrupt information exchange during Step D.

Observers in the Experimental Group whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers in the Experimental Group whose demonstrators ate cinnamon-flavoured chow (Mann Whitney U Test, $U = 8$, $p < .002$). Mean "percent demonstrators' diet eaten" calculated for the Experimental Group was significantly greater than 50 percent (Sign Test, $x = 2$, $p < .001$). Information transfer was not disrupted even though physical contact between demonstrators and observers was blocked during Step D, indicating that the message transmitted by demonstrators travelled through air. This result suggests that information exchange is mediated by olfactory cues.

Some authors have suggested that active communication regarding feeding success is an essential prerequisite to information centre functioning (Ward and Zahavi, 1973; Erwin, 1977). However, observers in the Experimental Group received information concerning the food that their demonstrators ate during Step C, even though the latter were anesthetized during Step D. Therefore, information exchange among rats can be a passive process during which demonstrators need not actively advertise their feeding success, but instead transmit the relevant information inadvertantly.

V OLFACTORY COMMUNICATION

The following series of experiments was designed to determine whether transmission of olfactory cues is necessary to permit information exchange between demonstrators and observers.

EXPERIMENT 6

If information exchange is mediated solely by olfactory cues, one would expect anosmic observer rats to be incapable of receiving information transmitted by their demonstrators. Consequently, Experiment 6 investigated whether anosmic observers would exhibit a preference for the food that their demonstrators ate during Step C of the General Procedure.

Method

Subjects

Subjects were Long-Evans rats randomly assigned to either the Experimental or Control Group consisting of 18 pairs each.

Apparatus

The apparatus described under General Method was used.

Procedure

The General Procedure (see Figure 5) was adhered to except for the following changes. On the afternoon of the third day of the General Procedure (Step A), observers in the Experimental Group were rendered anosmic. The treatment procedure, developed by Alberts and Galef (1971), consisted of running the bent tip of a catheter into the mouth along the hard palate of an etherized subject until the rounded apex was felt to enter the esophagus at the caudal end. The catheter was then retracted so that the tip entered the nasal cavity via the posterior choanae located behind and above the palate. Zinc sulfate solution (5 percent wt/vol) was then injected until 8 drops drained out the external nares. The rat's mouth was aspirated to remove excess solution and the rat was held head down to facilitate drainage from the nares until recovery from anesthesia.

Observers in the Control Group received the same treatment as observers in the Experimental Group except that physiological saline was substituted for zinc sulfate.

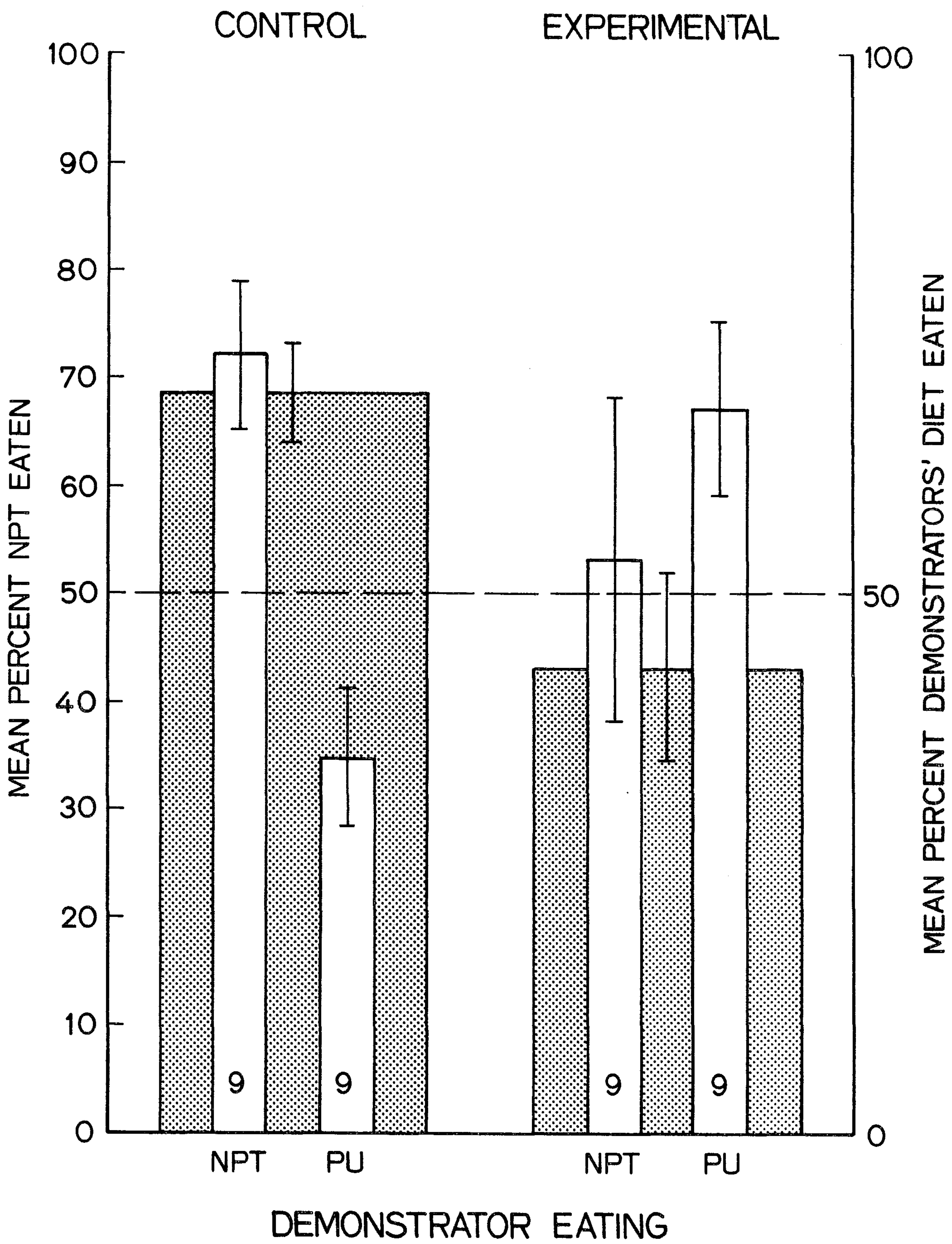
Half of the demonstrators in each group ate Normal Protein Test Diet (Teklad Mills, Madison Wisconsin) plus four percent granulated sugar (referred to below as Diet NPT) and the other half ate powdered Purina Laboratory Chow.

Results and Discussion

The results of Experiment 6 are presented in Figure 9. Observers in the Control Group whose demonstrators ate Diet NPT consumed significantly more Diet NPT than did observers in the Control Group whose demonstrators ate powdered Purina Laboratory Chow (Mann Whitney $\underline{U}$ Test, $\underline{U} = 4$, $\underline{p} < .002$). Mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, $\underline{x} = 3$, $\underline{p} = .008$). Treatment with physiological saline did not interfere with information exchange between demonstrators and observers during Step D.

Figure 9: Experiment 6

Stippled bars indicate the mean percentage of observers total food intake that was the same flavour as the food that their demonstrators ate. Open bars indicate the mean percentage of observers' total food intake that comprised Diet NPT, for observers whose demonstrators ate either Diet NPT or powdered Purina Laboratory Chow. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.



CONTROL
EXPERIMENTAL
MEAN PERCENT NPT EATEN
MEAN PERCENT DEMONSTRATORS' DIET EATEN
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100
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NPT
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DEMONSTRATOR EATING

Observers in the Experimental Group whose demonstrators ate Diet NPT did not consume significantly more Diet NPT than did observers in the Experimental Group whose demonstrators ate powdered Purina Laboratory Chow (Mann Whitney U Test, $U = 35$, $p > 0.1$). Mean "percent demonstrators' diet eaten" was not significantly different from 50 percent (Sign Test, $x = 10$, $p > 0.6$). These results suggest that anosmic observers are incapable of receiving information regarding the food that their demonstrators ate during Step C.

If, however, anosmic observers were unable to discriminate between the flavours of Diet NPT and powdered Purina Laboratory Chow, one could argue that these subjects had received the message during Step D but were unable to distinguish between the two foods during Step E. Experiment 7 addressed this possibility.

EXPERIMENT 7

Experiment 7 investigated whether anosmic rats could discriminate between the flavours of Diet NPT and powdered Purina Laboratory Chow.

Method

Subjects

Subjects were six week old Long-Evans rats individually housed in hanging cages (42 x 18 x 24 cm). They were randomly assigned to either the Experimental or Control Group, consisting of six subjects each.

Procedure

At noon on Day 1 of experimentation, subjects in the Experimental Group were rendered anosmic (Alberts and Galef, 1971). Subjects in the

Control Group received this same treatment procedure, except that physiological saline was substituted for zinc sulfate. All subjects were then returned to their home cages and allowed 6 hr. access to Purina Laboratory Chow pellets and water. Food pellets were then removed from subjects' cages and 18 hr. later, on Day 2 of experimentation, each subject was allowed 1 hr. access to Diet NPT in its home cage. Food cups containing Diet NPT were weighed before and after the access period and each subject ate at least 2.5 g. of the food. Immediately following consumption of Diet NPT, all subjects were administered an intraperitoneal injection of lithium chloride (10 ml/kg of 2 percent lithium chloride weight/volume solution) causing them gastrointestinal upset (Lavin, Freise and Coombes, 1980).

Following poisoning, subjects were deprived of food until the morning of Day 3, 20 hr. later. At this time two weighed food cups, one containing Diet NPT and the other containing powdered Purina Laboratory Chow, were placed in each subject's cage. The position of the food cups was balanced so that each flavour occurred equally often in the front and rear of the cages. Food cups were removed from subjects' cages and weighed after 3 hr. to determine the amount of each food each subject had consumed, and placed back into the cages in the reverse position where they remained for 4 hr. before being weighed again. The position of each subject's food cups was reversed to determine whether food preferences exhibited during the first 3 hr. were for the position of a food cup rather than the diet it contained.

Rats use taste cues in learning to avoid a novel flavour (CS) that has been paired with poison-induced illness (US) (Garcia and Koelling, 1966). Therefore, if anosmic rats were able to discriminate between the flavours of Diet NPT and powdered Purina Laboratory Chow, one would expect subjects in the Experimental Group to display an aversion to Diet NPT during preference testing.

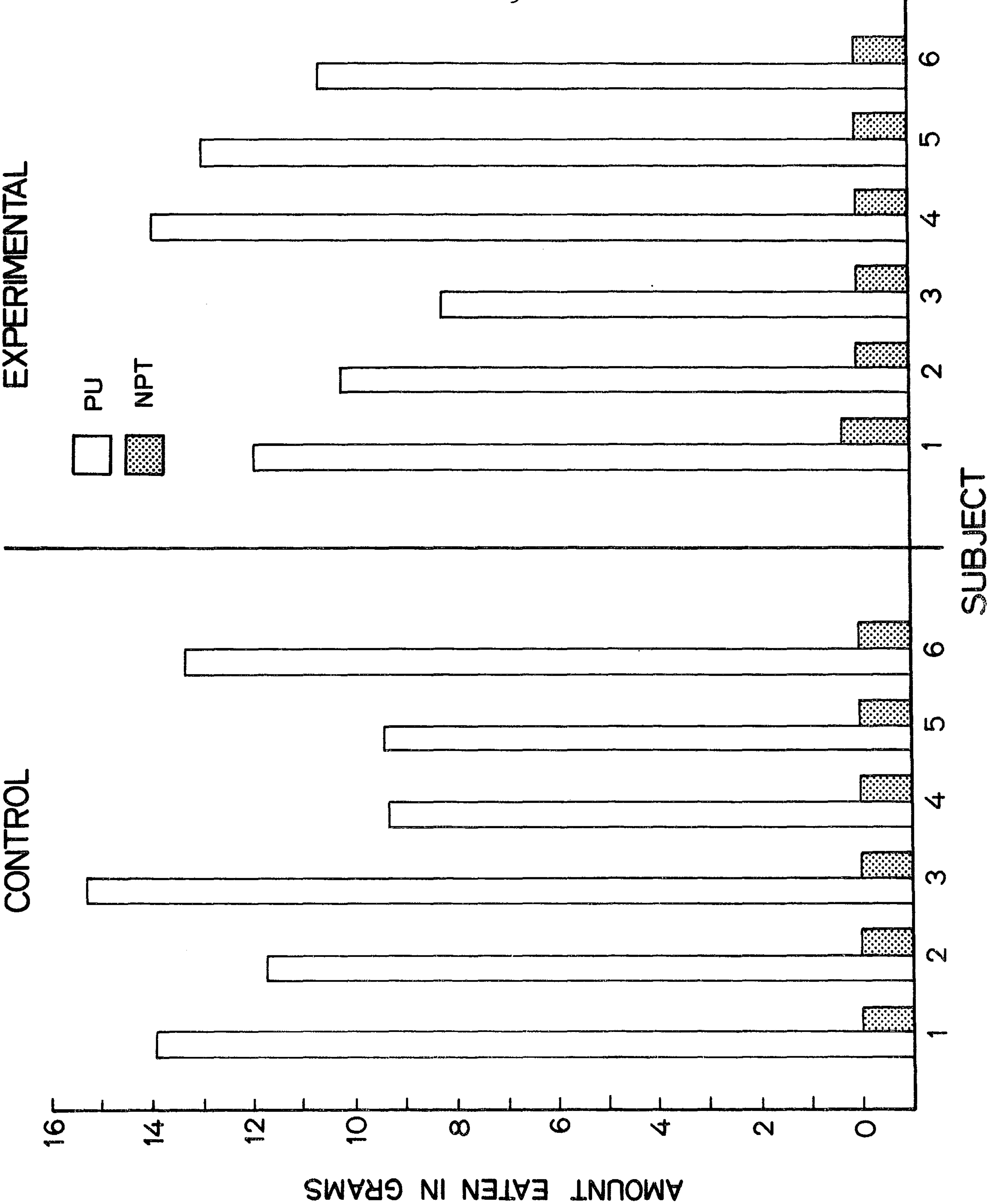
Results and Discussion

The results of Experiment 7 are presented in Figure 10. All subjects in both the Experimental and Control Groups ate very little or none of Diet NPT during preference testing, regardless of which side of the cage the food cup containing Diet NPT was placed. Furthermore, as can be seen in Figure 10, each subject ate at least 8 grams of powdered Purina Laboratory Chow, indicating that their appetities had recovered following lithium chloride poisoning. Avoidance of Diet NPT by subjects in the Experimental Group demonstrates that anosmic rats can discriminate between the flavours of Diet NPT and powdered Purina Laboratory Chow.

The results of Experiment 7 indicate that anosmic observers in Experiment 6 could discriminate between the flavours of Diet NPT and powdered Purina Laboratory Chow during Step E. Because anosmic observers in Experiment 6 did not exhibit a preference for the food that their demonstrators ate, one can conclude that these observers were incapable of receiving the message transmitted by their demonstrators. Transmission of olfactory cues is necessary to permit rats to exchange information at a central site regarding a distant food.

Figure 10: Experiment 7

Stippled bars indicate the amount of Diet NPT eaten by each subject and open bars indicate the amount of powdered Purina Laboratory Chow eaten by each subject.


CONTROL
EXPERIMENTAL
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NPT
AMOUNT EATEN IN GRAMS
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VI SOCIAL TRANSMISSION OF POISON AVOIDANCE

If an unpoisoned rat drinks a novel flavoured solution and is subsequently exposed to another familiar rat suffering from lithium chloride poisoning, the unpoisoned rat will display an aversion to the solution (Lavin, Freise and Coombes, 1980). The unpoisoned rat associates the novel flavour (CS) with the illness-induced cues of its sick partner (US).

Perhaps an observer rat, exposed to a poisoned demonstrator, would associate olfactory cues regarding the food its demonstrator had eaten with the demonstrator's illness, and consequently avoid this food. Such a mechanism in nature would seem adaptive. Receiving information from a conspecific at the burrow regarding both the odour of a distant toxic food and the negative consequences of ingesting it, would decrease the probability of a naive wild rat consuming this toxic food.

EXPERIMENT 8

Experiment 8 investigated whether an observer rat, exposed to a poisoned demonstrator that had recently ingested a novel food outside the home cage, would display an aversion to the food its demonstrator had eaten.

Method

Subjects

Subjects were Long-Evans rats randomly assigned to either the Experimental or Control Group. Each group comprised 12 pairs of subjects each.

Apparatus

The apparatus described under General Method was used.

Procedure

The procedure described in Experiment 2 (see Figure 3) was adhered to except for the following changes. Immediately after Step C, demonstrators in the Experimental Group were administered intraperitoneal injections of lithium chloride (10 ml/kg or 2 percent lithium chloride weight/volume solution), and demonstrators in the Control Group were administered intraperitoneal injections of physiological saline (10 ml/kg). Pairs of demonstrators and observers in both the Experimental and Control Groups were allowed to interact for 30 min. during Step D.

Half of the demonstrators in each group ate cinnamon-flavoured chow during Step C and the other half ate cocoa-flavoured chow.

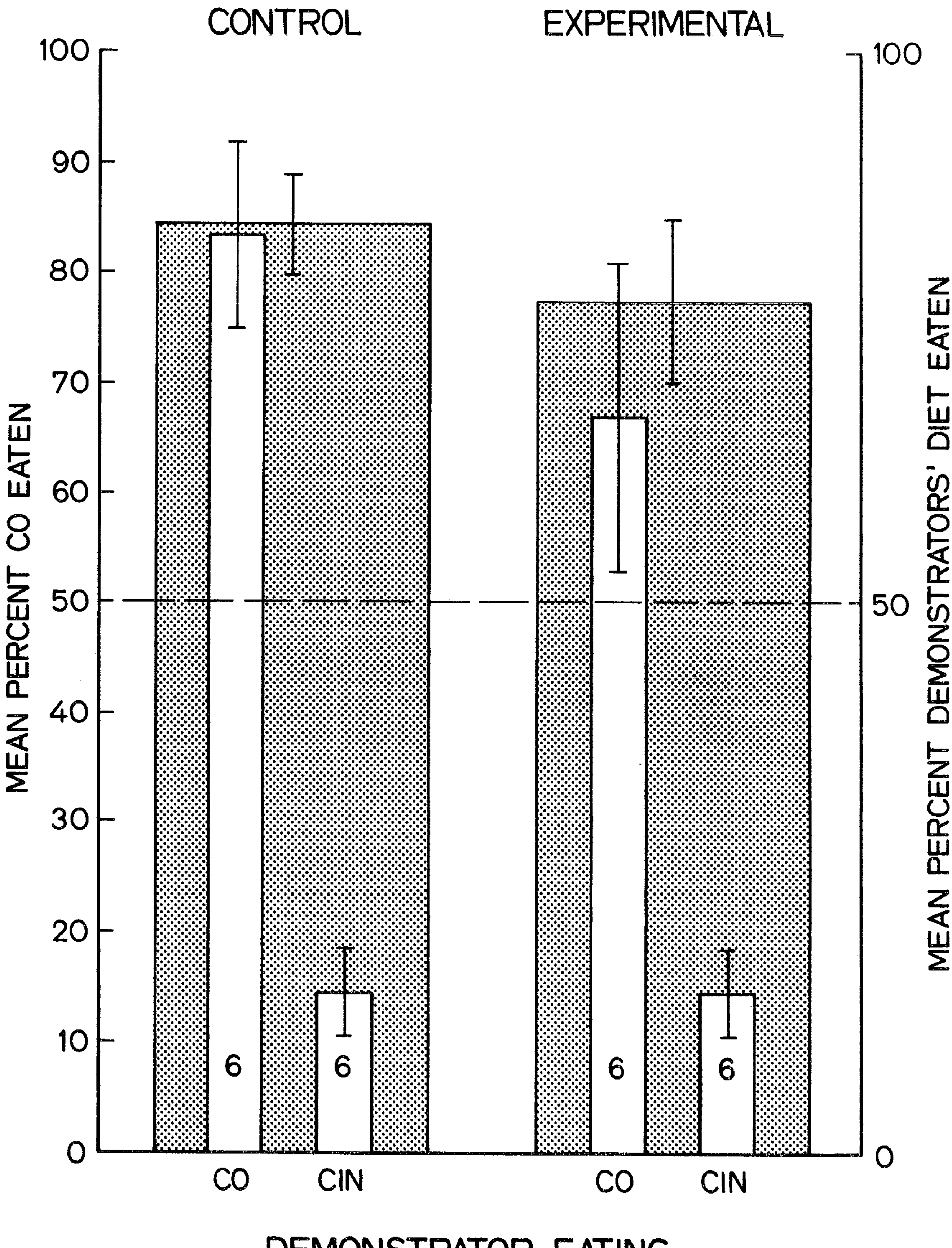
Results and Discussion

The results of Experiment 8 are presented in Figure 11. Observers in the Control Group whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers in the Control Group whose demonstrators ate cinnamon-flavoured chow (Mann Whitney $\underline{U}$ Test, $\underline{U} = 0$, $\underline{p} = .002$). Mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, $\underline{x} = 0$, $\underline{p} < .001$). Information transfer was demonstrated between observers and demonstrators in the Control Group.

Observers in the Experimental Group also exhibited a strong preference for the food that their demonstrators ate during Step C.

Figure 11: Experiment 8

Stippled bars indicate the mean percentage of observers' total food intake that was the same flavour as the food that their demonstrators ate. Open bars indicate the mean percentage of observers' total food intake that comprised cocoa-flavoured chow, for observers whose demonstrators ate either cocoa- or cinnamon-flavoured chow. Numbers on open bars indicate the number of pairs of subjects in the group. Flags indicate ± 1 S.E.M.



CONTROL
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MEAN PERCENT CO EATEN
MEAN PERCENT DEMONSTRATORS' DIET EATEN
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100
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CIN
DEMONSTRATOR EATING

Observers in the Experimental Group whose demonstrators ate cocoa-flavoured chow consumed significantly more cocoa-flavoured chow than did observers in the Experimental Group whose demonstrators ate cinnamon-flavoured chow (Mann Whitney $\underline{U}$ Test, $\underline{U} = 2$, $\underline{p} = .008$). Mean "percent demonstrators' diet eaten" was significantly greater than 50 percent (Sign Test, $\underline{x} = 2$, $\underline{p} < .04$). Preferences exhibited by observers in the Experimental Group for the food that their sick demonstrators had eaten, indicated that olfactory cues regarding the food were received by observers. However, they apparently did not associate these cues with their demonstrators' illness.

In the general poison avoidance literature, Hankins, Garcia and Rusiniak (1973) reported that rats readily form aversions to a novel taste that is followed hours later by illness, but that odour does not become aversive unless it is followed by illness immediately and repeatedly. Perhaps following repeated exposure to their sick demonstrators, observers might have displayed aversions to the food that their sick demonstrators had eaten.

GENERAL DISCUSSION

The present research investigated whether information concerning distant foods could be exchanged by domestic rats at a central site. Information transfer was demonstrated, as "observers" exhibited a preference for a novel food following brief interaction at the home cage with "demonstrators" that had recently ingested this food at a distant location. To permit development of this preference, transmission of olfactory cues concerning the food is necessary, but active communication regarding the demonstrator's feeding success is not.

The mechanism of olfactory communication could allow wild rats to use the burrow as an information centre. Experimental results reported here suggest that colony members could assess each others' feeding success simply by receiving olfactory cues transmitted inadvertantly by those that have recently eaten. Consequently, interaction at the burrow with a forager that had recently ingested a novel food could serve to facilitate less exploratory conspecifics' acceptance of this food. The results of Experiment 8 suggest that interaction with a sick forager might also facilitate a naive conspecific's acceptance of a toxic food. However, following repeated exposure to sick foragers that had consumed this food, or perhaps a period of interaction longer than thirty minutes, socially transmitted food aversions might have resulted.

If wild rats living in a patchy environment are able to learn the olfactory landscape of their ecological niche, and associate food odours with the particular locations in which these foods are intermittently found, olfactory communication at the burrow could also serve to signal replenishment of a previously available food source.

Determination of whether wild rats actually use the burrow as an information centre would require a field study that is beyond the scope of this thesis.

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