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Long-term reaction of the rat to conspecific (frustration) odor

H. WAYNE LUDVIGSON
Texas Christian University, Fort Worth, Texas 76129

RICK R. McNEESE
Sam Houston State University, Huntsville, Texas 77340

and

IRA COLLERAIN
San Antonio State School, San Antonio, Texas 78223

Rats' choices in a T-maze were observed to determine (a) their long-term tendencies, in the apparent absence of reinforcement, to approach or avoid a goalbox containing a "frustration odor" stimulus generated by prior placements into the box of other rats given frustrative nonreward, and (b) the extent to which preferences for one or the other goalbox persisted following cessation of odor placements. The initial response to frustration odor was avoidance, though it took a few trials to develop. Avoidance was short-lived for most subjects, diminishing quickly and turning to a stable approach reaction, although three subjects developed an equally stable avoidance. These changes in response direction appeared to result from altered perception or interpretation of the odor rather than changed responsivity or alterations in the odor product itself. Preferences for one or the other of the goalboxes per se were but little affected by experiencing odor there.

In 1966, McHose and Ludvigson, and Spear and Spitzner independently reported observations suggesting that the odor emissions of laboratory rats when "frustrated" may differ from their emissions when not frustrated. By now, quite a number of studies have supported the conclusion that differential treatments involving reward and nonreward yield differential odor emissions, though the question of which treatment(s) produce(s) distinctive odor emissions has often not been addressed (Amsel, Hug, & Surridge, 1969; Bloom & Phillips, 1973; Howard & McHose, 1974; Ludvigson, 1969; Ludvigson & Sytsma, 1967; McHose, 1967; Pitt, Davis, & Brown, 1973; Prytula & Davis, 1974; Seago, Ludvigson, & Remley, 1970). The studies that have addressed the latter question permit the conclusions that the rat emits a distinctive odor at least as a function of nonreward or extinction training (Collerain, 1978; Collerain & Ludvigson, 1972, 1977; Mellgren, Fouts, & Martin, 1973; Morrison & Ludvigson, 1970), and that the odor emission probably covaries with an emotional response to frustrative nonreward (Collerain, 1978; Collerain & Ludvigson, 1977; Howard & McHose, 1974).

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The initial response, i.e., the apparently unconditioned or preexperimental response, to this "frustration odor" is such as to suggest that the odor may be "aversive" or "alarming." Thus, encountering the odor slows the speed of goal-directed locomotion (McHose & Ludvigson, 1966; Pratt & Ludvigson, 1970; Wasserman & Jensen, 1969), the odor tends to be avoided or withdrawn from in a T-maze (Collerain & Ludvigson, 1972), hurdle jumping which removes the animal from the odor is enhanced (Collerain, 1978; Collerain & Ludvigson, 1977), the speed of leaving a chamber containing the odor is relatively faster than that of approaching it (Mellgren, Fouts, & Martin, 1973), and the odor results in various reactions often taken as indices of fear (Cattarelli, Vernet-Maury, & Chanel, 1974). However, the term "neophobic" response might be apt in that the tendency to escape or withdraw from the odor appears short-lived, at least under conditions in which the odor signals no adverse events (Collerain & Ludvigson, 1977).

The present experiments were aimed at studying further the long-term reaction to the odor. It was of interest to learn whether the odor would simply lose all control of the response, whether continued experience would reveal eventual attraction or even a second avoidance, and whether intervening tests without the odor would cause a recurrence of the

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avoidance response. As a by-product of investigating such matters, these studies also explored the question of whether a spatial locus, once associated with frustration odor, continues to exert a residual influence on behavior. This question is also relevant to the general study of the adaptation of the rat to an environment in which odorous substances appear and disappear over time. Thus, do short-lived odorous substances produce only short-lived, stimulus-bound reactions, or do the reactions outlast the substances, and, if the latter, by how long?

METHOD

Subjects

Experiment 1 used 54 rats and Experiment 2 used 30 rats, all male albinos from the Holtzman Company. The former were 75 days of age on Day 1 of the study, while the latter were approximately 150 days of age on Day 1. All subjects were individually caged, had continuous access to water when not in the apparatus, and, beginning on Day 1, were fed approximately 11 g of Purina Lab Chow daily. Feeding occurred about the same time each day following the period during which experimental treatments were administered.

Apparatus

The apparatus, previously described (Morrison & Ludvigson, 1970), was a T-maze that permitted paper, which lined the internal walls and covered the floor, to be removed and replaced as a means of odor control. Two removable circular food cups were used as containers for 45-mg Noyes food pellets.

Procedure

Table 1 provides an overview of the successive treatments given the groups of subjects in the two experiments. The animals of both experiments were divided randomly into different groups. In each experiment, 18 subjects were designated odor-producing or "odorant" subjects. In Experiment 1, there were also three groups of "test" animals (12 subjects each), and in Experiment 2, there was one such group. For one group of subjects (Group 3

Table 1
Succession of Treatments

	Experiment 1					
		Test Groups			Experiment 2	
Phase	Odorant Ss	1	2	3	Odorant Ss	Test Ss
Preliminary	G & H P Hab (Days 6-7)		G & H Exp		G & H (Days 8-9) P Hab (Days 10-11)	G & H Exp (Days 8-9)
A	4 R & 4 N* (Days 8-10)		4 PPT** No-O		Exp† (Days 12-13)	4 PPT†† No-O (Days 10-13)
B	4 R & 6 N (4 days)	O on P	No-O		4 R & 6 N (7 days)	O on P
C	1 R (6 days)	No-O	No-O		1 R (3 days)	No-O
D	4 R & 6 N (7 days)	O on P	No-O		4 R & 6 N (27 days)	O on P
E	4 R & 6 N (13 days)	No-O	O on P		4 R & 6 N (5 days)	O on NP
F	4 R & 6 N (16 days)	O on P	No-O		1 R (5 days)	No-O
G	4 R & 6 N (9 days)	O on P			4 R & 6 N (3 days)	O on NP
H	4 R & 6 N (5 days)	O on NP		G & H Exp (2 days) 4 PPT No-O (3 days)		
I	4 R & 6 N (5 days)	No-O		O on P		
J	4 R & 6 N (6 days)	O on P in T_2				

*Note—R = rewarded trial, N = nonrewarded trial, G & H = gentling and handling, Exp = maze exploration, P Hab = pellet habituation, Ss = subjects, O on P = odor on preferred side, O on NP = odor on nonpreferred side, O on P in T_2 = odor on preferred side in altered test situation, No-O = no intended odor present (no entry in a column indicates no treatment given in that phase). *Number of R and N placements per day. **Number of position preference tests per day. †Exploration of baited goalboxes. ††Number of position preference tests per day except for Day 13, on which three were given.*

of Experiment 1), the treatment described herein did not begin until 61 days after it began for the other groups of Experiment 1.

Pretesting: Experiment 1. On each of the 2 days (Days 6-7, preliminary phase in Table 1) immediately prior to the beginning of the experiment proper, all subjects received 2 min of gentling and handling, during which they were placed upon and removed from a flat surface approximately 10 times. During each of these days the test animals were individually permitted 5 min of free exploration of the empty T-maze and the odorant subjects received 10 45-mg pellets in their home cage prior to their daily ration to acquaint them with the to-be-used reward.

On Days 8-10 (Phase A), odorant subjects received 24 placements (8 per day) into the goalboxes of the maze; these placements were rewarded and nonrewarded according to a double-alternation schedule that began with reward on the first 2 days and nonreward on the 3rd. Placements alternated from one goalbox of the maze to the other after every four placements. A rewarded placement, here and throughout both studies, consisted of 30 sec of access to a cup of 45-mg food pellets; similarly, a nonrewarded placement was 30 sec in an empty goalbox.

Following completion of placements of odorant subjects during these days, the test animals received four tests per day in a clean maze (clean paper on floor and walls) to determine their position preferences prior to the introduction of frustration odor. A test, here and throughout both studies, consisted of placing an animal into the startbox of the maze, opening the exit door after the subject oriented toward it, permitting the subject to traverse the maze and to enter one or the other goalbox, and confining the subject therein for 10 sec after the door was closed. An animal's position preference was defined as the side chosen more frequently over the preference testing days or, in a few cases of equal choice, the side toward which preference tended in the latter half of the test. Intertrial interval within a day was about 50 min for the two groups of test animals that began the study since they were rotated in one large squad in this phase.

Pretesting: Experiment 2. As in Experiment 1, all subjects received gentling and handling for 2 days (Days 8-9), the odorant animals received 2 days of pellet habituation (Days 10-11), and the test animals received 2 days of maze exploration in a preliminary phase (Days 8-9). Details of the procedures were identical to those of Experiment 1.

Test animals received preference tests on Days 10-13 (Phase A in Table 1), four per day, except for Day 13, on which three were given, with an intertrial interval within a day of about 24 min. Odorant subjects in Experiment 2 did not receive the eight placements per day during these days as in Experiment 1; instead, they received on each of Days 12-13 5 min of free exploration of the goalboxes, one on one day and the other on the next, with food pellets available.

Testing: Experiment 1. The study proper began on Day 11 (Phase B) in Experiment 1. Odorant subjects received four rewarded (R) and six nonrewarded (N) placements per day in the pattern RNNRRNNRNN for 2 days and then NNRNNRRNNR for 2 days, all of which was then repeated. This schedule held throughout both studies, except for phases in which frustration odor was not needed for tests (e.g., Phase C of Experiment 1), during which time odorant subjects received one rewarded placement per day. The particular goalbox(es) in which N placements were given to a particular odorant subject was (were) determined by the position preferences of the test animals served by the given odorant subject. Rewarded placements for odorant subjects were given in both goalboxes according to a double-alternation sequence that reversed itself on successive days.

In Experiment 1, odorant subjects were rotated through placements in a fixed order such that a squad of nine all received their first trial before their second trial, etc. Interspersed, after nonrewarded placements for three consecutive odorant subjects, were test trials for reaction to frustration odor. A given test animal always followed the same odorants. It received three tests per day, one from each doublet of N placements in the daily pattern of odorant placements, with the tests utilizing the first, then the second, member of a doublet on alternate days. Following such tests, and following every third rewarded odorant placement as well, floor and wall papers were changed. When there was a second group of animals to be tested without odor in the maze, they were interspersed following tests with odor just after the change of paper. Except for the clean paper, tests for such "control" animals were identical to those for animals with odor present in terms of number and distribution of trials, etc. The within-day intertrial interval for test animals was held around 78 or 96 min, depending on interspersed schedules.

The study consisted of several phases in which tests were given with (a) frustration odor on test animals' preferred sides, designated "O on P" in Table 1 and in the figures, (b) frustration odor on test animals' nonpreferred sides, designated "O on NP," (c) no odor, i.e., clean paper, designated "No-O," or (d) a treatment designated "O on P in T2" in which frustration odor was placed on the preferred side as before, but then, for the test, the crossbar of the T-maze was covered with a black cloth to darken it and the maze was raised at the startbox so that the angle between the maze floor and the horizontal was about 7°. This last test was instituted at the end of Experiment 1 as a pilot attempt to determine whether alternation of the test situation would reinstate the avoidance displayed at the outset of the study; the maze remained unaltered for the placements of odorant subjects.

Testing: Experiment 2. Most of the treatments and procedures in Experiment 1 were also used in Experiment 2, although phases were not always identical in length (see Table 1 for details). Testing began on Day 14 (Phase B). Three subjects were assigned to a squad of odorants (unlike in Experiment 1, where nine odorants comprised a squad). When the single group of test animals was interspersed among the odorants as in Experiment 1, six squads resulted. The within-day intertrial interval was about 20 or 28 min, depending on the interspersed odorant schedule.

RESULTS

Figure 1 presents the groups' data from Phases A-I of Experiment 1; group data from the last phase, J, may be inferred from Figure 3. Similarly, Figure 2 presents the data from Experiment 2. In the figures, days are numbered beginning with the first test trials (Phase A). Also, the treatments during a phase are given at the top of the figures for convenience. By Phase G of Experiment 1, it became obvious that group functions would not be representative of three of the subjects of Group 1. Therefore, the data for these three subjects, which were responding similarly to one another, are plotted separately from the remaining subjects of Group 1 in Figure 3. The response measure was the daily mean percentage of test trials on which subjects avoided the goalbox that they initially preferred (i.e., chose the other goalbox). Thus, values below 50% indicate a preference for the initially preferred side.

Position Preferences

Panels A in Figures 1 and 2 present the data, obtained prior to the introduction of odor, that established the preferred sides of subjects in Groups 1 and 2 of Experiment 1 and of subjects in Experiment 2. Similar data for the subjects of Group 3 of Experi-

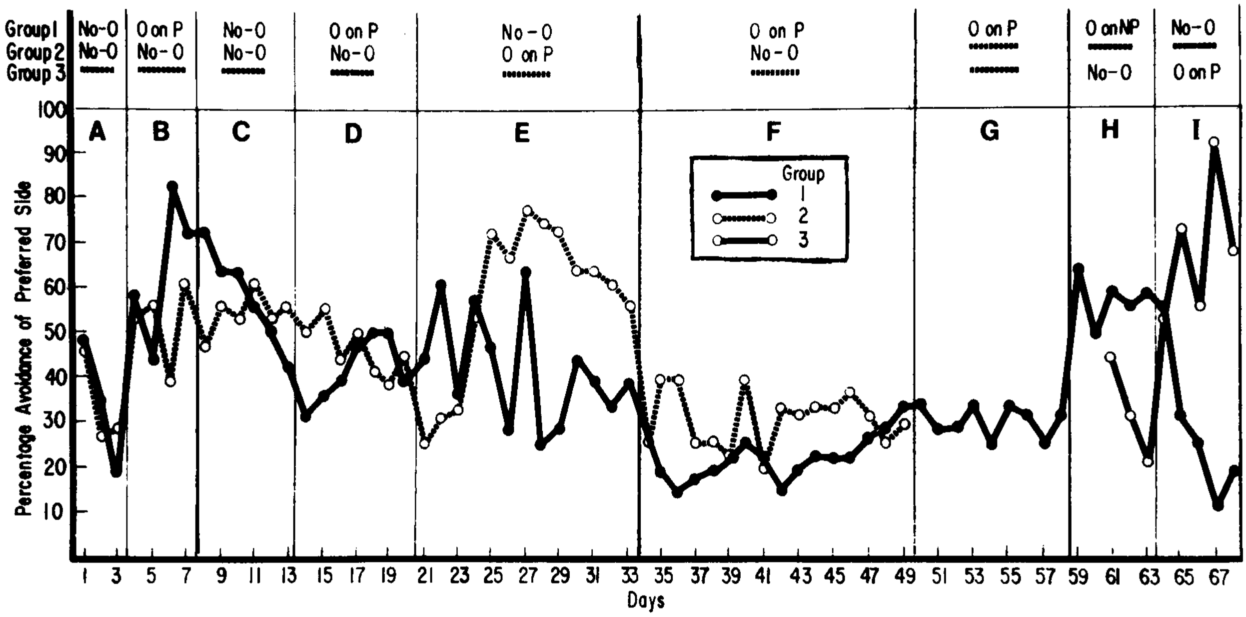

Figure 1. Percentage of trials on which the preferred side was avoided as a function of days during Phases A to I in Experiment 1. Treatments are indicated at the top: No-O means "no odor"; O on P means "odor on preferred side"; O on NP means "odor on nonpreferred side"; broken line means "no treatment during the indicated phase."

ment 1 may be seen in Panel H of Figure 1. As is evident from Figures 1 and 2, position preferences developed over trials, and they developed at the same average speed for the three groups of Experiment 1; in Experiment 2, the position habit appeared somewhat weaker.

The finding that the position habit developed over trials, though quite irrelevant to the purposes of this study, is nonetheless of interest in its own right. Major theories of animal discrimination learning (Spence, 1936; Sutherland & Mackintosh, 1971) have explained such "running away" of position preferences, which is characteristic of discrimination learning by rats, by appealing to the relatively greater effect of reward as compared with nonreward in the early stages of discrimination. In the present study, position preferences ran away in the absence of any obvious reward, since test animals were simply removed from the clean, empty, goalbox 10 sec after entry. Of course, it might be argued that such removal (and/or return to the home cage) actually constituted a reward. Nevertheless, the present data indicate that the running away of position preferences in typical discrimination problems may occur independently of the usual operations of reward, suggesting that theories of discrimination that causally relate the two may be in error.

Disruption of position preferences. Before turning to the results of main interest, the behavior of Group 2 of Experiment 1 during Phase B warrants discussion. Its treatment in Phase B was the same as in Phase A except that its tests were distributed among placements of odorant subjects and tests of Group 1 subjects. It appears that the position preferences that developed in Phase A were immediately disrupted by something at the outset of Phase B, resulting in about equal choice of the alternatives, and that only in Phase D did the position habits slowly begin to reappear, perhaps as Group 2 habituated to the disrupting influence.

What disrupted Group 2's position habits cannot be said. Various attempts to relate the disruption to possible odor traces from preceding subjects or slight changes in intertrial interval proved unproductive. In any case, the disrupting factor does not appear to have biased the choice of goalboxes for Group 2, but merely to have removed the position habit, since choice varied around 50%.

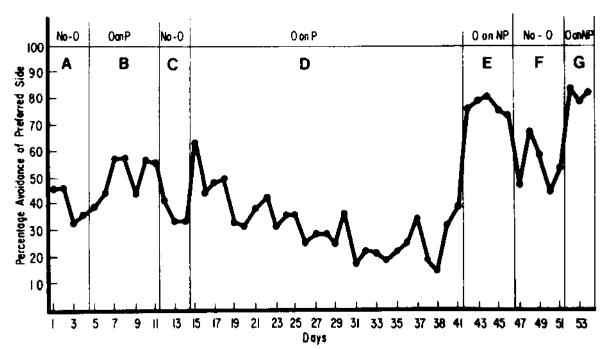

Figure 2. Percentage of trials on which the preferred side was avoided as a function of days during the several phases, A to G, of Experiment 2. Treatments are indicated at the top with the symbols having the same meanings as given in Figure 1.

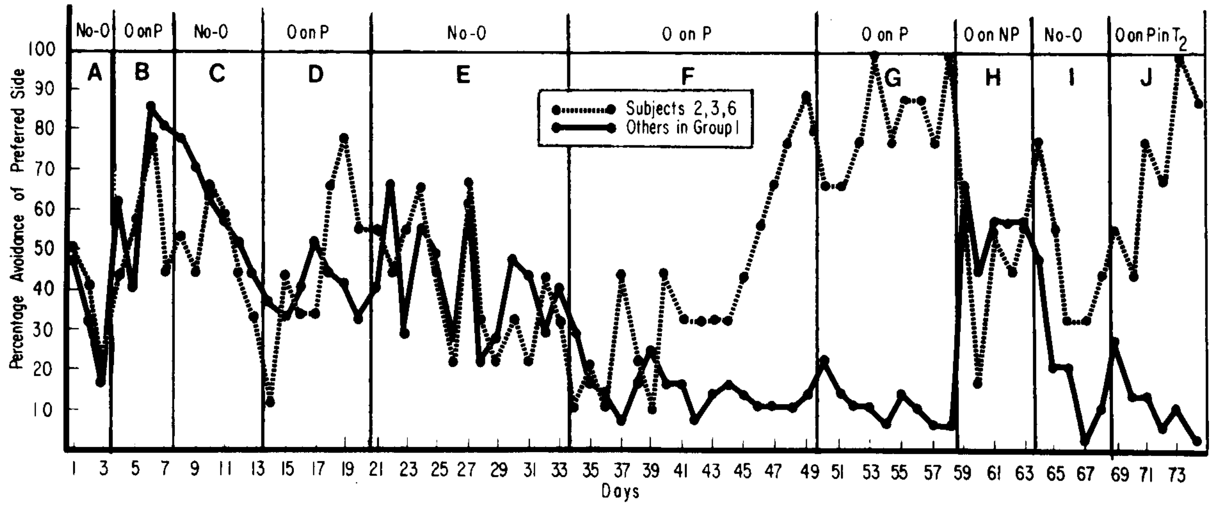

Figure 3. Percentage of trials on which the preferred side was avoided during the several phases of Experiment 1 for three subjects that displayed strong avoidance during Phase G and for the other subjects of Group 1. Treatments are indicated at the top; see Figure 1 for the meanings of the symbols.

Reactions to Odor

Initial Avoidance. Considering next the effect of the initial introduction of frustration odor into the preferred goalbox for Group 1 of Experiment 1 and for test subjects in Experiment 2, Panels B in Figures 1 and 2 suggest that an avoidance of or withdrawal from the odor developed over 3 days. A Mann-Whitney U test comparing Groups 1 and 2 of Experiment 1 on Days 6 and 7 indicated that the difference was significant [$U(12,12) = 21$, $p < .02$]. In Experiment 2, the withdrawal interpretation was supported, not only by the increase in avoidance with the introduction of odor but also by the significant drop in percentage avoidance from Days 7-11 to Days 12-14 as indicated by the Wilcoxon test [$T(12) = 7.5$, $p < .02$]. Similarly, when Group 2 of Experiment 1 experienced frustration odor for the first time (Panel E, Figure 1), they too developed an avoidance of it after 3 days in which there was a suggestion of an initial attraction. Over Days 25-33, Group 2 avoided the preferred side significantly more than Group 1 [$U(12,12) = .5$, $p < .002$].

Subsequent reactions and individual differences. In Phase D, frustration odor was introduced a second time into the preferred goalbox of test subjects. Avoidance temporarily reappeared in Experiment 2 [comparison of Days 14 and 15 with the Wilcoxon yielded a $T(10) = 8$, $p < .05$]. However, in Experiment 1, there was not much of an effect, considering the group as a whole. Considering separately the three atypical subjects mentioned above, it appears that they alone in Group 1 developed a withdrawal response after an initial brief "attraction" for or approach toward the odor (Figure 3). This same pattern was displayed somewhat more clearly by these three subjects in Phase F, where a strong avoidance developed after what appeared to be a period of attraction or perhaps conflicted response. The other subjects of Group 1 also displayed an almost immediate approach toward the odor in Phase F (see Figure 3), but for these subjects the attraction persisted throughout the remainder of the experiment. These latter subjects of Group 1 displayed significantly more choices of their preferred sides over Days 34-39 than did Group 2, which were responding to a clean maze [$U(9,12) = 24.5$, $p < .05$].

The subjects of Experiment 2 showed no evidence of this pattern of an initial attraction followed by avoidance, but they did avoid in the early phases, as noted above, and they also developed an attraction during Phase D that persisted throughout the study. Finally, there was no indication of an initial attraction, only an avoidance, in the response of the three atypical subjects of Group 1 in Phase J (Figure 3). That is, by Phase G, the reactions of the subjects of Group 1 appeared rather stable, attraction for the majority and avoidance for the three deviant ones. It may be noted, however, that comparison of Phase J with prior phases is somewhat hazardous, because test conditions of the maze were altered.

Stability of Odor Control of Responding

Odor potency after extended training of odorant rats. The finding that most subjects eventually changed their responses to frustration odor raised the question of whether the odor changed properties as the experiments progressed. It was possible that the odor lost some or most of the property that produced the initial avoidance of it as the odorant subjects were repeatedly placed into the goalboxes of the maze. Indeed, the odorant subjects might have adapted to nonreward to the point that it was no longer frustrative. Although no previous odor research from this laboratory had given evidence of this, the present studies administered more trials to odorant subjects than did previous ones. Therefore, in Experiment 1, a new group of test animals, Group 3, received position preference testing on Days 61-63 and tests for odor avoidance on Days 64-68. As may be seen in Panel I of Figure 1, a strong avoidance developed. A comparison of percentages of avoidance responses for Group 3 over Days 61-63 with Days 64-68 was significant [$T(12) = 2$, $p < .01$]. Thus, there was no evidence the odor changed in property, since it remained a repellent for naive subjects.

Tracking the odor. Compelling evidence that frustration odor continued to control responding throughout the studies arose from tests in which odor was shifted to the nonpreferred side of the maze (Panels H in Figures 1 and 3; Panels E and G of Figure 2). Subjects immediately shifted their choices, with most continuing to approach the odor and the three deviant subjects of Group 1 continuing to avoid it, though less strongly than before. In Experiment 1, a Wilcoxon test of Group 1 on Days 54-58 vs. Days 59-63 yielded significant results, in spite of the inclusion of the three atypical subjects which attenuated the effect [$T(12) = 13$, $p < .05$]. In Experiment 2, a test of Days 37-41 vs. Days 42-46 was easily significant [$T(12) = 0$, $p < .01$], as was a test of Days 49-51 vs. Days 52-52 [$T(11) = 1.5$, $p < .01$].

Reactions Conditioned by Odor

Effects of odor removal. A preference for one side of the maze, established by presentation of the odor, that persisted following the removal of the odor would suggest a conditioned reaction to one or both of the sides. In Phase C, frustration placements were discontinued for odorant subjects, and all test subjects were tested with clean paper. As may be seen in Panel C of Figure 1, the avoidance by Group 1 of their preferred side did not immediately disappear but, rather, slowly diminished over days. On Day 8, Group 1 remained above Group 2 but not significantly, as evaluated by a two-tailed Mann-Whitney test [$U(12,12) = 38.5$, $p < .10$]. Looking at Panel C in Figure 3, it appears that the lingering avoidance of the preferred side was stronger for the nine animals that eventually showed an attraction for the odor than for the three eventual avoiders. This result, then, provides a suggestion that frustration odor established a temporary conditioned avoidance of the originally preferred side. Little, if any, such effect is evident in Panel C of Figure 2. Also, when odor was removed from Group 2 of Experiment 1 on Day 34 (Panel F, Figure 1), avoidance immediately dropped. On the only other occasions when odor was removed following a phase of definite response to the odor (Phase F of Experiment 2 and Phase I of Experiment 1), performance immediately changed in the former but not in the latter; Group 1 remained on Day 64 significantly above the level to which it dropped on Day 65 according to the Wilcoxon test [$T(12) = 0$, $p < .01$]. Since, in this case, most subjects were tending to approach the odor prior to its removal, these data provide a hint of a temporary conditioned attraction. However, since the three deviant subjects were avoiding, not approaching, the odor during this period, they must be considered separately. As Panel I in Figure 3 indicates, they displayed an immediate approach to the side on which the odor had just been placed during Phase H. Such a reaction was the opposite of any conditioned reaction established during Phase H, but of course it is what one would expect if the avoidance established during Phases F and G were exerting a dominant conditioned influence.

Effects of shifting odor placement. Considering next the immediacy of the change in response when the odor was shifted from one side to the other, it may be seen, in Panels H in Figures 1 and 3 and Panel E in Figure 2, that subjects immediately shifted their responses to a level typical of that supported by the new odor location. However, it may be noted in Figure 3 (Panel H) that Group 1 subjects did not display the extreme preferences after the location change that they did before the change, which could be interpreted as evidence of a long-lived conditioned reaction, especially since it does not seem to be merely the consequence of original position preferences (witness the data of the three deviant subjects). In contrast, subjects of Experiment 2 showed a dramatic shift to a preference level slightly more extreme than preshift. Thus, the evidence for conditioned preferences was minimal and by no means a typical finding.

Altered Test Situation

There was little indication that altering the test situation by tilting the maze and covering the arms with black cloth produced any effect, except, perhaps, a slight transitory disruption (see Panel J, Figure 3). It had been speculated that the original avoidance of the odor might reappear in a "new" situation for subjects that had come to approach the odor. Clearly, that did not happen, although a more drastic change in test conditions might show such an effect. The present study was limited in the extent to which conditions could be altered for test subjects by the necessity of maintaining placement conditions for the odorant subjects unaltered. As for the three subjects that had developed a lasting avoidance, they again showed such a development. Since this aspect of this work was exploratory in nature, it will not be discussed further herein.

DISCUSSION

Initial Reactions to Odor

Taken together, the several transitions from no odor to odor suggest that the initial response to frustration odor is one of avoidance, though this may take a few trials to develop, and that it is not a long-lived reaction. Only in Group 2 of Experiment 1 was there any indication that this initial avoidance might be preceded by a short phase of attraction, and this evidence was merely suggestive (Panel E, Figure 1).

That the avoidance should have taken some trials to develop is somewhat surprising, since two previous studies from this laboratory, one identical to the present experiments in most respects, found avoidance from the outset (Collerain & Ludvigson, 1972, 1977). However, Collerain (1978) has reported increased avoidance as experience with frustration odor increased. It could have been that the animals of the present studies learned over trials how to avoid the odor effectively. This learning interpretation is consonant enough with the immediate recurrence of avoidance in Experiment 2 upon the reintroduction of frustration odor (Panel D, Figure 2). However, the persistent recurrence of the gradual buildup of avoidance displayed by the three deviant subjects of Group 1 of Experiment 1 (see Panels B, D, F, and J of Figure 3) favors an interpretation appealing to an accumulation of some sort of "intolerance" of the odor, at least for these subjects. This conclusion is strengthened by the facility these subjects displayed in switching choices when the odor was switched to the opposite goalbox (Panel H, Figure 3): clearly, by that time, these subjects knew very well how to avoid the odor, yet a few days later (Panel J, Figure 3) they again displayed a gradual buildup of avoidance.

Long-term Reactions to Odor

Following the period of initial avoidance, the avoidance declined and there gradually appeared a rather strong and persistent attraction for the odor in most subjects. In striking contrast, a few subjects did not develop a permanent attraction; rather, after a period of high variability, there emerged a stable avoidance tendency. This constitutes a rather dramatic and unusual instance of individual differences in which variations occur, not merely in the magnitude or intensity of a response, but in the direction of a response to a stimulus. As such, it poses some interesting questions regarding why such differences should emerge in the absence of differential treatments.

While not answering such questions, these studies do speak clearly to a question about the nature of the mechanism of habituation to the odor left unanswered by the Collerain and Ludvigson (1977) study. There, it was not clear whether, with repeated exposure to the odor, the return to baseline of hurdle-jumping speed resulted because (a) broadly speaking, the test animals' "perception" or "interpretation" of the odor changed, perhaps from one of an "aversive" to a "neutral" odor, or (b) the odor lost control of responding as the escape response itself became refractory. The former interpretation might be thought of as appealing to a kind of stimulus satiation and the latter to a kind of response satiation or Hullian reactive inhibition. The present observation of continued control of responding by the odor following initial habituation rather effectively rules out the response satiation interpretation. The change, then, in avoidance or approach responses to the odor with repeated exposure to it appears to be a consequence of altered perception of the odor, not a change in the response, per se.

Stability of the Odor Stimulus and Frustration Theory

Given the clear avoidance of the odor exhibited by naive subjects late in testing (cf. Panel I, Figurel), it seems safe to conclude that the odor stimulus itself had not significantly changed, even after 570 placements of an odorant subject through Day 63 just prior to testing. It may be noted that this finding bears upon a fundamental assumption of frustration theory (Amsel, 1958). While one might suppose that, with repeated exposure to a partial-reward schedule, a "tolerance" for nonreward might develop via a lessening of the frustration reaction, frustration theory has never embraced such a view. Instead, it has assumed a frustration reaction tied to the magnitude of reward expectancy, which, in the present case, should be stronger or undiminished with continued training. Given that avoidance by test animals is positively related to a frustration reaction of odorant animals, the present observations are quite consistent with frustration theory. They also extend a related inference from the work of Collerain and Ludvigson (1977), who reported evidence for an increase in potency of frustration odor through 112 partially rewarded trials.

Reactions Conditioned by the Odor

Evidence that preferences for spatial loci are conditionable through exposure to frustration odor was minimal, although there were some suggestions of such an effect. For the most part, the odor seemed to function as a well-discriminated stimulus, with the response, whether approach or avoidance, being rather bound to the odor.

The Question of the Uniqueness of these Reactions to Frustration Odor

It should be noted that these studies did not compare the long-term reaction to frustration odor with reactions to other odors. Rather, for practical reasons, they looked only at frustration odor. The question immediately arises, then, as to whether these same patterns of results might not occur using any conspecific odor. Previous research clearly suggests that this would not be the case, at least for the initial reaction to the odor: Collerain and Ludvigson (1972) found avoidance in the same T-maze used herein for frustration odor but not "reward odor" (odor from rewarded rats) or "neutral odor" (odor from rats given neutral placements); Collerain and Ludvigson (1977) found enhanced escape from frustration odor but not from neutral odor from well-habituated donors, and they found slowed escape from reward odor; Collerain (1978) found a clear difference in escape from frustration odor and neutral odor, with the latter producing at best a very transitory, early, weak enhancement; Mellgren, Fouts, and Martin (1973) found slower approach to than escape from frustration odor, and the reverse pattern for reward and neutral odors; McHose (1973) found preferences for reward and frustration odors to differ for animals with certain reinforcement histories; and several studies from the laboratory of Cattarelli, Vernet-Maury, and Chanel (e.g., 1974) have reported both behavioral and physiological differences in response to reward odor and what they term "frustrated rat" odor. Of course, the question of the precise differences in reaction to these odors over the long term must await further work.

Interestingly, were one to attempt to obtain data bearing on such a question, one would be disposed, for reasons of good design, to compare reactions to several odors in a single experimental session. However, we have on occasion in our laboratory experienced real difficulty in controlling odor contamination among treatments in such a study. This suggests that the present approach of testing only a single odor may, in fact, yield "cleaner" data (though even here, all problems may not be eliminated, as suggested by the behavior of Group 2, Experiment 1, Phase B—behavior possibly caused by odor contamination).

Neophobic reaction? Related to the question of the uniqueness of the reaction to frustration odor is that of whether the term "neophobic" is appropriately applied to the initial avoidance reaction. As indicated above, this avoidance reaction would not be expected from certain other conspecific odors, suggesting either that the term is inappropriate or that frustration odor is more novel than other conspecific odors at the moment of testing. The present data cannot resolve this matter, but they do contribute two important observations to the general topic: (a) Although the initial avoidance followed by its habituation fits the concept of a neophobia, the eventual attraction toward the odor must be described in other ways; and (b) for some minority of subjects, an aversion to frustration odor develops that clearly does not fit the neophobic description.

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