ODOR OF FRUSTRATION AS IT RELATES TO THE NUMBER OF REINFORCED TRIALS PRIOR TO FRUSTRATIVE NONREWARD

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ABSTRACT

ODOR OF FRUSTRATION AS IT RELATES TO THE NUMBER OF REINFORCED TRIALS PRIOR TO FRUSTRATIVE NONREWARD

By

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While a number of studies have demonstrated that rodents secrete an odorous substance as a function of frustrative nonreward, little is known about the response properties of odor emission. The purpose of the present study is four-fold:

(1) To determine if the concentration of odor-of-frustration is systematically related to the number of reinforced trials preceding frustrative nonreward.

(2) To determine if the odor concentration on the second trial of frustrative nonreward is greater than that emitted following the first exposure to frustrative nonreward.

(3) To determine if the paper covering the floor under the odorant animal acts as a depository for the odorous substance.

(4) To determine the pheromonal reaction of a male albino rat detecting the odor of a nonfrustrated male conspecific.

To this end, Ss from five odorant groups were placed, individually, into the center chamber of a three-chambered box for six trials per day over nine consecutive days. The Ss of each group received a pre-determined number of nonreinforced

trials (0, 18, 36, 48, 54), with the remainder of the 54 trials (54, 36, 18, 6, 0) reinforcing approach toward the food cup. Frustrative nonreward followed the final reinforced trial of day nine.

The existence of odor of frustration, and its concentration, was measured in terms of the latency of a naive detector S to leave one of the end chambers and enter the odorized center chamber. Latency of the detector to leave this odorized area was also used as an index of odor concentration, since previous studies had shown that conspecifics find odor of frustration mildly aversive.

It was found that:

(1) Odorant groups differed in latency to approach the food cup on day nine. This was interpreted in terms of differences in level of "food expectation".

(2) Amount of urine excreted by the odorants following frustrative nonreward was directly related to the number of reinforced trials prior to frustrative nonreward. This was interpreted as showing differences in level of frustration following frustrative nonreward.

(3) Latency of the detector Ss to enter, then leave the odorized center chamber was not systematically related to the number of reinforced trials the odorant Ss received prior to frustrative nonreward.

(4) Rats detecting odor of a nonfrustrated male conspecific tend to approach faster and escape slower than rats detecting odor of a clean chamber.

(5) Exhausting the odorized air of the center chamber following frustrative nonreward, but prior to detector testing, yielded a non-significant tendency to approach more slowly, and leave faster than detector Ss of the control group.

(6) Detectors were slower to enter but faster to leave an area infused with odor-of-frustration secreted as a function of the second trial of frustrative nonreward, relative to detectors receiving odor-of-frustration from odorants receiving their first trial of frustrative nonreward.

Discrepant findings between comparable studies were discussed in terms of procedural differences. An improved methodology based on the findings of the present study was proposed. And a brief summary of phenomena related to odor-of-frustration was given.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

A number of investigations have provided evidence for the existence of odors secreted by an individual rodent as a function of operations designed to produce frustration, i.e., nonreinforcement in a situation previously associated with reinforcement.

In general these demonstrations have taken one of two forms. First, it has been shown that a nonfrustrated conspecific makes an immediate and characteristic response upon receipt of an odor associated with frustrative nonreward. When an odor elicits a characteristic response from a conspecific it is termed a pheromone (Karlson & Luscher, 1959). A second type of supportive evidence has come from those studies which report that experimental animals can use the odor produced by a frustrated conspecific as a cue for the solution of a discrimination learning problem.

For example, Morrison & Ludvigson (1970) successfully trained female albino rats to choose a food baited goal box in a T-maze conditional discrimination problem when using odor-of-frustration as a cue. Forty-eight Ss were separated into four groups of twelve Ss each. The first group (NC) received odor-of-frustrated-conspecific versus odor-of-clean paper. A second group (RN) received odor-of-frustrated

conspecific versus odor-of-rewarded conspecific. And a third group (RC) received odor-of-rewarded conspecific versus odor-of-clean paper. The fourth group received only odor-of-clean paper as a control for non-experimental discriminative cues such as odor of food pellets emanating from the baited goal box. Odor-of-reward and odor-of-frustration were presumed to be secreted or excreted by a food deprived odorant animal placed at the choice point of the T-maze. The presentation of food to the odorant animal was intended to elicit odor-of reward, while frustrative nonreward was intended to elicit odor-of-frustration. The above chance performance of the NC and RN groups was interpreted by Morrison and Ludvigson as showing a cue function for odor-of-frustration. However, the use of compound cues in this study makes the evidence equivocal. For example, the NC group could have learned the T-maze problem using the species-specific scent of the individual odorant animals.

Several spontaneous alternation studies have shown that rats tend to avoid an area infused with their own scent (c.f., Schultz & Tapp, 1972) but to approach an area containing the scent of other conspecifics (Reiff, 1956). Bower & Alexander (1967) found that mice could distinguish between odors associated with two conspecifics in a Y-maze discrimination problem. Archer (1968) showed that odor of a strange male mouse caused an increase in aggressive behavior between male cage mates. Taken together, these studies support the possibility that "odor-of-frustration" might better be labelled "odor-of-frustrated-rat" with the characteristic scent of the

odorant conspecific contributing to stimulus control of the choice behavior of the indicator animal in the Morrison and Ludvigson study.

A similar problem arises in determining the nature of the cue controlling the choice responses of the second indicator group. Recall that this group received odor-of-a frustrated rat versus odor-of-a-reinforced rat. While Morrison & Ludvigson interpret the successful performance of this group in terms of cue control by odor-of-frustration an alternative explanation is possible. Southhall & Long (1969) showed that rats could use the odor from a single pellet as a cue to solve a T-maze discrimination problem. It seems possible that group two of the Morrison and Ludvigson study (the RN group) solved the conditional discrimination problem using odor of food or food particles rather than odor-of-frustration. In spite of the evidence cited above, Morrison and Ludvigson found that the RC group receiving odor-of a reinforced conspecific versus odor-of-clean paper did not choose the baited goal box significantly above chance. It is not clear whether the discrepancy in findings is due to methodological differences in studies or an odor insensitivity by the Ss of the RC group. Using essentially the same apparatus and design, McHenry (unpublished research) was unable to replicate the Morrison and Ludvigson findings when the characteristic scent of rat was common to the two cue values of the successive conditional discrimination, i.e., odor-of-frustrated rat versus odor-of-a nonfrustrated rat.

In general, the use of a learned response confounds the

learning process with the relationship between the odor of frustration and the unconditioned response to that odor. Under certain circumstances it may be impossible to determine whether the topography of a learned odor indicator response is due to learning variables or detection of the odor.

For example, a number of studies have used the "double alternation" learning paradigm in providing evidence for the existence of an odor associated with non-receipt of an "expected" reward (Ludvigson & Sytsma, 1967; Ludvigson, 1969). Typically this procedure involves the double alternation of reward (R) and non-reward (N) in an RRNN pattern of successive events in the goal box of a straight alley. A second characteristic of these studies is that homogeneous goal box events are arranged such that each S in a squad receives a given ordinally numbered trial before any S receives the next trial, and the goal box event of a given trial is the same for each S. A number of studies have shown that rats need an external cue to learn this pattern (Bloom & Capaldi, 1961), with learning manifested by significantly slower running speeds on non-reinforced trials relative to running speeds on reinforced trials. Ludvigson & Sytsma (1967) have shown that when the above conditions are met, i.e., double alternation paradigm with homogeneous goal box events, rats show patterned running in the area of the goal box. Seago, Ludvigson & Remley (1970) have implicated an odor cue from the preceding conspecific by showing that anosmic rats do not show patterned running under the double alternation condition.

An unambiguous interpretation of the outcome of these studies is that rats give off a substance which perseverates after the frustrated animal is removed, and that the presence of this substance is associated with one type of behavior by the detecting animal, and a different type of behavior in its absence. Unfortunately, this type of study reveals nothing about the relationship between odor emission, odor-of-frustration and the response or class of responses made by a conspecific detecting odor-of-frustration. Both pheromonal properties and the cue properties of odor-of-frustration would be expected to elicit responses incompatible with approach toward the goal box, so that increased running time in the presence of the odor is not an unambiguous demonstration of the aversive properties of the odor when using this paradigm.

Rather than imposing a learned indicator response (discrimination paradigm) upon the odor detector, a number of investigators have used designs showing the interaction between learned responses and responses elicited by odor of frustration. McHose & Ludvigson (1966), for example, trained an experimental group to run in two discriminably different alleys, one of which was associated with a small magnitude of reward (s- alley) and the other associated with a large magnitude of reward (s+ alley). McHose and Ludvigson found that the control group which received an intermediate but equal amount of food in each alley ran slower in the s- alley than in the s+ alley. Presumably this effect was due to an odor given off by the experimental animals in the s- alley.

A related effect has been demonstrated by Wasserman &

Jensen (1969) which they term the "pseudo-extinction effect". Essentially this refers to the finding that "continuously rewarded rats show a decrease in running speed on a runway recently traversed by other rats undergoing experimental extinction" (p. 1307). This decrease in running speed was confined to the goal area where odor-of-frustration would presumably be strongest. Since Ss running speed did not decrease on those trials where the preceding odorant animal was reinforced it is unlikely that the effect was due to the characteristic scent of the conspecific.

Evidence supporting the existence of an odor associated with non-receipt of an "expected" reward also comes from a study carried out by Mellgren, Fouts & Martin (1973). Water deprived odorant rats received twenty-four continuously reinforced trials in the center compartment of a three-chambered box. They then received a series of trials of non-reinforcement in the same center compartment. When detector Ss were placed in the start box (one of the end chambers) and permitted entrance into the odorized center chamber their latency to enter the odor laden center chamber was significantly longer than detector Ss exposed to odor of a nonfrustrated rat. Latency to leave the center chamber by "escaping" to one of the end chambers was significantly shorter for those detectors exposed to odor-of-frustration, relative to the performance of those detectors receiving the scent of a nonfrustrated conspecific.

To date, the study of odor of frustration has been limited to demonstrations of its existence. Determining the response

characteristics of odor emission as it relates to the operation of frustrative nonreward has been hampered by the need to use an indicator response of a conspecific receiving odor-of-frustration. Most responses can be measured using devices that relate to the response in a known way, e.g., clocks and counters. Unfortunately, odor-of-frustration cannot yet be measured using a mechanical device which gives a one-to-one relation between a dial reading and some value of a response parameter. The only "device" which is sensitive to odor of frustration is another rat which makes an unconditioned response upon detection of the odor. Unlike the clocks and counters, it is not known how changes in the indicator response relate to changes in some characteristic of odor emission.

An incidental finding of the previously cited study by Seago, et. al. (1970) points to a possible indicator response, namely, latency to approach an area infused with odor-of-frustration, which may be sensitive to graded changes in the concentration of the odor. Recall that four groups of rats were tested in a straight alley using a double alternation paradigm. The Ss of two groups were made anosmic as a consequence of olfactory bulb removal; the remaining two groups were tested intact, and presumably were macrosomatic. The normal Ss showed patterned running as expected while the anosmic animals didn't. But of particular interest was the additional finding that the magnitude of patterning (difference between latency to enter the goal box on reward versus nonreward trials) was a function of the number of preceding Ss on a given trial, i.e.,

the S run seventh showed stronger patterning than the S run second. Such a finding suggests that either: (1) odor of frustration accumulated as successive Ss were tested on a given trial and that latency to approach an area infused with this odor is a function of the odor concentration, i.e., a pheromone effect, or (2) a greater concentration of the odor provided a more easily detected cue signaling nonreinforcement in the goal box area, or (3) perhaps both of these factors were operating in additive fashion. In any case it is clear that the indicator response was sensitive to the concentration of the odor. This finding may permit a study of the response properties of odor emission, especially as it relates in parallel fashion to the traditional response measures indicative of a frustration effect, e.g., running speed in alley two of a double-alley apparatus (Amsel & Rousell, 1952) or bar press amplitude (Netterman & Mintz, 1965).

Amsel (1958) has proposed that the magnitude of the frustration effect of "invigorating responses which follow (frustrative nonreward)" depends upon the strength of the anticipation of reward, $r_g - s_g$ (Spence, 1956). The strength of $r_g - s_g$, in turn, is determined by such factors as magnitude of reward, and number of reinforced trials. Peckham & Amsel (1967) has confirmed that the frustration effect is influenced by reward magnitude, and a number of studies have found that number of reinforced trials prior to frustrative nonreward is positively related to the strength of the frustration effect (Hug, 1970; Stimmell & Adams, 1969; Yelen, 1969).

Yelen (1969) trained three groups of rats in a double

alley apparatus constructed such that the goal box of alley one also functioned as the start box for alley two. Each group of rats was given 12, 36, or 60 trials with a 97 mg. Noyes food pellet consistently available in both goal boxes. The Ss of all three groups were then shifted to a 50% reinforcement schedule for goal box one, with goal box two baited on all trials. The magnitude of the frustration effect, as manifested by significantly faster alley two running speeds following goal box one nonreinforcement versus goal box one reinforcement, was directly related to the number of prior reinforced trials. The frustration effect was largest for the 60 reinforced-trials-group, second largest for the 36 reinforced-trials-group, and smallest for the 12 reinforced-trials-group.

In summary, a number of studies have demonstrated the existence of an odor associated with frustrative nonreward, and the time has come to begin a study of the response characteristics of odor emission. Yelen (1969) has shown that the response of running following frustrative nonreward is influenced by the number of reinforced trials preceding frustrative nonreward. The purpose of the present study was to determine the extent to which odor-of-frustration is similarly influenced by this variable. Odor concentration was measured in terms of the latency of an odor detecting S to approach an area infused with odor-of-frustration emitted by an odorant animal receiving different numbers of prior reinforced trials. Since Seago, et. al. (1970) showed that approach latency is sensitive to odor-of-frustration concentration,

the function relating latency of approach by odor detecting Ss to number of prior reinforced trials of the odorant group should give an indication of odor concentration as it relates to the number of prior reinforced trials.

METHOD

Subjects:

One hundred and eight male, albino rats (Sprague-Dawley strain) served as Ss. Each S was experimentally naive, and was 95 to 105 days old at the beginning of experimentation. Upon arrival at the laboratory each rat was housed individually in an 8" X 10" metal cage, and provided with *ad libitum* food and water for a five day period. At the completion of this period each S was reduced to approximately 80% of its free feeding weight by imposing a 10 gram per-day deprivation schedule.

Apparatus:

The testing apparatus consisted of a three-chambered box, with each chamber measuring 11" X 7½" X 8" high. Adjoining chambers were constructed of ¼" clear plexiglas, and were separated by 7½" X 8" high guilletine doors, also constructed of clear plexiglas. Each chamber was covered by a hinged, plexiglas lid measuring 11" X 8". Strips of water proof butcher paper overlayed with absorbent Scott toweling covered the floor of the apparatus. Clean paper could be pulled from paper rolls located at one end of the apparatus through a slot located at the base of one end of the chamber; paper soiled with urine and boli could be pulled from the apparatus through a slot

located at the other end of the apparatus. Forty-five mg. Noyes food pellets were delivered down a ½" (O.D.) rigid plastic tube into a plastic food dish with a removable, clear plastic top. The food dish, measuring 1" X 2", was located in the center chamber, and was attached to one of the side walls. Latency of response measures for the detector Ss were taken by using microswitches attached to the guilletine doors and one photo-relay located 4½" inside the center chamber, with a second photo-relay 4½" inside the "goal box". Each microswitch and photo-relay was part of the timing circuitry programmed through 28 v. electro-mechanical components. Two clocks, capable of resolving .01 seconds provided measures of response latency. Oder laden air was removed from the chamber by using two 28 v. blowers. A 1 5/8" rubber hose connected the input port of one blower to the 1 5/8" exhaust hole cut in the end wall of the goal chamber. A similar blower and hose arrangement provided room air into the chamber through a 1 5/8" hole cut in the start box end wall.

Procedure:

The 108 Ss were randomly divided into five groups of odor emitters and eight groups of odor detectors. The size, treatment and function of each of the thirteen groups was as follows:[1]

(1) A group of eight detector rats received oder of a clean (center) chamber in order to provide reference data for

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[1] At the end of the description for each group is a code enclosed in parentheses. This code will be used as a group label, and is intended as a mnemonic device to help the reader recall the function and treatment assigned each group.

group three. (D-OCC) refers to Detector - Odor of Clean Chamber.

(2) A group of four nonfrustrated odorant Ss was placed in the center chamber in order to provide a scent characteristic of a nonfrustrated male rat. (O-O R) refers to Odorant - O Reinforcement in the center chamber.

(3) A group of eight detector rats received odor of a nonfrustrated conspecific so as to provide data on the characteristic response elicited by odor of a nonfrustrated male; and secondly, these Ss provided "reference data" for the detectors which received odor of a frustrated male rat. (D-O R) refers to Detector - receiving odor associated with O Reinforcement.

(4) A group of eight odorant animals received 48 nonreinforced trials, followed by 6 reinforced trials, and finally frustrative nonreward. (O-6 R) refers to Odorant - 6 Reinforcements in the center chamber.

(5) A group of eight detector rats received odor-of-frustration from the Ss of group four. (D-6 R) refers to Detector - receiving odor associated with 6 Reinforcements.

(6) A group of eight odorant Ss received 36 nonreinforced trials, followed by 18 reinforced trials prior to frustrative nonreward. (O-18 R) refers to Odorant - 18 reinforcements in the center chamber.

(7) A group of eight detector rats received odor-of-frustration from the Ss of group six. (D-18 R) refers to Detector - receiving odor associated with 18 Reinforcements.

(8) A group of eight odorant Ss received 18 nonreinforced

trials followed by 36 reinforced trials prior to frustrative nonreward. (O-36 R) refers to Odorant - 36 Reinfercements in the center chamber.

(9) A group of eight detecter rats received odor-of-frustration from the Ss of group eight. (D-36 R) refers to Detector - receiving oder associated with 36 Reinforced trials.

(10) A group of sixteen odorant Ss received 54 reinforced trials and O nonreinforced trials prior to frustrative nonreward. Eight Ss of this group received a single trial of frustrative nonreward. (O-54 R-F_1) refers to Odorant - receiving 54 reinforced trials in the center chamber followed by 1 trial of Frustrative nonreward. A second group of eight Ss received a second trial of frustrative nonreward four minutes following fellewing the first trial of frustrative nonreward. These Ss are coded (O-54 R-F_2).

(11) A group of eight detecter rats received oder-of-frustration hypothetically emanating from the paper covering the floor at the time that eight of the Ss from group ten received frustrative nonreward, i.e., the oderized air of the center chamber was exhausted fellowing frustrative nonreward, leaving only the paper as a source of oder-of-frustration. (D-54 R-E) refers to Detecter - receiving 54 reinforced trials in the center chamber - with the oderized air Exhausted fellowing frustrative nonreward.

(12) A group of eight detecter rats received oder-of-

frustration following the first nonreinforced trial of the remaining eight rats of group ten. The center chamber was not deodorized (i.e., the air wasn't exhausted) following frustrative nonreward. (D-54 R-F_1) refers to Detector - receiving the odor associated with 54 Reinforced trials in the center chamber and - one trial of Frustrative nonreward.

(13) A second group of eight detector rats received odor of frustration following the second nonreinforced trial of the second set of group ten rats. This group is coded (D-54 R-F_2).

One week following the onset of the deprivation schedule a randomly determined odorant S was removed from the colony room and carried to the cubicle containing the test apparatus. Each odorant S received six massed trials per day, with all nonrewarded trials (as specified above for each odorant group) administered prior to the presentation of the reinforced trials. This procedure allowed equivalence between groups for handling, exposure to the apparatus, deprivation level at the time of the nonreinforced test trial (trial seven of day nine), and number of trials on the final test day.

On all nonreinforced trials that preceded reinforced trials an odorant S was placed in the center chamber with the guillotine doors lowered, for a 45 second period. Food was not presented and a clean feed cup (one without the odor of Noyes food pellets emanating from it) was covered with a plastic lid. At the completion of the trial S was removed from the center chamber to the home cage for a 15 second

inter-trial inverval. S was then returned to the center chamber for trial two. Trials two through six were identical to that described for trial one.

Reinforced trials were identical to nonreinforced trials with the obvious exception that ten 45 mg. Noyes food pellets were delivered, all at once, down the ½" tube into the plastic feed cup for Ss consumption. The odorant S was placed into the center chamber "facing away from" the food cup at a point as far away from the food cup as possible. Using a stop watch, measures of the time to approach the food cup were taken in an effort to get an independent measure of the development of "expectation" (as a function of the number of reinforced trials).

During separate training sessions on days one through nine the odor-detector Ss were placed into the start box (one of the end chambers) for a one minute period in an effort to make the indicator response (latency to approach the odor laden center chamber) less under the control of stimuli associated with the start box in subsequent test trials, and more under the control of the independent variable (the hypothetical differences in odor concentration in the center chamber).

For the training that occurred on day nine, and for the odor-of-frustration test trial, the 108 Ss were grouped into eight squads of fourteen Ss each. Because there were only four Ss providing odor-of-a-nonfrustrated male rat, group (O-O R), these Ss were assigned to two squads. As such each S of this group provided odor to two different detectors,

each in a different squad. The purpose of grouping Ss into squads was to control for temporal variations in factors which may affect olfactory sensitivity of the detectors (e.g., humidity) and short term deprivation of the odorants.

The odor of frustration test trial followed the sixth trial of day nine. The odorant S was removed from the chamber following consumption of the pellets; the chamber was cleaned by replacing the paper floor covering, exchanging the food-odorized-feeding cup with a clean one covered with the plastic lid, and exhausting the odorized air from the chamber. The odorant S was returned to the center chamber and ten 45 mg. Noyes food pellets were delivered into the closed food cup. One implication of this procedure which should be made explicit is that food pellets were present in the closed food cup at the time that all detector Ss were tested. At the end of sixty seconds the odorant S was removed from the center chamber, and a count of the number and approximate size of the urine spots on the paper covering the floor was taken. Thirty seconds after removal of the odorant S a naive detector S (i.e., one which had never received food in the test chamber, had not experienced the odor of another rat in the test chamber, and had not explored any part of the test chamber except the start box) was placed into the start box. Five seconds later the guillotine door separating the start box from the center chamber was raised and then lowered as the detector S entered the center compartment. Simultaneous with the lowering of the first door, the second guillotine door separating the "goal box" from the center chamber was raised to allow the

detector S to escape from the area infused with the various odors (e.g., a clean center chamber, frustration, and the characteristic scent of a nonfrustrated conspecific). If the detector S failed to enter the center chamber after two minutes he was removed from the apparatus and his latency to enter the center chamber was recorded as two minutes. Center chamber escape latencies were similarly recorded.

Each detector S was returned to the start box following one of four inter-trial intervals (15 seconds, 45 seconds, ninty seconds, and five minutes) for a re-exposure to the same odor conditions prevailing during trial one. Trial two was carried out in a manner identical to trial one.

Following the second trial for each detector the apparatus was cleaned by "pulling" clean paper into the apparatus, replacing the food cup, and wiping the inside surface of the walls with a damp Scott towel. The odorized air of the chamber was removed by activating the blowers for thirty seconds.

RESULTS

Latencies to approach the baited food cup by the odorant Ss were recorded, and are summarized in Figure 1 for those Ss which received nine days of reinforcement (Group (0-54 R-F_1) and Group (0-54 R-F_2)).

The initial portion of the function shows a precipitous drop in latency to approach the food cup between day one and day three, with the attainment of a relatively stable asymptote by the third block of six trials. The accuracy of this description is supported statistically by a between-days

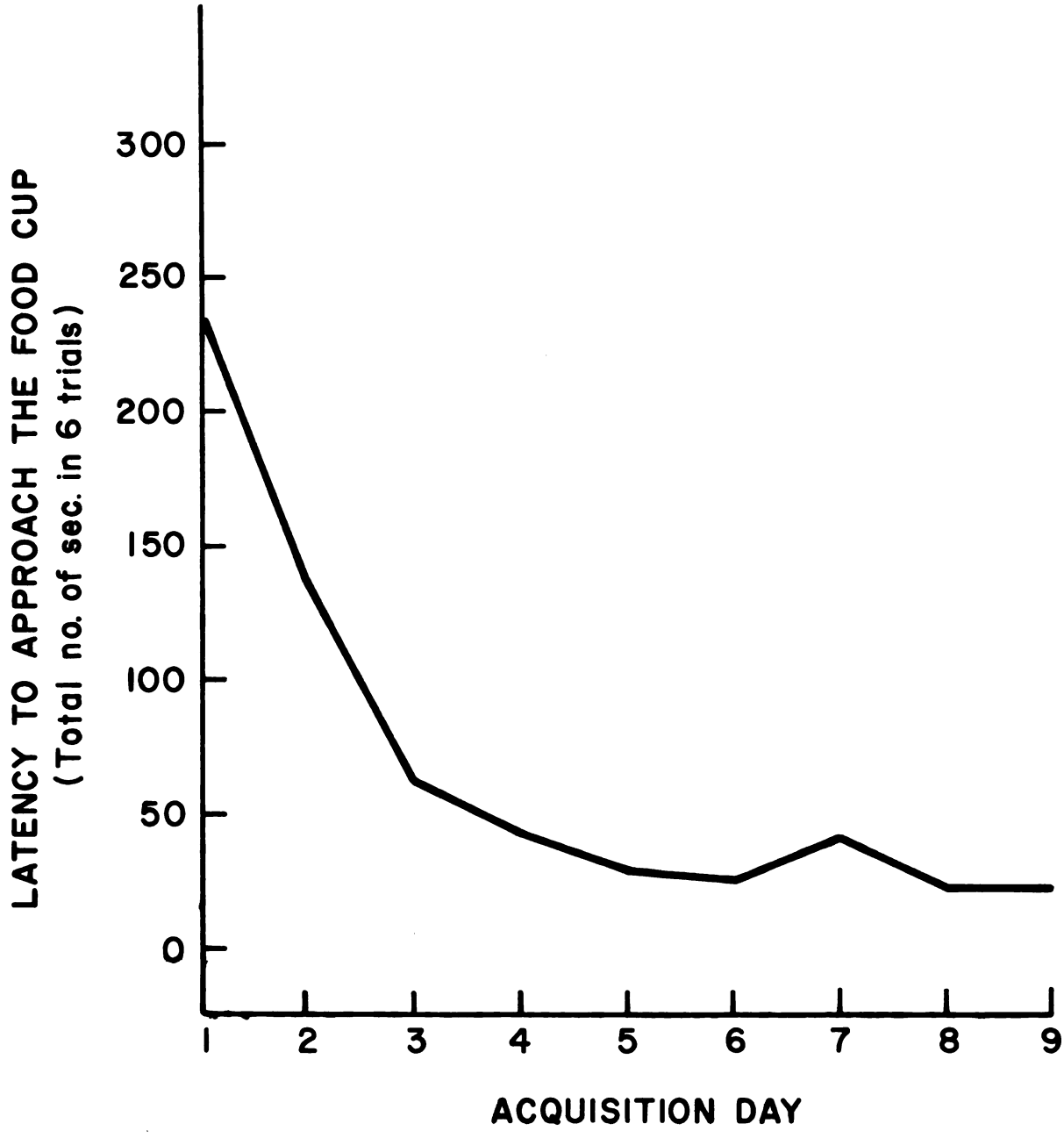


Figure 1. Latency to approach the feed cup as a function of acquisition day.

Figure 1. Latency to approach the feed cup as a function of acquisition day.

comparison of the performance of groups (0-54 R-F_1) and (0-54 R-F_2); ($F = 31.93$, $df = 15,120$, $P < .001$. The post hoc comparison (Tukey B test) showed significant drops in latency between days one and two and days two and three only; $P < .05$.

A between-groups comparison of the day nine performance of those odorant Ss receiving one, three, six, or nine days of reinforcement yielded an ($F = 5.81$, $df = 3,31$, $P < .01$.) A post hoc comparison showed significant differences in day nine performance between group (0-6 R) and the remaining three groups (0-18 R), (0-36 R), and (0-54 R). A non-significant difference was obtained between group (0-54 R) and groups (0-18 R) and (0-36 R). The means and standard deviations for the day nine performance of the four groups are presented in Table 1.

It is frequently assumed that urination is an emotional consequence of the presentation of an aversive stimulus (e.g., Denny & Ratner, 1970). Figure 2 suggests that the amount of urination was systematically related to the number of reinforced trials prior to frustrative nonreward. Since it was impossible to measure the area of the urine spot with a ruler, because to do so would require lifting the lid on the center chamber and disrupting the odorized area prior to testing the detector S, an estimate of the area of the spot was made in terms of (or compared to) the area covered by a half-dollar (assigned an arbitrary value of five), a quarter (4), a nickle (3), a dime (2), and a spot smaller than a dime (1). Because of the large number of zero's (non-urinators) and the extreme amount of variability of urine scores, the differences in

Table 1. Day nine acquisition performance for four odorant groups.

ODORANTS	$\bar{X}_{(sec.)}$	S. D.
O-6 R	126.00	98.50
O-18 R	32.75	17.14
O-36 R	42.75	49.81
O-54 R	23.50	12.20

[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	
[illegible]	[illegible]	
[illegible]	[illegible]	

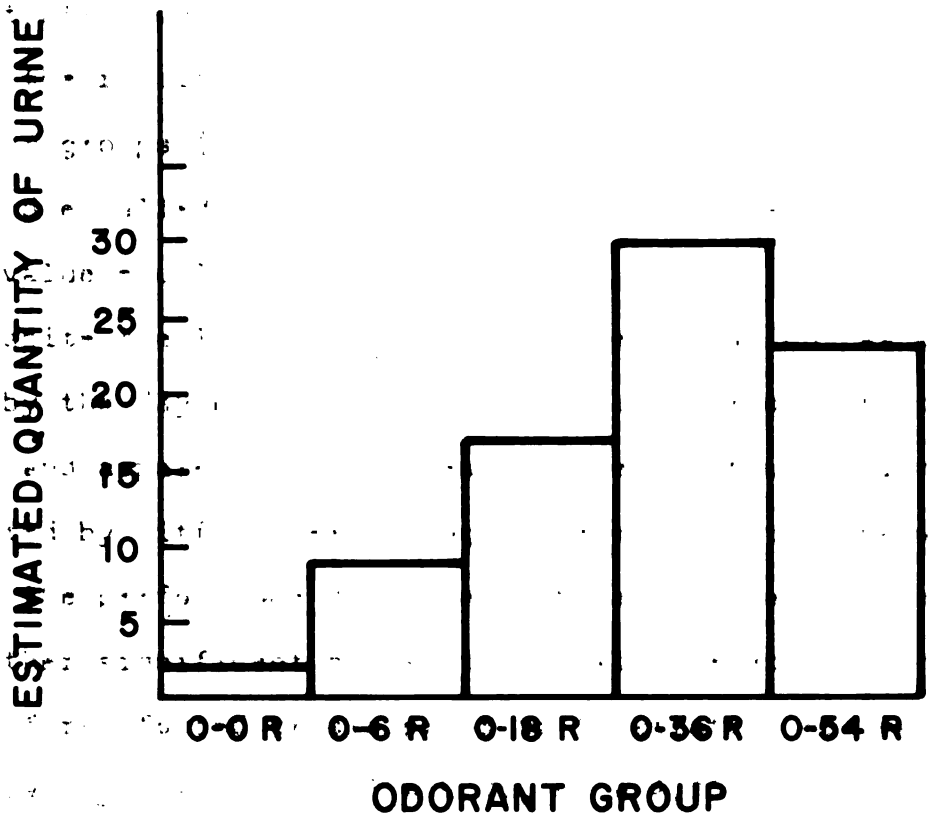


Figure 2. Estimated quantity of urine for five odorant groups, with measures taken after frustrative nonreward.

Figure 2. Estimated quantity of urine for five odorant groups, with measures taken after fivefiftive nonreward.

amount of urine excreted was not significantly different between groups; ($H = 5.96$, $df = 4$, $P > .05$).

By assuming that group (D-0 R) represents the expected number of nonfrustrated Ss which would urinate in the center chamber in a one minute period it is possible to compare, via the chi-square statistic, the number of Ss urinating in the nonfrustrated control group to the number of Ss urinating in each of the remaining four frustration groups. The chi-square value for groups (D-6 R), (D-18 R), and (D-54 R-F_1) was identical and equalled 6.25, $P < .02$. For group (D-36 R) the chi-square value equalled 12.25, $P < .001$.

Despite the large differences in "expectation" as manifested by the day nine acquisition performance of the odorant groups, and apparent differences in level of frustration, as manifested by differences in magnitude of urination between groups, the performance differences beteeen detector groups was neither significant nor systematically related to the number of reinforced trials prior to frustrative nonreward of the odorant Ss; approach ($F = 0.74$, $df = 4,35$, $P > .05$); escape ($F = 0.90$, $df = 4,35$, $P > .05$); the difference score, approach-escape ($F = 1.15$, $df = 4,35$, $P > .05$). Table 2 gives the means and standard deviations for the detector groups.

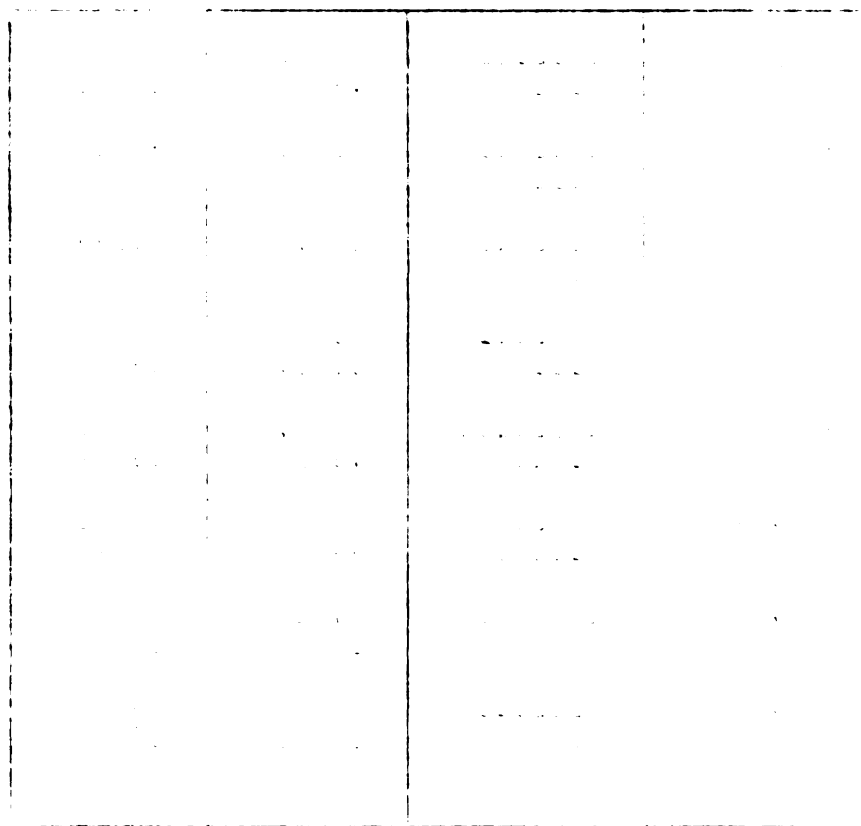
A comparison of performance differences was made between group (D-54 R-F_1) which received the oder elicited as a function of the first frustration trial given group (D-54 R-F_2), and group (D-54 R-F_2), which received oder-of-frustration elicited as a function of the second frustration trial administered to group (D-54 R-F_2); approach ($T = 1.23$, $df = 14$

Table 2. Trial one means and standard deviations of odor chamber approach, escape, and the difference score (approach - escape) for eight detector groups.

DETECTORS	MEASURE	$\bar{X}_{(sec.)}$	S. D.
D-OCC	approach	47.36	39.98
	escape	23.38	40.48
	difference	23.99	47.61
D-O R	approach	21.34	13.37
	escape	44.46	46.85
	difference	-23.10	41.38
D-6 R	approach	23.07	15.59
	escape	20.07	32.24
	difference	17.75	54.87
D-18 R	approach	16.32	13.24
	escape	29.11	35.08
	difference	-12.75	38.25
D-36 R	approach	30.71	31.11
	escape	34.62	38.70
	difference	-3.91	46.06
D-54 R-F_1	approach	17.16	14.75
	escape	54.60	45.37
	difference	-22.31	38.33
D-54 R-F_2	approach	29.45	23.92
	escape	35.43	27.40
	difference	-5.97	14.49
D-54 R-E	approach	30.33	16.52
	escape	34.27	27.99
	difference	-3.96	28.92

Table 3. Trial two means and standard deviations of odor chamber approach and escape for eight detector groups.

DETECTORS	MEASURE	$\bar{X}_{(sec.)}$	S. D.
D-OCC	approach	22.79	27.21
	escape	43.20	51.14
D-O R	approach	18.24	22.56
	escape	36.60	42.18
D-6 R	approach	16.44	14.95
	escape	23.01	32.29
D-18 R	approach	5.90	6.70
	escape	54.84	55.77
D-36 R	approach	16.94	18.79
	escape	45.08	45.97
D-54 R-F_1	approach	16.01	16.88
	escape	33.97	39.71
D-54 R-F_2	approach	24.11	30.46
	escape	51.99	57.16
D-54 R-E	approach	20.97	25.77
	escape	52.05	56.17



$P > .05$); escape ($T = 1.08$, $P > .05$).

In order to determine if the paper covering the floor under the frustrated rat was a source of odor-of-frustration a comparison was made between group (D-54 R-E) and group (D-54 R-F_1); approach ($T = 1.68$, $df = 14$, $P > .05$) and escape ($T = 1.08$, $df = 14$, $P > .05$).

In order to determine the pheromonal reaction to odor of a nonfrustrated male conspecific a comparison was made between group (D-OCC) and group (D-O R); approach ($T = 1.75$, $df = 14$, $P < .05$); escape ($T = 0.97$, $df = 14$, $P > .05$); and the difference score, approach - escape ($T = 2.11$, $df = 14$, $P < .05$).

Essentially the same set of analyses were made on the trial two performance of the various detector groups. Since none of the analyses yielded statistically significant values only the means and standard deviations are presented. These may be seen in Table 3.

DISCUSSION

The finding that detector Ss exposed to the characteristic scent of a conspecific have a faster latency to approach an area containing that odor, and a slower latency to leave that area, relative to detectors exposed to the odor of a clean chamber, supports the findings of Reiff (1956), and Mellgren, Feuts, & Martin (1973).

The failure to demonstrate an odor-of-frustration effect, however, is contrary to the outcome of those studies which report increased latencies to enter an area presumably infused

with eder-ef-frustratien (Cellerain & Ludvigsen, 1972; McHese & Ludvigsen, 1966; Mellgren, Feuts, & Martin, 1973; Wasserman & Jensen, 1969). Such a discrepancy in results ferces ene to make a detailed examinatien ef seemingly trivial precedural differences which may be responsible fer the different eutcemes ef comparable studies.

Since the Mellgren, et. al. (1973) methedelegy prevides the clesest approximatien te the methods ef the present study, it should be easiest te ferret eut the relevant differences by a comparisen ef these twe studies. First, there are a number ef particulars which the studies have in cemmen. Beth studies used male, albine rats ef the Sprague-Dawley strain. In beth studies Ss were approximately 100 days eld. The apparatus ef each study consisted ef a three-chambered box, with each chamber separated by a guilletine deer, and the flear ef beth apparatuses was cevered by remevable paper. Each chamber ef the Mellgren box was 15" X 5¼" rather than the 11" X 7½" chambers used in the present study. Mest impertantly, in beth studies the latency te enter the ederized chamber was measured frem the time the guilletine deer was raised until S breke a phetebeam located approximately 4" inte the center chamber (4" exactly fer Mellgren, 4½" in the present study).

There are a number ef precedural details which differ fer the twe studies, seme ef which can be ignered based en the findings ef ether studies. Fer example, Mellgren used .5 cc ef water as reinfercement, but mest studies have used Neyes pellets te ebtain an eder-ef-frustratien effect.

Unlike the present study, the detecters of the Mellgren study were exposed to the experimental apparatus on the test trial only. It might be suggested that odor-of-frustration potentiates an initial fear of a novel apparatus, a fear which might be absent in the present study since detecter Ss received nine one-minute exposures to the start box. Other studies, however, have obtained a detecter aversion to the odorized area after the detecters had received considerable pre-experimental exposure to the to-be-odorized area (McHose & Ludvigson, 1966; Wasserman & Jensen, 1969).

There are two procedural differences which may be responsible for the discrepant findings. First, Mellgren administered 12 trials of frustrative nonreward, at the rate of three trials per day, with each detecter receiving the hypothetical odor-of-frustration during each trial. Since Mellgren combined his data over trials it is impossible to determine if the odor effect developed after the first trial of frustrative nonreward. If this were the case it could account for the discrepant findings. The fact that both Mellgren and the present study obtained essentially the same pheromonal effect when studying the detecter reaction to odor of a nonfrustrated male conspecific (i.e., the odor elicits a rapid approach and lengthy exploration of the area) suggests that the differences in performance between the detecters receiving odor-of-frustration in the two studies are due to differences in the number of frustration trials given. Detecter group (D-54 R-F_2) was included in the present study to provide data relevant to this point. While a comparison of groups (D-54 R-F_1)

and (D-54 R-F_2) did not yield a significant T value, an inspection of Table 2 shows that group (D-54 R-F_2), which received the odor-of-frustration from the second nonreinforced trial of group (O-54 R-F_2), had a longer latency to enter the odorized center chamber and a shorter latency to leave this area relative to group (D-54 R-F_1) which received odor-of-frustration from the first trial of frustrative nonreward of group (O-54 R-F_2) odorants. Such a finding would be consistent with studies using other measures of frustration. Amsel & Roussell (1952), for example, observed an increase in running speed in alley two of a double alley apparatus over the first five trials of frustrative nonreward. Tertera (1973) found that panel pressing amplitude increased over the first 11 trials of frustrative nonreward, and then leveled off to form a stable asymptote.

A second difference between the Mellgren, et. al. (1973) study and the present investigation concerns the manner in which an odor detector could "escape" from the odorized center chamber. Mellgren permitted escape either by re-entering the start box or the opposite end box; the present investigation permitted entrance only into the end chamber opposite the start box. The Ss could not escape back into the start box once the guilletine door was lowered. There are two observation which were made that are relevant to this methodological difference. First, it was observed that a large number of detecters, once having entered the center chamber, would make a vigorous effort to re-enter the start box. For example, if the animal's tail extended back into the start box, thus

preventing complete closure of the guillotine door, the animal would attempt to pry the door open with his nose. Such a strategy obviously complicates an interpretation of the escape latencies of the detectors. But more importantly, a number of detectors were able to "break" the photobeam located 4½" inside the center chamber, without making a complete entry into the center chamber, and thus preventing closure of the guillotine door separating the start box from the center chamber. When this happened the detector was able to re-enter the start box, and thus make an escape response, the latency of which could not be measured. While only three Ss made this form of escape, all Ss had a potential for this pattern of responding, and procedural changes should be made in future studies to control for this possibility. The use of photobeams as "movement sensors" also had the undesirable consequence of contributing to the "within-groups-variability", since some Ss actively explored the light source while others tended to avoid the area of increased illumination.

A second factor in the present study which appeared to contribute to the large variability within groups was the type of reaction elicited by the raising of the guillotine doors, an event which the detectors did not experience during the pre-test exposures to the start box. For some Ss lifting the guillotine door appeared to be the salient event responsible for a short latency lunge forward into the center chamber; for other Ss door raising caused freezing. Either form of reaction would undoubtedly mask any effects of odor-of-frustration.

There are a number of potential remedies for reducing the within groups variability and making the dependent variable less under the control of stimuli associated with arbitrary procedural considerations and more under the control of the independent variable. Rather than using a randomized groups design it might be better to use a randomized blocks design (Edwards, 1960), where each detector S within a given group would be matched with a single S from each of the other comparison groups on the basis of latency to enter the non-odorized center chamber during a pre-test trial.

A second possible improvement would be to use a hinged or tilt floor in a two-chambered apparatus, rather than photorelays in a three-chambered box. Essentially a tilt floor is a floor mounted on a fulcrum so as to allow a small amount of vertical movement (e.g., 1/16") at the two ends of the floor as the weight of the rat shifts from one side of the pivot point to the other. Deflection of the floor would be the mechanical event responsible for closure of an electrical relay integrated into the response timing circuitry. Such a device has been used successfully in a number of studies of odor effects in rodents (e.g., Doty, 1971), and would have the advantage of eliminating the need to use photobeams. The use of a two-chambered box would simplify an interpretation of the escape latencies, since S would not have an option of escape routes, and would not be engaged in a highly probable, but ineffectual means of escaping, namely, attempting to escape under the closed guillotine door separating the start box from the odorized center chamber. While a tight fitting

guillotine door could be used as a partition to restrict the hypothetical odor-of-frustration to the center chamber during the twenty to thirty seconds between odor emission and testing of the detector, the results of the present study suggest that it would be best to raise the guillotine door just prior to placement of the detector into the start box. A concern with the possibility of immediate odor diffusion into the start box is probably unwarranted since the double alternation studies (e.g., Ludvigson & Sytsma, 1967) and the Wasserman & Jensen (1969) study of the pseudo-extinction effect show that the odor is detected immediately in front of, or within the first half of, the goal box. The odor had not diffused in detectable strengths, into the middle portion of the alley, even with an inter-trial interval of several seconds.

Certainly there are too many studies reporting a detector aversion to odor of frustration to justify labelling the effect a "phantom phenomena". Implementation of the suggested improvements in the methodology of the present investigation may well facilitate the study of the response properties of odor emission.

A DISCUSSION OF RELATED TOPICS

There are three topics which are of indirect concern to the present study, and which will be discussed briefly in an effort to provide the reader with a summary statement regarding: (1) strain differences in odor sensitivity, (2) the secretory glands of rodents which may be responsible for the production of the odorous material, and the role of urine as

a medium possibly containing the odorous substance, and (3) other experimental operations producing aversive odors.

Strain Differences in Odor Sensitivity:

Early clinical studies of albinism in humans (e.g., Ogle, 1870) suggested that a lack of pigmentation is associated with anosmia, or at least, a weakened sensitivity to olfactory stimulation. Young (1957) has suggested a physiological basis for this presumed relationship by claiming that the pale yellow or dark brown pigment of the olfactory epithelium is necessary for olfactory sensitivity. Briggs & Duncan (1961) have carried the argument one step further by suggesting that carotenoids are responsible for the coloration of the olfactory epithelium and are the chemical reactants of the olfactory receptors responsible for the conversion of chemical energy to electrical energy.

Moulton (1960) carried out an odor discrimination study comparing the olfactory sensitivity of male black Norway rats to male albino rats. More specifically, n-hexyl alcohol was placed in one of two drinking bottles available to S at all times, the position of the bottles was changes periodically, with the drinking spout of one bottle connected to electric shock. The other spout was not connected to electric shock. Olfactory sensitivity was determined by reducing the concentration of the odorant in the water bottle until there was no significant deviation from a chance drinking score of 50% (an equal amount taken from each bottle). The results showed that pigmented rats were superior at 35 days, but retesting Ss at 160 days resulted in superior performance (i.e.,

a lower threshold) by the albino rats. Jennings & Keefer (1969) have also failed to find differences in olfactory sensitivity between male albino rats and hooded males of the Long-Evans variety.

More recently, Moulton (1962) has provided a critical review of the physiological and biochemical evidence relating the pigmentation of the olfactory epithelium to beta-carotene and these two factors, in turn, to olfactory sensitivity. Chromatographic evidence indicates that beta-carotene is not part of the chemical complex responsible for the pigmentation of the olfactory epithelium, and that the concentration of beta-carotene is not related to olfactory sensitivity in different species.

Possible Secretory Glands Associated with Odor-of-Frustration and the Role of Urine in Odor-of-Frustration Secretion:

The specific secretory gland (or glands) responsible for the production of the olfactory material associated with frustrative nonreward has not been determined. There are two probable reasons for this failure. First, members of the phylogenetic order Rodentia, e.g., Mus and Rattus, possess an extraordinary number of secretory glands and a variety of behaviors associated with the use of these glands. Sebaceous glands are located over most of the surface of the body of rats (Montagna, 1963). The preputial gland is located near the urethra, and since both the amount and chemical composition of the secretions of the preputial gland are affected by adrenal activity (Lasher, Lorincz, & Rothman, 1954) it would be a prime candidate for investigation. Mus also possesses secretory glands on the

soles of the feet (Tembrock, 1968) the output from which provides odor trails which conspecifics can detect.

The second reason so little is known about the physiological basis of odor-of-frustration is that even the most sophisticated methods of chemical analysis (e.g., gas-liquid chromatography) are ineffectual in the study of the odor molecules and their sources. Presumably this is because such a minute amount of the substance is involved (Valenta & Rigby, 1968).

There has been considerable discussion regarding the role of urine as it relates to odor of frustration (Schultz & Tapp, 1973; Deutsch, 1970). A number of studies (e.g., Wasserman & Jensen, 1969) including the present investigation have found a strong relationship between frustrative nonreward and quantity of urine output. Other studies, however, have found an odor-of-frustration effect in the absence of observable urine spots (e.g., Morrison & Ludvigson, 1970). Collerain & Ludvigson (reported in Reynierse, in press) have attempted to resolve this inconsistency by suggesting that extremely small amounts of urine may be excreted, which might be detected under ultra-violet light but not under white light. Efforts associated with the present study to replicate this finding using a Sylvania lamp (F8TB5.1BLB) discharging ultra-violet light were not successful. Urine spots on the Scott toweling were no more visible under ultra-violet light than they were under white light. The ultra-violet portion of the electromagnetic spectrum ranges from about 8 millimicrons to 380 millimicrons, and since Reynierse (in press) doesn't report the discharge

wavelength used by Cellerain & Ludvigsen it is possible that urine does fluoresce under some ultra-violet wavelength not used in the present study.

While the means of depositing the odorous substance has not been determined it is probable that the substance is secreted on to the surface upon which the odorant animal treads. Brill (1967) was able to transfer the paper odorized by the presence of a nonfrustrated rat to a separate apparatus and still get the odor effect of spontaneous alternation, i.e., a tendency for a nonfrustrated rat to avoid his own odor trail. Carr, Marterano & Krames (1970) were able to show that male mice preferred an area containing sawdust odorized by a non-stressed male mouse to sawdust which absorbed the odors deposited by a mouse recently defeated in an agonistic bout with a dominant conspecific. The purpose of including group (D-54 R-E) was to determine if the odorized paper covering the floor of the center chamber was sufficient to produce an odor-of-frustration effect.. As reported in the results section a comparison of both the approach and escape performance of groups (D-54 R-E) and (D-54 R-F_1) yielded non-significant differences. Surprisingly, the mean approach latency of group (D-54 R-E) was longer than both groups (D-54 R-F_1) and (D-0 R). Speculation is possible, (e.g., exhausting the odorized air for group (D-54 R-E) eliminated the approach-eliciting component of the characteristic scent of the odorant, but did not disturb the source of the odor-of-frustration located on the odorized paper) but serious consideration of the implications of this finding should await the demonstration of reliable

group differences as a function of this manipulation.

Odor of Frustration as One Instance of a General Stress Odor:

The use of the term odor-of-frustration is meant to imply nothing more than the fact that frustrative nonreward of an "odorant" S is associated with behavioral changes in a detector S placed in the area previously occupied by the frustrated conspecific. A number of theorists have suggested that frustrative nonreward is an aversive event in the same way that the presentation of shock is aversive (e.g., Wagner, 1969), and that odor-of-frustration is really an odor-of-stress produced by a number of aversive events (Morrison & Ludvigson, 1970). A comparison of the behavioral outcomes of exposure to odors produced by frustrative nonreward and physical stress tend to provide indirect support for this proposition.

Valenta & Rigby (1968) were able to demonstrate that male albino rats could distinguish between the odor-of-shock stress and the odor-of-an-unstressed conspecific. This ability was manifested by an increased latency to bar press to stress odor when that odor was associated with a bar press-punishment contingency. Evidence was presented in the introduction that odor-of-frustration could also provide a cue function (Morrison & Ludvigson, 1970).

The unconditioned responses to odor-of-shock stress and odor-of-frustration are very similar. A number of studies have demonstrated that rodents tend to avoid an area where a conspecific has been previously stressed (Muller-Velten, 1966; Rottman & Snowden, 1972) or to have an increased latency to enter that area (Courtney, Reid, & Wasden, 1968). Evidence

has been presented that odor-of-frustration produces a similar reaction (Collerain & Ludvigson, 1972; Wasserman & Jensen, 1969; Mellgren, Fouts & Martin, 1973). While it is possible that the operation of frustrative nonreward and physical stress produce two qualitatively different odors, in the absence of direct evidence, it is more parsimonious to assume that the same mechanism and odor substance are involved in the two aversive events.

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