Different odors in rats from large and small rewards

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Although rats emit different odors in a goalbox upon receipt of unsignaled reward and non-reward, recent studies have failed to find odor differences from unsignaled large and small reward, apparently disconfirming the generalization that frustration-producing manipulations lead to a distinctive emission. Experiment 1 tested the hypothesis that providing discriminative runway signals, permitting subjects to anticipate the large and small rewards, would lead to different odor emissions. Results supported the hypothesis: donor rats emitted odors sufficiently different to provide cues for differential responding in test subjects. However, an attempt to replicate the recent observations on unsignaled rewards suggested that these, too, occasioned goalbox emissions. Therefore, Experiment 2 again gave donors unsignaled large and small reward, but increased the incentive for discrimination in test rats. Test subjects readily discriminated, confirming the conclusion that large and small rewards occasion different emissions even without discriminative signals and supporting a frustration-odor interpretation.

Although many studies have found that laboratory rats excrete different odors upon receipt of unsignaled reward and nonreward on a partial reinforcement schedule (e.g., Amsel, Hug, & Surridge, 1969; Howard & McHose, 1974; Ludvigson, 1969; Ludvigson & Sytsma, 1967; McHose & Ludvigson, 1966; Pitt, Davis, & Brown, 1973), recent data have suggested that similar schedules of large and small rewards do not occasion different odors (Burns, Thomas, & Davis, 1981; Davis, Burns, Howard, & Voorhees, 1982; Davis & Weaver, 1981; Davis, White-side, Bramlett, & Petersen, 1981). This latter suggestion is surprising, since prior studies employing frustrative treatments have found evidence for distinctive odor emissions, and large versus small incentive contrast has usually been considered a frustrative operation. Davis et al. (1981) suggested their data could reflect a "lack of perfect correspondence between the elicitation of frustration and odor production" (p. 381).

Davis et al. (1981) suggested that although reward magnitude contrast per se fails to occasion differential odor, entrance into an empty goalbox prior to the delivery of a relatively small reward after a delay interval certainly does. Rather than accompanying frustration, then, the emitted odor might be playing the adaptive role of "signaling *no reward* to conspecifics" (p. 381, *italics added*). The "food vs. no food" hypothesis elaborated by

Voorhees and Remley (1981) as an alternative to a "frustration odor" interpretation, though not addressed to the Davis et al. results, could be construed as compatible with them. They suggested that a rat may emit an "ethologically significant odor (pheromone) when encountering food, thereby signaling the location of food to conspecifics," and that "when encountering food stimuli . . . , but no food, the rat emits a pheromone signaling 'food is no longer at this location' to conspecifics" (p. 169). The provocative suggestion of Davis et al. is that the odor emission, while varying with presence versus absence of reward, does not vary with greater-than-zero magnitude of reward. Presumably, upon receipt of a small reward a rat might register a discrepancy between expected and received reward and even exhibit a frustration response, but not emit a "frustration odor" so long as some reward was present. The implication for adaptation would presumably be that gene pool survival is more served by signals of food and no-food-when-expected, than by signals of relative food abundance or accompanying emotional reactions.

Given the importance of the differential-reward manipulation for our understanding of odor functioning, as well as frustration and perhaps even adaptation, further analyses seem imperative. In the recent problematic studies, the rewards were unsignaled—only upon arrival in the goalbox could the rat learn whether large or small reward awaited it, and at that point the rat could immediately consume the reward.¹ Perhaps the reward process produced by receipt of small reward is antagonistic to frustration-odor production, as, indeed, it may be to frustration (cf.

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Daly & Daly, 1982, p. 452; Ludvigson & Gay, 1967). Though receipt of small reward may inhibit frustration odor, anticipation of small reward may not. Therefore, Experiment 1 tested the hypothesis that anticipation of a small reward, aroused by a reward signal some distance from the goal, leads to a frustration-odor emission, whereas unsignaled receipt of small reward does not.

It may be noted that the topic of anticipatory odors, odors emitted as a response to a signal of a goal event, has remained virtually unexplored since the first study in this series (McHose & Ludvigson, 1966). That study involved anticipatory odors and contrasting reward magnitudes. However, delay of reward, that is, entry into an empty goalbox, was involved also, rendering it uncritical for the issue at hand.

EXPERIMENT 1

To determine whether anticipations of large and small rewards generate different odor emissions, a standard differential conditioning procedure in a runway was used with donor subjects. As these subjects (Group LB) emerged from the startbox, they received a discriminative cue (a light-buzzer combination) announcing whether the impending goal event was large or small reward. Following each donor, a test subject received a trial with the same goal event, large or small reward, received by the donor. However, the test subject's only discriminative stimuli for the goal events were differential odors, if they existed, emitted by the previous donor. Any such odors emitted during the donor's anticipation would initially be encountered near the start end of the runway. Thus, if anticipations of large and small rewards generate different odors, the test animals (Group SO) would receive "start odor" cues and should display discriminative responding throughout the runway.²

Treatment for the third group of subjects, the unsignaled group, was like that in Davis et al. (1981). These subjects, run in succession, received the same rewards as the other groups, with all receiving either large or small on a given trial. However, the only discriminative cues signaling these events were different odors, if they existed, emitted by preceding members of the group as they received reward. Thus, this group (Group GO), having only "goal odor" cues, would not be expected to display differential responding, were the Davis et al. (1981) results to be replicated, or would display only a late-runway discrimination, were odors to arise from unsignaled rewards.

Method

Subjects. Subjects were 38 experimentally naive male rats from the Holtzman Co., about 90 days old at the outset. Approximately 2 weeks prior to gentling and handling, a limited food regimen was begun which reduced their weights to 85% of their preexperimental ad-lib levels. Water was continuously available.

Apparatus. A 2.13-m alleyway, fully described in Eslinger and Ludvigson (1980), was used. Stainless steel inserts lined the goalbox walls and floor; white paper flooring covered all sections. Pho-

tocells located 50, 75, 136, and 166 cm from the start door permitted measurement of start, run, and goal speeds, expressed in centimeters per second. In addition, a start-door microswitch allowed an orient speed measure expressed as 100/sec. Light, diffused through Plexiglas from a string of 100-V 7-W lamps located 50 cm above the top of the runway, could be lighted as a subject emerged from the startbox. Similarly, a buzzer, located on the outside of the startbox, could be activated.

Procedure. The subjects received 2 min of gentling and handling on Days 1 and 2, and 5 min of apparatus habituation on Days 3 and 4. The subjects were placed singly into the middle of the runway with all retrace doors open, facing the startbox with the light cue on on Day 3 and facing the goalbox with the light cue off on Day 4. After habituation, the subjects received four 45-mg Noyes pellets in the home cage.

The subjects were assigned randomly to three groups. Group LB had light and buzzer cues as signals for goal events. For half the group, they signaled large reward (20 45-mg food pellets from the Noyes Co.); for the other half, they signaled small reward (1 pellet). Groups SO and GO received light-buzzer presentations uncorrelated with goal events, as indicated in the schedule below.

Squads of rats, called LB+, LB-, and GO, were constituted in each of two replications. The rats received trials in rotation within squads. That is, all members of the squad received a trial before the squad, in the same order, received another trial, and all members of a squad received daily trials before the rats in the next squad received their trials. The six subjects that ran in Squad LB+ were the animals from Group LB in Positions 1, 3, and 5 and the animals from Group SO in Positions 2, 4, and 6. For this squad, light and buzzer signaled large reward for Group LB's members. Squad LB- was similarly composed, but light and buzzer signaled small reward for the Group LB members. Seven subjects, all from Group GO, made up Squad GO. Data from the first subjects in Squads GO were omitted, since these subjects were solely odor donors for subsequent squad members. In Replication 1, order of running of Squads LB+ and LB- alternated daily; Squad GO rotated through first, second, and third positions every 3 days. In Replication 2, running order of Squads LB+ and LB- also alternated daily, but Squad GO was run separately, approximately 120 days after Squads LB+ and LB- began training.

The subjects received two large (L) and two small (S) reward trials per day. On S trials, time in the goalbox was 30 sec, and on L trials, time in the goalbox was as long as needed to consume the reward, which was approximately 30 sec. Subjects within a squad received the same goal event on a given trial. The following daily reward sequences were repeated every 6 days: LSSL, LLSS, SLLS, SSLL, LSLs, and SLsL. For Groups SO and GO, the following uncorrelated cue sequences were repeated every 6 days: CCCC, CCCC, CCCC, CCCC, CCCC, where C means light-buzzer and $\bar{C}$ means no light-buzzer.

During training, the subjects were transported, via a carrying cart, to a holding room adjacent to the experimental room. A white-noise generator masked auditory cues in the holding room. A subject was carried to the experimental room in its home cage, given one trial, and then either returned to the holding room (Replication 1) or placed in a carrying cart outside the room (Replication 2).

To begin a trial, the experimenter placed a subject into the startbox facing away from the start door. When the subject faced the door, the experimenter opened it, and, if scheduled, delivered light-buzzer cues until the subject was removed from the goalbox. Orient speed was timed from startbox placement to start door opening. When the subject entered the goalbox, the experimenter closed the goal door and delivered reward via a pellet dispenser. On the rare occasions in early training in which an animal dawdled in a section of the alley to the extent that 60 sec elapsed on a clock, it was gently nudged forward into the next clock section.

To remove odors after completion of a trial for a squad, food cup, metal insert, and paper flooring were removed, runway air was evacuated for 60 sec, and clean cup, insert, and flooring were put in place.

Results and Discussion

Group LB, the donors for Group SO, readily utilized the light-buzzer cue to anticipate the reward conditions by running fast to large reward and slowly to small reward, as is evident in Figure 1. Analyses of variance of the data from Group LB over the last 18 days, using the pooled interactions with subjects as the error term and collapsing across replications, confirmed that speeds were faster on large-reward trials in all measures except orient speed [$F(1,385) = 212.8, 186.5$, and 116.2 for start, run, and goal measures, respectively; $p < .001$].

Since Group LB clearly anticipated the large and small rewards, any differential odor production that might have accompanied the differential response should have been emitted in the alleyway and been available for detection by subjects in Group SO. That such differential odors in fact were emitted is evidenced by Group SO, as revealed in Table 1, since their only cues for differential behavior were the odors left by Group LB. Analyses of Group SO's data, in the manner of the analyses of Group LB's data, yielded significantly faster responding on large-reward trials in all response measures. Therefore, large and small rewards appear to occasion different odors while their receipt is being anticipated.

In contrast with recent data, results from Group GO suggested that even actual receipt of different reward magnitudes, as opposed to anticipation of them, produces differential odor, since the only basis for discrimination

Table 1
Mean Speed for Groups SO and GO on Large (L) and Small (S) Reward Trials for the Four Response Measures over the Last 18 Days of Experiment 1, Along with F Values for L-S Comparisons

Measure	Reward	Group			
		SO		GO	
		Mean Speed (m/sec)	F	Mean Speed (m/sec)	F
Goal	L	55.3	40.67†	43.6	14.74†
	S	47.5		40.8	
Run	L	87.2	13.26†	77.2	13.77†
	S	82.0		73.3	
Start	L	40.7	19.4†	33.0	n.s.
	S	37.7		31.7	
Orient	L	68.6	5.55*	61.2	n.s.
	S	65.3		58.8	

Note— $df = 1,385$. * $p < .05$. † $p < .001$. n.s. = $p > .05$.

in this group was, by design, odor cues from prior animals' goal experiences (see Table 1). Supporting this conclusion is the observation that discrimination occurred in only those alley segments, goal and run, in which the odors should have been maximal. These data, then, conflict with those from Davis's laboratory. Since our conditions for Group GO were highly similar to those of the Davis studies, the reason for the conflict is not apparent. It may be noted that the size of the effect in our data was small; presumably the effect is not easy to detect with this procedure.

EXPERIMENT 2

Experiment 1 not only indicated that different odor emissions result from anticipation of large as opposed to small reward, it also suggested that odor emissions are different even after receipt of unsignaled large and small rewards. Since this latter effect was small, and its occurrence is in conflict with observations from the Davis studies, a second experiment was undertaken to explore just this effect. In order to provide a more sensitive test of this effect, some subjects (test subjects) were given added incentive to respond differentially to any odors generated by large versus small reward. That is, in Experiment 1 and in the Davis studies, squad members in succession received identical treatments on a given trial, making each rat simultaneously a donor for subsequent rats and a test rat with respect to odors emitted by preceding rats. Thus, the incentive conditions for responding differentially to odors from large and small reward were these same large and small rewards. In Experiment 2, squads of four rats received trials in rotation, with the first three members of the squad treated as before, that is, given large and small rewards. However, the fourth rat in the squad received large reward and nonreward. These latter "test" rats, therefore, had greater differential incentive for displaying discrimination of any different odors emitted by the preceding donors on large- and small-reward trials.

Figure 1. Orient speed (100/sec) and start, run, and goal speeds (cm/sec) for Group LB. Ordinates for orient and run speeds are at the left; ordinates for start and goal speeds are at the right.

Method

The method was identical to that of Experiment 1 except for the following. The subjects were 24 rats. Light/buzzer cues were not provided; the lights over the runway were constantly illuminated. The rats were assigned randomly to four groups: D1, D2, D3, and Test. Each of six squads contained four rats, one from each group, with trials for squad members given in a fixed, repeated order indicated by the listing of groups, above. The squads received training in different random orders over a 9-day period, and then the schedule was repeated.

On half the trials, the subjects received the large reward; on the other trials, the subjects in Groups D1, D2, and D3 received the small reward, but Test subjects received an empty food cup. Confinement in the goalbox was about 30 sec on all trials. On a given trial, all subjects in a squad received either the large reward or the small (or zero) reward. As a control for extraneous cues, the subjects began a trial in one antechamber, were transported singly to the experimental room, and were placed in a third room after the trial. Thus, no rat was in the presence of another that had finished a trial just prior to its trial.

Training phase. On the 1st and 2nd days, the rats received only one and three rewarded trials, respectively. Thereafter, for 24 days, the following daily trial sequences, which equated first-order conditional probabilities within days, were used, where L and S designate large and small (or zero) reward, respectively: LLSLSS, LLSSLS, LLSSSL, LSSSLL, SLLLSS, SLSSLL, SSLLSL, and SSLSLL. These daily sequences were ordered randomly and independently for squads over days. Odors were removed as in Experiment 1 after each trial for a squad.

Control phase. To be certain odor cues were in control of discrimination, odors were removed on half the trials for 4 days following training. That is, on half the trials, odors were removed after each subject's run, instead of after runs by all four subjects of a squad as had otherwise been done. Only four trials were given per day, utilizing the following daily sequences of large and small (or zero) reward: LSS $\bar{L}$, SLL $\bar{S}$, LSL $\bar{S}$, SL $\bar{S}$ L, where $\bar{S}$ and $\bar{L}$ refer to trials on which odors were removed. Squads received different orders of these sequences over days. Odors were removed in the same manner as before.

Results and Discussion

Training phase. The data from the test subjects revealed significantly faster speed on rewarded trials than on nonrewarded trials [$F(1,20) = 12.79$, $p < .01$] in the goal speeds over the last 14 days of the training phase (see Figure 2). Since the cues for this differential responding must have come from preceding donor subjects that had experienced large and small rewards, it may be concluded that these reward events generate different odors even after they occur. The rather sizable difference that occurred in this study, compared with the small differences from Group GO in Experiment 1, can presumably be attributed to the greater difference in incentive for detecting odor differences.

Other differences between speeds on favorable versus unfavorable reward trials were not significant in any group. One additional result was noteworthy: Group D1 ran considerably faster than other groups on both large- and small-reward trials at the goal end of the alley. The fact that the three groups that might have displayed a differential response, assuming the presence of differential odor cues, all ran considerably more slowly overall in the goal measure than the one group (D1) that had no differential cues available suggests that even donor Groups

Figure 2. Orient speed (100/sec) and start, run, and goal speeds (cm/sec) for Group T during training (Blocks 1-13) and control (Blocks 14-15) phases. Ordinates for orient and run speeds are at the left; ordinates for start and goal speeds are at the right.

D2 and D3 were developing or attempting a discrimination. That is, when a discrimination occurs in this type of task, it tends to be accompanied by a general slowing of response (cf. Ludvigson & Sytsma, 1967), presumably because of the time needed to detect and process the discriminative cues.

Control phase. Data from the control phase, in which odors were removed from the alley on half the trials, are presented for Group T in the right-hand panels of Figure 2. The sizable difference in goal speed on reward and nonreward trials evident at the end of the training phase persisted on trials in which odor cues were undisturbed, but completely disappeared on trials in which odors were removed. Using a pooled error term of all interactions with subjects, the interaction between goal events and presence-absence of odor was significant in goal speeds [$F(1,75) = 8.72$, $p < .01$]. In the other measure suggesting a discrimination, goal speeds for Group D2, the results were similar [$F(1,75) = 7.04$, $p < .01$] for the goal events $\times$ presence-absence of odor effect. The control phase thus substantiated the inference that different odors were emitted as a result of unsigned differential reward magnitude.

GENERAL DISCUSSION

The most immediate importance of the present studies is as a counterbalance to the view that large and small

rewards, delivered immediately upon completion of an instrumental response, do not engender differential odor, and that, therefore, odor arising from nonreward may not be a perfect correlate of frustration processes. Results of the present studies should at least argue against a hasty rejection of the "frustration odor" hypothesis.

The present data not only stand in opposition to those that suggested that receiving differential reward produces no odor differences, they also clearly demonstrate for the first time that anticipation of differential reward produces differential emissions. That is, the present studies permit inferences of odor emissions stemming from both unsignaled goal events and signals of goal events.

Why the present data are in fundamental disagreement with the Davis studies is uncertain. However, aside from subtle procedural differences such as number and order of large and small rewards in a day, these considerations seem relevant: (1) The odor differential from large and small reward may be small; for reasons discussed above, our Experiment 2 used a more sensitive measure than did other studies. (2) Prior studies showing no effect of large and small reward, when employing a procedure in which the subject is both donor and test animal, cannot distinguish between absence of different odors and absence of different responses to odors as the cause; only in Experiment 5 of Davis et al. (1981) were these factors separated and absence of differential odor implicated for four test rats, three of which could have failed to display differential performance because of generalization decrement. (3) In some, though not all, of Davis's results, a small effect in the expected direction appears, although it is not reported as significant.

Like most behavioral studies, these studies speak only indirectly to the nature of the odor differential. However, they do lead to an inference which most prior behavioral studies do not permit. In the present studies, the following are among the potential sources of odor differentials: (1) different amounts of time available for the concentration of a single substance that the rat constantly emits at a given rate, (2) different rates of emission of a single substance produced by different amounts of bodily movement, (3) different rates of emission of a single substance initiated by the rewards or signals thereof, and (4) qualitatively different emissions initiated by the rewards or signals thereof, with or without accompanying differences in rates of emission. These will be considered in turn.

(1) The first obviously includes odors associated with the subject as an individual, a member of a certain species or sex, and so forth. In addition, since a "constantly" emitted substance would only have to be constant for the duration of a session or even a trial, this category also includes undifferentiated anticipation of reward, large or small, and undifferentiated anticipation of frustration for small reward. This category could be the source of an odor differential in Group LB (Experiment 1). However, it is not likely the source of the differential in Group GO (Experiment 1) or Group T (Experiment 2), because time

in the goalbox was roughly the same on all trials. In Group LB, the odor differential arose from anticipation of rewards in the runway, not just from receipt of reward in the goalbox. In addition to discounting this category on grounds of parsimony, it seems implausible even for Group LB. Although subjects in Group LB spent more time in the runway on large- than on small-reward trials, the difference was small, for example, about .4 sec per 10 cm of traversal at maximum discrimination in the start section.

(2) The second source of an odor differential, emission rate correlated with amount of movement, is possible for Groups GO and T, since for them more movement in the goalbox occurred on small- than on large-reward trials, but implausible for Group LB. Again, the small runway time difference on large- versus small-reward trials indicates only a small difference in movement vigor. Incidentally, since most prior studies have manipulated goalbox odors, the data of Group LB are among the few available to test the movement hypothesis.

(3) Different emission rates of a single reward-initiated substance, or "odor of reward," has difficulty explaining the data of the control phase in Experiment 2. Removing odor cues resulted in response speeds equal to or faster than speeds to odors from large-reward trials in those response measures giving evidence of discrimination, notably the goal speed for Group T (see Figure 2). If different amounts of an odor of reward had controlled the discrimination, introducing a "clean" odor (background odor only) should have produced slow responses, because clean (absence of relevant odor) should be more similar to the lesser amount of odor of reward.³

(4) The present data are most readily explained by the postulation of qualitatively different odors on large- and small-reward trials, such as odor of reward versus frustration odor. The small difference in time in the runway on large- and small-reward trials poses no problem. Similarly, the control-phase results, where removal of relevant odor cues led to fast responses, seem explicable only under the assumption of an important role for a distinctive cue occurring on small-reward trials. In fact, the results are precisely what would be expected had frustration odor on small-reward trials been the only effective cue, with odor of reward absent, below threshold, or of very low salience. Frustration odor would also be implicated if the rat processed the stimuli such that the effective cues were presence versus absence of the S- discriminandum, the signal of the less desirable alternative.

In sum, then, these studies support the postulation of a qualitatively distinct "frustration odor." Although an "odor of reward" may well be emitted, postulation of such an odor is insufficient to explain these data, and, at best, an odor of reward seems to have been relatively ineffective in controlling discriminative behavior.

The exact meaning of "frustration odor" implied by these results, as well as its relevance for adaptation and ethological functioning, can be clarified by reference to contemporary learning theory (e.g., Mackintosh, 1983).

Experience with a reinforcer may be assumed to produce in the animal a representation of the goal experience, a representation that not only determines the nature of learned behavior but in this case may be assumed to control, or at least accompany, odor emission. Such a representation might include (1) sensory attributes of the goal experience itself, (2) the animal's expectancy of reinforcement prior to the delivery of the reinforcer, and (3) the animal's affective reaction to the goal experience.

What the Davis studies seemed to suggest was that a reward odor emission was triggered by, or covaried with, the mere presence of sensory attributes arising from food, irrespective of attributes encoding quantity of food, expectancy of food, or the affective reaction. The present work rejects that inference: the odor "trigger" must be (1) the affective reaction, or (2) food attributes, including quantity, along with expectancy. The expression "frustration odor" is probably best reserved for the former of these possibilities, but clearly the second possibility (perceived quantity discrepancy) is not ruled out by the present data, despite the use for convenience of the expression "frustration odor." The distinction between these two mechanisms, expressed by Voorhees and Remley (1981) in slightly different language, may be reflected in ethological functioning, that is, in the reactions of conspecifics to the emitted odors. Presumably, rather different effects might be expected, with that of a true frustration odor perhaps extending to general aggregation and social interaction, and that of a signal of relative food abundance restricted to foraging. Either effect, however, might be ethologically significant in the sense of affecting adaptation and survival. It remains for further work to determine which mechanism is, in fact, involved and exactly how adaptation is affected.

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NOTES

1. Clarification of "unsigned" goal events in this context is in order. In some studies (e.g., Morrison & Ludvigson, 1970), odors are emitted by a donor subject without the availability of a prior discriminative signal of the particular goal received. In this case, unsigned goal events are clearly the controlling factors. However, in the Davis and present studies of "unsigned" goal events, the situation is more complex. Here, the method is that introduced by Ludvigson and Sytman in 1967 and widely used thereafter: for efficiency, rats are run in an alley in succession, all receiving the same goal event on a given trial. The first subject serves solely as a donor, but subsequent subjects both respond to previously emitted odors and themselves donate emissions. The second subject has available, at the goal end of the runway, the first subject's goal odor, that is, an odor from an unsigned goal event. The second subject can, and certainly does, utilize that goal odor as a signal of its impending goal event. Its emission may, therefore, be at least partly an anticipatory odor arising from the first subject's odor signal. In this sense, the third and subsequent subjects might be responding to odors from signaled plus unsigned goal events. We nonetheless believe this method should be considered as "unsigned" for two reasons: (1) Some odor from unsigned events must be present or discrimination could not be displayed; anticipatory odor might or might not be present; and (2) the odor and goal event are spatially close, leaving the rat little opportunity to emit an odor to the signal independent of its emission to the goal event.

2. Test subjects might also display unlearned reactions to the odors, as in the Mchose and Ludvigson (1966) study. Unlearned and learned reactions to the odors would be compatible in that effects on performance would be in the same direction. Since the present interest was in detecting odor differences, the common practice of making no attempt to separate the two reactions was followed. It may be noted, however, that the unlearned reaction is weak and usually short lived (e.g., Ludvigson, McNeese, & Collerain, 1979), and can be counteracted by learned reactions (Eslinger & Ludvigson, 1980). "Patterned responding" of the type exemplified here almost certainly reflects a learned reaction almost exclusively. Conclusions would, of course, be unchanged were both reactions operating.

3. Exactly the same reasoning rules out control of discrimination by different amounts of vestigial food odors.