AN ABSTRACT OF THE THESIS OF



Traditional animal learning theories have predominantly been based upon research which failed to account for the influence of odor cues exuded by animal subjects. A review of the literature clearly indicated that odor cues are a scientifically viable phenomenon and that such cues should be incorporated into the theoretical framework of factors involved in animal learning.

The present study sought to contribute to the general body of knowledge concerning odor-based responding by investigating the effects of Elavil on double-alternation patterning in albino rats. The runway performances of Elavilinjected subjects were compared to those of saline-injected subjects. All subjects were run contiguously (in fixed order), under a double-alternating (i.e., RRNNRRNN) sequence of goal events. A second phase, during which the druginjection conditions were reversed, was included as part of the experimental design.

It was shown that subjects trained under the effects of Elavil did not display patterned responding during the first phase, but did develop double-alternation patterning when they were shifted to the saline-injection condition in Phase 2. On the other hand, saline-trained subjects patterned appropriately in the first phase, and maintained that patterning when they were shifted to the Elavil-injection condition in Phase 2. These results were discussed in light of the proposed ceiling-effect hypothesis and frustration theory.

ODOR PRODUCTION AND UTILIZATION AS A FUNCTION OF ELAVIL INJECTION

A Thesis

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by

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CHAPTER 1

INTRODUCTION

Psychologists conducting laboratory experiments using animal subjects have traditionally assumed that the performance of one subject on a given trial is functionally isolated from the subsequent performance of conspecifics. According to this perspective, any improvement in performance from one trial to the next must be attributed to the use of memory, or some such hypothetical construct. However, over forty years ago, DeMand (1940) demonstrated that the performance of albino rats in a multiple-arm-maze-learning task was mediated by the subjects' utilization of animal odor trails which the experimenter systematically varied across experimental groups. The conclusion reached by DeMand was that the validity of the measurements of learning employed by traditional learning theorists, such as Hull and Tolman, may be greatly influenced by distinctive animal odor trails. DeMand's findings implied that learning theories formed on the basis of animal research which ignored olfactory variables may be ideologically confounded. Unfortunately, DeMand's cautions were largely unheeded until recently.

The "odor hypothesis" was revitalized when McHose and Ludvigson (1966) found that nondifferentially reinforced (control) rats tested in a straight alleyway apparatus developed differential responding if they traversed the runway

after differentially reinforced (discrimination) subjects (i.e., control animals ran faster when preceded by discrimination subjects receiving reward than when preceded by nonrewarded discrimination subjects). This differential responding was tentatively attributed to odors exuded by the discrimination subjects which, presumably, functioned as discriminative stimuli for the control animals. A concurrent, and independent, research endeavor (Spear & Spitzner, 1966) corroborated these findings.

More conclusive evidence for the odor hypothesis was provided by Ludvigson and Sytsma (1967). These investigators demonstrated that rats were capable of learning a doublealternation pattern of reward (R) and nonreward (N) when subjects were trained under homogeneous trial-administration conditions, an odor-maximizing technique. Subjects run under heterogeneous (odor-minimizing) trial-administration procedures were unable to learn the appropriate response pattern. Further support for the olfactory nature of these results was furnished by Seago, Ludvigson, and Remley (1970), who showed that rats rendered surgically anosmic (olfactory bulbs removed) were incapable of learning this pattern of instrumental behavior, regardless of the trial-administration procedure employed.

Obviously, such odor research potentially poses monumental problems for contemporary learning theories developed from animal research which did not employ adequate controls for odors. For example, Capaldi (1966, 1967, 1971) has proposed a sequential theory of learning which assumes that R and N goal events act as distinctive stimuli for the recall of internal memories. These R and N memories subsequently form an effective stimulus complex which serves to predict impending goal events. The sequential theory was based upon, and readily predicts, single-alternation-patterned responding However, Bloom and Capaldi (1961) have shown that, in rats. when external visual cues, such as runway color, remain constant for both R and N trials, rats are unable to utilize internal memories to learn double-alternation responding. Therefore, the Ludvigson and Sytsma (1967) findings, previously cited, suggest definite limitations to the applicability of the sequential theory of learning. Additional odor studies (e.g., Davis, Prytula, Doughman, & Perry, 1975; Pavlik & Collier, 1975; Prytula, Davis, Allen, & Taylor, 1980) are further supportive of the notion that memory-based explanations of animal behavior are less than adequate. Likewise, the frustration theory proposed by Amsel (1958) must be seriously questioned because supportive studies have lacked appropriate odor controls.

Given the drastic implications of odor research regarding the formulation of accurate theories of learning, numerous studies have been conducted to establish and evaluate the parameters of the odor phenomenon. For example, one group of studies (e.g., Prytula & Davis, 1974; 1976) examined the relationship between patterned responding and the presence of "odor-donor" animals. Previous research (e.g., Ludvigson,

1969; Ludvigson & Sytsma, 1967) established patterned responding only in the goal section of the runway apparatus, where the odors of contiguously run animals were most concentrated. Prytula and Davis (1974) introduced the technique of placing odor-donor animals in the startbox of a straight alleyway in an attempt to establish differential running behavior throughout the apparatus. These investigators found that when the odor-donor reinforcement schedule was positively correlated with the schedule of run subjects (i.e., odor-donor, RRNNRRNN; run subjects, RRNNRRNN) appropriate alternating responding occurred in all segments of the runway. However, when the reward schedules of odor-donor and run subjects were negatively correlated (i.e., odor-donor, NNRRNNRR; run subjects, RRNNRRNN), an immediate and pronounced disruption of double-alternation performance was observed throughout the runway. A similar study (Prytula & Davis, 1976) employing the startbox odor-donor technique examined the effects of partially correlated odor-donor and run subject reinforcement schedules and presented results comparable to the earlier study (Prytula & Davis, 1974). These studies clearly demonstrate that odors exuded by one group of subjects (i.e., odor-donors) can function as discriminative stimuli for a separate group of rats (i.e., run subjects). It was further demonstrated that double-alternation performance can be established and subsequently disrupted, virtually at will, in those runway segments (i.e., start and run) not normally affected by odors exuded by run subjects.

Other odor studies have been designed to investigate the biological significance of odor production and utilization. Mellgren, Fouts, and Martin (1973), for instance, demonstrated that rats which encountered the odor of nonreward in the middle segment of a three-compartment apparatus were reluctant to enter the middle compartment and exited relatively rapidly once there. On the other hand, it was shown that, when the middle segment contained reward odor, rats entered relatively quickly and were reluctant to leave once there. Such results led these researchers to suggest that odors exuded by rat subjects experiencing R and N goal events elicit unconditioned (unlearned) approach and avoidance responses, respectively. Similarly, studies employing a forced-choice, T-maze apparatus (Collerain & Ludvigson, 1972; Means, Hardy, Gabriel, & Uphold, 1971; Morrison & Ludvigson, 1970) have consistently shown that rats tend to avoid that arm of the maze in which nonreward odor is present. These studies provide additional evidence that rat odors indeed have unlearned biological significance. Further studies (Davis, Prytula, Harper, Tucker, Lewis & Flood, 1974; Davis, Prytula, Noble, & Mollenhour, 1976) have investigated the biological motivational specificity of exuded odor cues. These studies reported that double-alternation patterning was observed in rats only when the deprivational states (food-deprived or water-deprived) of odor-donors and run subjects were positively correlated. Appropriately patterned responding did not occur when the odor-donors and run subjects experienced dissimilar deprivation conditions.

These findings suggest that the utilization of odor cues is largely biological-drive-state dependent.

In order to evaluate the extent of biological limitations on odor-based-responding, Eslinger and Ludvigson (1980a) established conditioned responding to odor cues. These investigators demonstrated that rats can learn one odor-cue pattern (e.g., R odor cues signal R goal events for run subjects) and, subsequently, learn to reverse that discrimination and respond to the opposite odor-cue pattern (e.g., R odor cues signal N goal events for run subjects). Such findings indicate that, even though odor cues may be biologically significant, they can also function as conditioned stimuli. Further, Phillips (1968) reported that odor cues affect the rate of acquisition of visual discriminations. Therefore, these studies strongly suggest that learning, in rats, cannot be constrained to a single, simple relationship between strictly biological functions and/or factors.

Another area of odor research has investigated the generalizability of the rat-odor phenomenon. The use of odors as discriminative stimuli has also been demonstrated in hamsters (Durup, 1964), Mongolian gerbils (Topping & Cole, 1969), and albino mice (Davis, 1970). Cross-species generalization was established by Davis, Crutchfield, Shaver, and Sullivan (1970), when they showed that albino rats developed appropriate double-alternation patterning as a function of odor cues exuded by Mongolian gerbils. It has also been demonstrated (Pratt, Note 1; Prytula, 1975) that a rat is

capable of utilizing its own odor in forecasting the nature of an impending goal event. Further, Eslinger and Ludvigson (1980b) have shown that rats respond differentially to conspecific odor cues regardless of gender factors, familiarity with the odor-donor, or the individual characteristics of odor-donors. Obviously, the generality of the odor hypothesis has been extended by such research. That extension further implies that odor cues must be regarded as a potentially significant variable in runway investigations of learning.

In addition to the behavioral investigations of odor production and utilization, several studies have sought to determine physiological and chemical characteristics of exuded animal odors. Pitt, Davis, and Brown (1973) demonstrated that rats cannot develop appropriate patterning when a wire-mesh lid covers the runway apparatus, but do display patterned responding when the runway is covered by Plexiglas. These researchers suggest, therefore, that exuded odors are extremely volatile. The volatility of rat odors was also demonstrated by McNeese (Note 2) and Taylor and Ludvigson (1980a; 1980b). McNeese and Ludvigson (Note 3) suggested that odors of reward and nonreward cannot be attributed to any known or suspected glandular function. These researchers showed that gonadectomized and preputialectomized rats did not differ from sham operates in learning an odor discrimination. Thus, the precise origin of exuded odors has yet to Perhaps the most informative physiological odor be found.

study was conducted by Voorhees (Note 4). Using the singlecell recording technique with cells in the rat olfactory bulb, this investigator found that R and N odors produced distinctively different patterns of cellular activity. Further, Voorhees concluded that goalbox odors are quite unique from food or urine odors and that goalbox odors are the direct product of particular goal events. Physiological and chemical approaches to odor research, though immature and, as yet, inconclusive, have further implicated exuded goalbox odors as significant variables to be considered in runway studies.

Rather than simply attempting to refute more traditional approaches to animal research, one of the primary goals of odor research has been to establish better defined conditions upon which more accurate theories of learning can be developed and based. Odor researchers have not suggested that odor cues be manipulated as an independent variable in all runway studies, but rather that they must be considered and, at the least, controlled. To this end, several investigators have offered constructive advice for the control of exuded odors. For example, McHose (1969) and Ludvigson (1969) have suggested that odor cues can be neutralized by running trials so that odors exuded by one rat cannot be differentially associated with the goal events experienced by other subjects. Further, Phillips and Bloom (1971) demonstrated that odors can be controlled and patterned responding disrupted by eliminating odors via a small exhaust fan mounted within the apparatus.

Another control procedure has been evaluated by Marrero, Davis, and Seago (1973). It has been shown that rats rendered surgically anosmic are unable to utilize odor cues (see Seago et al., 1970). However, Marrero et al. (1973) cautioned that this technique is not a refined control because the behavioral effects of such surgery have not been fully explored. The investments made by odor researchers in developing constructive advice for the application of knowledge gleaned from studies of the odor phenomenon are indicative of the importance of odors as a significant variable in animal research.

As evidenced by the preceding text, odor research has contributed much to the general body of knowledge regarding animal learning and behavior. As is often the case with any scientifically viable phenomenon, attempts have been made to incorporate the production and utilization of exuded odors within a theoretical framework. Such attempts have chiefly focused upon examining the possibility of a link between odor production and Amsel's (1958, 1962, 1967) frustration theory. This theory suggests that the receipt of nonreward in a previously rewarded situation results in an emotional reaction (frustration), and that this reaction is positively correlated with the degree of expectation and magnitude of reward. Collerain (1978) and Collerain and Ludvigson (1972) have suggested that the demonstrated aversion to the odor of nonreward is indicative of the frustrative nature of such odors. In another study, Collerain and Ludvigson (1977) used the hurdle-jump apparatus as a measure of frustration. These

investigators showed that hurdle-jump (escape) speeds were negatively correlated with the presumed degree of frustration of odor-donors. Additional studies (Thomas, Riccio, & Meyer, 1977; Valenta & Rigby, 1968) have indicated that odors exuded by rats under stressful (and presumably frustrating) conditions can be effectively utilized as discriminative cues. In support of the frustration interpretation, Howard and McHose (1974) have shown that nondrugged run subjects failed to develop double-alternation patterning when following odordonors injected with sodium amobarbital. They concluded that sodium amobarbital reduced the emotional response to frustrative nonreward in the donor animals and, thus, reduced the production of odor cues to be utilized by the run animals. Likewise, Davis and Prytula (1979) demonstrated that, when odor-donors were injected with chlorpromazine (Thorazine) and placed in the startbox, nondrugged run animals that followed them failed to develop appropriate patterning in the start and run sections of the alleyway apparatus. In contrast, run subjects did respond appropriately when following salineinjected, startbox-placed donors. However, when the salineinjected donor animals were shifted to Thorazine injection conditions, appropriate responding was maintained by the run These findings suggest that the correspondence animals. between odor production and frustration is less than perfect. Had the Thorazine injections diminished the frustrative response to nonreward, patterned responding should not have been maintained when the subjects runway-trained under

saline-injection conditions were shifted to Thorazine. It should be noted that both the Howard and McHose (1974) and Davis and Prytula (1979) studies evaluated the performance of nondrugged run subjects which followed drugged donor animals. In light of the fact that odor cues appear to be drive-state dependent (Davis et al., 1974; Davis et al., 1976), Davis, Thomas, Whiteside, Seago, and Prytula (Note 5) investigated the effects of testing Thorazine-injected run animals as a homogeneous group. These researchers indicated that animals tested under the effects of Thorazine were capable of acquiring double-alternation patterning when odor conditions were made as homogeneous as possible. It was further shown that the response latencies of Thorazine-injected subjects were significantly slower than those of saline-injected subjects. These findings led to the tentative conclusion that the drug state may have imposed a ceiling effect upon the performance of those subjects. In that patterning was developed earlier in training by the Thorazine subjects, it was also suggested that the inhibitory tendencies imposed by this ceiling effect may well have caused the Thorazine subjects to attend and respond to odor cues in an augmented fashion. The ceilingeffect hypothesis was further supported by the finding that the runway speeds of the Thorazine animals increased when they were shifted to saline conditions.

Assuming that the ceiling-effect hypothesis is correct, it would be predicted that rats tested under the influence of a drug having the effect of raising the performance ceiling

would find it more difficult to inhibit responding (on N trials) and develop patterning. Because the catecholamine antagonist, Thorazine, has the effect of lowering the performance ceiling, it may be predicted that a catecholamine agonist, such as the tricyclic compound amitriptyline HCL (Elavil), might serve to raise it. Davis, Whiteside, Dickson, Thomas, and Heck (1981) have provided defensive burying data supportive of this contention. These researchers indicated that Elavil-injected rats responded more vigorously and to a greater degree in a burying task than did saline-injected control animals. Therefore, it was the purpose of the present study to investigate the effects of Elavil on odor-based double-alternation patterning in rat subjects tested in the alleyway apparatus. Two phases comprised the present study. In the first phase, two homogeneous groups of subjects were tested, in fixed order, under the conditions of Elavil and saline injections, respectively. In accord with the ceilingeffect hypothesis, it would be predicted that appropriate double-alternation patterning would be developed in Phase 1 only by the saline subjects. During Phase 2, the injection conditions were reversed, while the running order remained the same. Based on the findings of Davis and Prytula (1979), previously discussed, it would be predicted that the saline subjects (shifted from Elavil) would develop double-alternation patterning soon after the initiation of Phase 2. It would further be predicted that the Elavil animals (shifted from saline) would display slightly elevated runway speeds,

but would maintain their strongly established doublealternation responding.

CHAPTER 2

METHOD

Subjects

Fourteen 90-day-old male albino rats purchased from the Holtzman Company, Madison, Wisconsin, served as subjects. All subjects were individually caged, with water available on an ad libitum basis. One week prior to the initiation of pretraining procedures, all subjects were placed on a food deprivation schedule which maintained them at 85% free feeding body weight for the duration of the experiment.

Apparatus

The apparatus consisted of a single straight runway (11.4 cm wide x 12.7 cm high), having a grey startbox (28.1 cm), a black run section (91.4 cm), and a black goalbox (30.5 cm). Masonite guillotine doors separated the startbox and goalbox from the run section. Raising the start door activated a microswitch, which in turn started the first timer. The interruption of a series of photoelectric cells located 15.2, 92.4, and 116.8 cm beyond the start door provided start, run, and goal times, respectively. These times were recorded on all trials. A plastic receptacle recessed into the end wall of the goalbox served as the goal cup. A thin sheet of transparent plastic covered the top of the apparatus, thus maximizing the concentration of odors and preventing their dissipation.

Procedure

Prior to pretraining, each subject was randomly assigned to one of two equal-sized (n=7) groups, Group E-S [designated to receive Elavil (E) injections during Phase 1 and saline (S) injections during Phase 2] or Group S-E (designated to receive S injections during Phase 1 and E injections during Phase 2). Subjects within each group were randomly assigned a permanent number (Group E-S, 1-7; Group S-E, 8-14).

A pretraining phase (4 days) immediately preceded Phase 1 of the experiment proper. On Days 1 and 2 of pretraining, each subject was handled and tamed. Throughout pretraining (Days 1-4), subjects were habituated to the 45-mg Noyes reward pellets in the home cage at the completion of the daily pretraining session. Pellet habituation consisted of introducing a metal receptacle containing 12 reward pellets into the home cage. The receptacle was removed only after the pellets had been consumed. Each subject was placed in the apparatus for a 5-min exploration period on Days 3-4. During exploration, the guillotine doors were permanently raised and all photoelectric cells and timers were operative.

During the experiment proper, all subjects received eight runway experiences (4 R and 4 N) daily in a doublealternation (RRNNRRNN) sequence. On all days of the experiment, subjects were run as a single squad in sequential numerical order (1-14). To administer an R or N event, the appropriate subject was removed from the home cage and placed into the startbox of the apparatus. After a 3-sec confinement period, the doors were raised and the subject allowed to traverse the runway. If the subject remained in the start or run sections of the alleyway for longer than 180 seconds, it was gently coerced into the next section and a time of 180 seconds was recorded for that runway segment. For R events, 12, 45-mg Noyes pellets were placed in the goal cup prior to putting the subject into the startbox. Subjects were confined to the unbaited goalbox for 30 seconds on N events. To effectively isolate the odor conditions within each trial (i.e., the sequential administration of an R or N event to all 14 subjects), the runway was thoroughly swabbed with a damp sponge and aired for 5-min prior to the running of a trial.

During Phase 1 (12 days, 96 trials), Subjects 1-7 (Group E-S) received daily intraperitoneal injections of Elavil 1 h prior to experimental testing, while Subjects 8-14 (Group S-E) received daily intraperitoneal injections of .09% isotonic saline 1 h prior to testing. Each injection was administered at the rate of 2 mg per kg body weight. Subjects were weighed, and appropriate dosages computed, on a daily basis. Phase 2 (6 days, 48 trials) consisted of the reversal of injection conditions. Therefore, even though running order remained unchanged, Elavil-injected subjects (Group E-S) immediately preceded saline-injected subjects (Group S-E) during Phase 1, but immediately followed such subjects during Phase 2.

CHAPTER 3

RESULTS

Because the runway was swabbed and aired prior to the administration of each trial, the first animal in Group E-S (Subject 1) was designated as an "odor-donor" for Subjects 2-7. Even though the runway was not cleaned before testing Group S-E, Subject 8, being the initial animal run under a different drug condition, functionally served the role of "odor-donor" for Subjects 9-14. Since the primary concern of the present study was the utilization of exuded odors, the data collected from the donor subjects (1 and 8) were subsequently omitted from statistical analyses and graphs.

To achieve metric uniformity, all latencies were reciprocated and multiplied by the appropriate constant (.3046) to yield speed scores in meters per seconds. For purposes of statistical facilitation, prior to analysis and graphing, the speed scores for each subject's daily eight-trial sequence were combined in the following manner: The first two trials were averaged to yield a composite (R_1) score, the third and fourth trials were averaged to yield a composite (N_1) score, the fifth and sixth trials were averaged to yield a composite (R_2) score, and the last two trials were averaged to yield a composite (N_2) score. Hence, the daily performance for each subject was reduced to four composite scores $(R_1, N_1, R_2, and$

 N_2) for each section (start, run, and goal) of the runway. In turn, these composite scores were averaged within the appropriate group (E-S or S-E) to yield group mean start, run, and goal speed scores. Mean speed scores, by group, for the start, run, and goal sections of the runway apparatus are shown in Figures 1-3, respectively, for both phases of the experiment.

Analyses of variance incorporating one between subjects factor, Groups (E-S vs S-E); and two within subjects factors, Double-Alternation (DA) Performance (R_1, N_1, R_2, N_2) and Days, were performed on the speed data beginning at Day 7, the point at which appropriately patterned responding appeared to have been established in the goal measure by Group S-E. The Newman-Keuls procedure was employed to test specific contrast effects in all cases.

Phase 1

Analyses of the speed scores for the start and run measures failed to yield significant main-effect differences for the Groups [<u>start</u>, F(1,10) = 1.98, p > .05; <u>run</u>, F(1,10)= 2.12, p > .05], DA Performance [<u>start</u>, F(3,30) = 1.73, p > .05; <u>run</u>, F(3,30) = 1.38, p > .05], and Days [<u>start</u>, F(5,50) = 1.11, p > .05; <u>run</u>, F(5,50) = 1.06, p > .05] factors. Likewise, none of the two-way interactions, nor the threeway interaction, were found to be significant. Goal-measure analysis, on the other hand, yielded significant Groups, F(1,10) = 6.55, p < .05, and Groups by DA Performance, F(3,30) = 7.95, p < .01, effects. Subsequent tests of specific contrast effects revealed that the R speeds of Group S-E were significantly (p < .01) faster than their N speeds and that no such differential responding occurred in Group E-S. Thus, the statistical analysis of the Phase 1 data leads to the conclusions that only Group S-E displayed appropriate doublealternation patterning and that Group E-S approached the goal faster than did Group S-E. Graphical support for these statistical conclusions is certainly demonstrated in Figure 3. Phase 2

Start and run measure analyses did not yield significant main-effect differences for the Groups [start, F(1,10) = 2.31, p > .05; run, F(1,10) = 1.78, p > .05, DA Performance [start, $\underline{F}(3,30) = 1.06$, $\underline{p} > .05$; \underline{run} , $\underline{F}(3,30) = 1.42$, $\underline{p} > .05$], and Days [start, F(7,70) = 1.33, p > .05; run, F(7,70) = 1.82, p > .05] factors. As in Phase 1, none of the possible interactions were found to be significant for the start and run data. In the goal measure, statistical analysis revealed significant DA Performance, F(3,30) = 26.93, p < .01, and Groups by DA Performance by Days, F(15,150) = 1.87, p <.05, effects. Tests of specific contrast effects indicated that, for both groups, all R speeds were significantly (p < .05) faster than all N speeds, with the minor exception that the N_1 speed on Day 1 for Group E-S did not differ significantly from the R speeds on that day. Other significant contrast effects were obtained which did not pertain to the display of appropriate doublealternation patterning and, hence, were not considered to be relevant. The major conclusion to be drawn from the statistical analysis of the Phase 2 data is that appropriate doublealternation patterning was developed by Group E-S and maintained by Group S-E.

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CHAPTER 4

DISCUSSION

To reiterate, the purpose of the present study was to investigate and evaluate the effects of Elavil on odor-based double-alternation patterning. Further, the present study sought to evaluate the state-dependent, ceiling-effect, and frustration explanations of odor-based responding. Though no significant differences were found in the start and run measure data, the Phase 1 goal data (see Fig. 3) are certainly in accord with the ceiling-effect hypothesis. On the other hand, it will be shown that the frustration interpretation may be less than adequate.

During Phase 1, Group E-S failed to develop patterning, whereas patterned responding was displayed by all subjects in Group S-E. Also, Group E-S subjects were shown to approach the goal faster than Group S-E subjects. These results are certainly supportive of the ceiling-effect hypothesis, which would predict that raising the performance ceiling via injections of Elavil might result in faster speeds, an inability to inhibit responding, and the failure to develop appropriate patterning. Of course, another interpretation would be that Group E-S subjects did not produce or utilize odors. This interpretation is supported by the visual inspection of the speeds of the first animal in Group S-E (Subject 8), which

indicated that this subject responded nondifferentially throughout Phase 1.

However, a consideration of the Phase 2 data suggests that odors may well have been produced by Group E-S during Phase 1. For example, the patterning of Group S-E, established in Phase 1, was not affected when these subjects were shifted to Elavil injections in Phase 2. Had the Elavil injections precluded the production of odors, then patterning should also have been disrupted. Similarly, the very rapid development of patterned responding by Group E-S in Phase 2 suggests that these animals had in some manner become sensitized to the salience of odor cues during Phase 1. The shift to saline injections, theoretically, served to lower their performance ceiling and allowed them to inhibit responding on N trials.

The inspection of the speeds of Subject 8 further revealed that this animal also failed to develop differential patterning in Phase 2. Because Subject 8 always followed subjects tested under a different drug-injection state, it might be argued that the differences in drug states rendered the odor cues exuded by previous animals ineffective for this subject. The deprivation-state experiments (Davis et al., 1974; Davis et al., 1976) certainly indicate that this is a plausible interpretation.

Turning to a frustration interpretation of these results, several predictions would seem logical. For example, if Elavil injections served to eliminate or reduce the frus-

trative reaction to N goal events, then no patterning would be predicted for Group E-S during Phase 1. Such a prediction is corroborated by the results of the present study. In this light, it would be further predicted that patterning would be disrupted in Group S-E during Phase 2. This most certainly Therefore, the results of the present study did not occur. suggest that frustration interpretations may not be totally adequate to explain all aspects of odor-based responding. Additional research projects (Burns, Thomas, & Davis, in press; Davis, Whiteside, Bramlett, & Petersen, in press) have also suggested that certain predictions made by frustration theory, regarding the nature of a frustrative goal event, are not borne out by laboratory results. Given this discrepancy between frustration theory and odor research data, it would seem inappropriate to label nonreward odor cues as "frustration odors" (see Collerain & Ludvigson, 1972). It seems obvious that further research designed to ascertain the precise nature and function of such odors is required.

The conclusions of the present study are threefold. First, it is concluded that odor-based patterning is not readily established when subjects are initially trained under the effects of Elavil and that such patterning, once established, is quite insensitive to shifts in drug state. Second, it is suggested that the ceiling-effect hypothesis is more applicable to the present data than a frustration-theory interpretation. Finally, it is concluded that animal odors are a genuine phenomenon to be considered in laboratory animal research and that this phenomenon must be incorporated into the general framework of animal learning theory.

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APPENDIX: FIGURES

Figure 1. Mean Start Speeds for Groups S-E and E-S During Phases 1 and 2.

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MEAN SPEED (METERS/SEC.)



Figure 2. Mean Run Speeds for Groups S-E and E-S During Phases 1 and 2.

MEAN SPEED (METERS/SEC.)



DAYS

Figure 3. Mean Goal Speeds for Groups S-E and E-S During Phases 1 and 2.

MEAN SPEED (METERS/SEC.)



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DAYS