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Motivational Specificity of the Signal Value of Odor Cues: A Reconsideration and Extension

by
Melanie S. Weaver and Stephen F. Davis*

Over 40 years ago, J.W. DeMand (1940) published a study indicating that maze learning of the albino rat could be influenced by the presence of animal odor trails. Utilizing an elevated multiple-T maze and three groups of rat subjects, DeMand demonstrated that those animals given an odor trail marking the true path through the maze achieved faster times and made fewer errors than did those animals receiving no odor trails or odor trails marking blind alleys. These results indicated that certain measurements of learning may be greatly influenced by these uncontrolled animal odors. DeMand further suggested that the response being measured may not, in fact, be the actual learning ability of the animal but, rather, the olfactory acuity of the animal. DeMand's contention would appear to be rather straightforward and of some importance; since, uncontrolled, these odors could pose great potential interpretation problems for animal researchers. Unfortunately, DeMand's contention, as well as his study, went unheeded until almost 30 years later when Ludvigson and Sytsma (1967) and Ludvigson (1969) demonstrated that rat subjects were capable of mastering a double-alternation pattern of reward and nonreward through the use of olfactory cues. In these two studies a straight runway, divided into start, run, and goal segments, served as the experimental apparatus. All subjects were administered eight daily trials in a double-alternation (DA) sequence of reward (R) and nonreward (N) (i.e., RRNNRRNN). Specifically, all subjects within a group received the same condition (R or N) on a given trial with all subjects receiving the first trial before any subjects received the second

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trial, and so forth. The runway was swabbed with a damp sponge only *between* trials, thus allowing any odors that were present to accumulate. Eventually, a pattern of running fast on R trials and slowly on N trials developed in the goal segment of the runway.

Stemming from these two seminal publications (Ludvigson & Sytsma, 1967; and Ludvigson, 1969), an accumulating body of research has been gathered investigating the properties of and the experimental conditions under which these odors occur. This growing body of literature has come to be known as the "odor hypothesis" and its data support the contention that rat subjects exude either quantitatively and/or qualitatively different odors on R and N occasions. Further, if these odors are allowed to persist they can influence the behavior of subsequent conspecifics. It is readily observed that the development of appropriate patterned responding (i.e., fast to R and slow to N) occurs only under odor maximizing conditions and not odor minimizing conditions. The typical odor maximizing and odor minimizing DA sequences used in such odor studies are shown in Part A of Table 1. Part B of Table 1

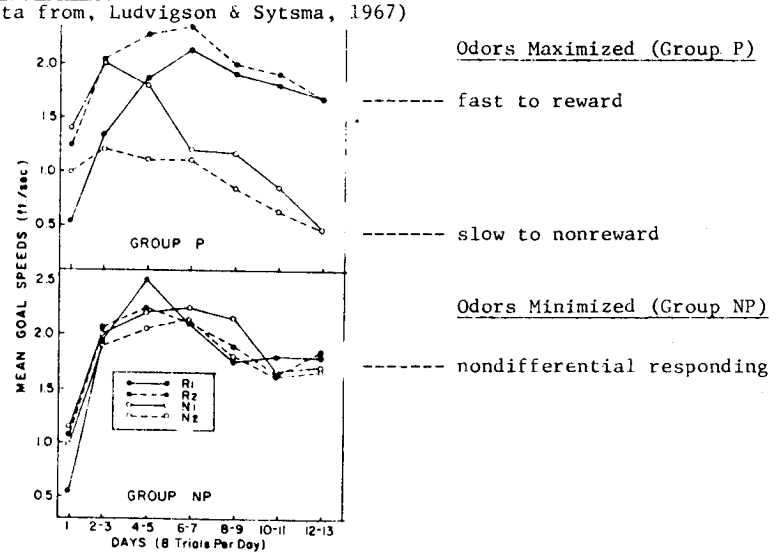
TABLE 1

A. Odor-Maximizing and Odor-Minimizing Double-Alternation Schedules (from, Ludvigson & Sytsma, 1967)

		Trial								
GROUP	S	1	2	3	4	5	6	7	8	
P	1	R	R	N	N	R	R	N	N	ODOR-MAXIMIZING
	2	R	R	N	N	R	R	N	N	
	3	R	R	N	N	R	R	N	N	
	4	R	R	N	N	R	R	N	N	
	5	R	R	N	N	R	R	N	N	
	6	R	R	N	N	R	R	N	N	
	7	R*	R*	N*	N*	R*	R*	N*	N*	
NP	1	R	R	N	N	R	R	N	N	ODOR-MINIMIZING
	2	R	N	N	R	R	N	N	R	
	3	N	N	R	R	N	N	R	R	
	4	N	R	R	N	N	R	R	N	
	5	R	R	N	N	R	R	N	N	
	6	R	N	N	R	R	N	N	R	
	7	N*	N*	R*	R*	N*	N*	R*	R*	

*Any odors that are present in the apparatus are allowed to accumulate from S 1 to S 7 within the respective groups. Typically, the apparatus is swabbed following S 7 (last S in the group). Hence, S 1 is always tested in a clean, odor-free apparatus.

B. Double-Alternation Responding Under Odor-Maximizing and Odor-Minimizing Conditions
(data from, Ludvigson & Sytsma, 1967)



graphically depicts the results of DA patterning for both sequences. The first animal in a group, which is typically tested in a clean odor-free apparatus and considered to be an odor-donor for the following subjects, never displays differential responding (e.g., Prytula, Davis, Allen, & Taylor, 1980; Prytula, Davis, & Fanning, 1981). Moreover, if these odors are allowed to dissipate from an enclosed apparatus (Pitt, Davis, & Brown, 1973) or if the runway is swabbed after each animal patterned responding does not occur.

In addition to the data reported by Ludvigson and Sytsma (1967) and Ludvigson (1969), several other studies suggest that rats experiencing R and N treatments exude differential odors that subsequent conspecifics can utilize as disciminative cues for corresponding R and N goal events. For example Prytula et al. (1980) trained two groups of animals under one of two different alternating sequences of R and N; single-alternation, SA, (RNRNRNRN) and double-alternation, DA, (RRNNRRNN). Following acquisition of appropriate patterned responding each group was shifted to the opposite schedule. Those animals initially trained under the SA schedule immediately displayed DA patterning. Likewise, those animals initially trained under DA patterning immediately displayed SA patterning. Due to the immediate shifts in behavior, these results strongly suggest that odor cues and not memory are the mediating factor(s) in the development of patterned responding. Seago, Ludvigson, and Remley (1970) presented further support for the "odor hypothesis" by indicating that when normal and anosmic (olfactory bulbs removed) rats were trained in a DA sequence of R

and N, the bulbectomized subjects were capable of discriminating and demonstrating appropriate patterned responding *only* when a light cue was added on N trials (see also, Marrero, Davis, & Seago, 1973). In accordance with these findings Voorhees and Remley (1981), through single cell recordings of the rat's olfactory bulb, suggested not only that these odors are different from each other and can serve as discriminative cues, but also that R and N odors are detected at the mitral cell level.

It further has been demonstrated that R and N odors may also serve to elicit unconditioned approach and avoidance responses, respectively (e.g., Mellgren, Fouts, & Martin, 1973; Collerain & Ludvigson, 1972). When odor-donor subjects are placed in a chamber and allowed to exude an odor corresponding to a goal event (R or N), subsequent subjects placed in the same chamber will display faster escape speeds from N odors than from R odors. This finding suggests that odors produced when a rat receives nonreward are aversive stimuli and that odors produced by a rat receiving reward may be attractive stimuli.

The use of odor-donor subjects generated several interesting avenues for investigations into the nature of these odor cues. For example, it has been observed in several studies (see Ludvigson & Sytsma, 1967; Prytula et al., 1980; Seago et al., 1970) that the discriminative effects of these odors, especially those of nonreward (Taylor & Ludvigson, 1980), exert their most pronounced effects in the goal segment of the straight runway apparatus. As the R and N events are directly experienced in the goal box, this finding is not completely unexpected. However, Prytula and Davis (1974, 1976) have demonstrated that appropriate DA responding can be established in the start and run segments of the runway by placing odor-donors in these respective locations. When odor-donor R-N schedules are positively correlated with those of the subjects that actually traverse the runway (e.g., a donor R trial is followed by a run-subject R trial, etc.), appropriate patterned responding develops in these designated segments. More specifically, if odor-donors are placed in the startbox, patterning will be established in all segments. However, if odor-donors are placed in the run segment, patterned responding will be established only in the run and goal segments. When the odor-donor schedule is changed to correlate negatively with that of the run subjects (e.g., a donor R trial is followed by a run-subject N trial, etc.), an immediate and pronounced disruption in DA responding occurs in all segments of the runway.

Eslinger and Ludvigson (1980a) carried the analysis of the discriminative functions of these odors one step further. These researchers demonstrated that rat subjects can utilize R and N odor cues interchangeably. Utilizing donor-test triplets, rats disciminated R and N *goal* events based upon the opposite odor cues by running fast to N odors and slow to R odors. Hence, the use of opposite reward-event schedules for donor and test animals did not preclude the development of discrimination. As these data may appear to contrast somewhat with the Prytula and Davis (1974, 1976) studies which suggested that odor cues must be redundant in order to be utilized effectively, it would appear that the specific precedure for running the odor-donors and run-subjects must be taken into consideration. The Eslinger and Ludvigson (1980a) study utilized odor-donor triplets, sequentially placing two odor-donors in the goalbox and adminstering each one either an R or N treatment. One test subject was then allowed to traverse the runway to receive either the same or opposite treatment. The runway was then swabbed before the next triplet was run. On the other hand, Prytula and Davis (1974, 1976) placed their odor-donors in the start or run segments and *each* was then followed by a run subject that was allowed to traverse the entire runway. Under these conditions the runway was not swabbed until all test subjects had been run, thus allowing odors to accumulate in the goal segment, thereby signalling the actual impending goal event.

The development of DA responding in *all* segments of the runway does not appear to be limited to the situation using odor-donor subjects. In particular, Prytula et al. (1981) established patterning in all segments of the runway through the use of one large squad of animals which was conceptually divided into two groups: low odor buildup (intial animals) and high odor buildup (terminal animals). With the larger group there would be, theoretically, a greater buildup and/or accumulation of odors in the goal area. In turn, these more potent odors would be expected to disseminate farther from the goal area toward the run and start segments to establish and maintain appropriate responding in these sections. These predictions were substantiated. To further support this contention, Prytula et al. (1981) found that when naive animals were placed in initial and terminal positions of the squad, the terminal animals exposed to the intensified odor conditions developed patterning more rapidly than the initial naive animals in the squad. These later results, along with those of Prytula and Davis (1974, 1976), indicate that the rat may be biologically "prepared" to respond appropriate-

ly to R and N odors. It will be recalled that the studies by Mellgren et al. (1973) and Collerain and Ludvigson (1972) yielded data supportive of such a preparedness interpretation. In contrast, the Eslinger and Ludvigson (1980a) study, in which animals were trained to approach N odors and avoid R odors, would suggest that the adaptive significance of these odors may well exceed the simple relationship of approaching an R odor and avoiding an N odor.

As can be seen, much is already known about the properties of these proposed R and N odor cues and the experimental conditions under which they are exuded. However, much less is known about their source and/or specific chemical nature. It appears that R and N odors are not only different from each other, but also differ from the odors of food and urine (Voorhees & Remley, 1981). Although the exact source of these odors has not been located, McNeese and Ludvigson (Note 1) reported that they are not a function of the preputial gland or of the androgen-dependent accessory glands. Studies involving visible observation of urine (Eslinger & Ludvigson, 1980a) and flourescent emissions, as an indicant of urine (McNeese & Ludvigson, Note 1), also have yielded negative results. Further, Mellgren et al. (1973) have eliminated feces as a possible source of odor. As the odors exuded by rat subjects appear to be partially airborne but intially deposited on the apparatus flooring (Taylor & Ludvigson, 1980b), Weaver, Whiteside, Janzen, Moore, and Davis (1982) investigated the footpad sweatgland as a possible source of odor. Unfortunately, precluding odors exuded from the feet resulted in a significant intensification of patterned responding, suggesting that the odor exuded from the feet is a form of natural animal odor which serves to partially mask the odors of reward and non-reward. Hence, no sound conclusions can presently be made with regard to the source of these odors.

The "odor hypothesis" has been extended and generalized to include the concept of interspecific odors (Davis, 1970; Davis, Crutchfield, Shaver, & Sullivan, 1970). Moreover, it has been demonstrated that individual and sex differences appear to be functionally unimportant (Eslinger & Ludvigson, 1980b) in both the production and discriminative use of R and N odors. By interchanging odor-donors *after* the subjects had developed appropriate patterned responding with a *particular* donor, male and female test rats responded to donor odors in a similar manner regardless of gender factors, familiarity with the donor, or individual characteristics of the donors.

However, with regard to rats trained under different deprivation states the generalizability of R and N odors does not seem to apply. This consideration brings us to the line of experimentation most directly related to the present research, motivational specificity. Motivational specificity suggests that rat subjects deprived of food will not attend to or utilize odor cues exuded by water-deprived rats and vice versa. The initial report proposing that odors may be motivationally (i.e., deprivation state) specific would appear to be that of Davis, Prytula, Harper, Tucker, Lewis, and Flood (1974). Davis et al. (1974) conducted a three-phase study utilizing food-deprived startbox-placed odor-donor subjects and water-deprived runway-trained test subjects. During Phase 1, odor-donor and run-subject pairs received positively correlated reinforcement schedules (RRNNRRNN). Subsequently, there was a shift from water deprivation to food deprivation for the run subjects. The data from Phase 1 indicated that the run subjects displayed appropriate DA responding *only* in the goal measure of the runway. This is to be contrasted with the data from the shift phase which indicated that appropriate patterned responding was developed in *all* segments of the runway when all subjects were tested under the same deprivation state (food-deprivation). A follow-up study, conducted by Davis, Prytula, Noble, and Mollenhour (1976), replicated the Davis et al. (1974) findings. This study was conducted similarly to the Davis et al. (1974) experiment with the exception that all subjects were shifted to water-deprived during the final phase. Taken collectively, these data would appear to support the contention that odors produced by odor-donor subjects are attended to and utilized as discriminable cues by runway subjects *only* when the deprivation states of these two sets of animals coincide.

Eslinger and Travis-Neideffer (Note 2) have reported a partial replication of the Davis et al. (1974,1976) studies. This study was designed not only to replicate but also to rule out the possibility that the previous data may have been due to the specific training procedures utilized by Davis et al. (1974, 1976). [For purposes of clarity the experimental designs used in the Davis et al. (1974, 1976) and the Eslinger & Travis-Neideffer (Note 2) studies are shown in Table 2.] Specifically, Eslinger and Travis-Neifeffer

TABLE 2

Experimental Design - Davis et al., 1974

	Phases 1 & 2	Phase 3
	Donor - Food Deprived Test - Water Deprived	Donor - Food Deprived Test - Food Deprived

- During Phases 1 and 3 both odor-donor and test subjects received their eight daily trials in a positively correlated sequence (RRNNRRNN).
- During Phase 2 the odor-donor schedule was shifted to negatively correlate (NNRRNNRR) with that of the test subject (RRNNRRNN).

Experimental Design - Davis et al., 1976

	Phases 1 & 2	Phase 3
	Donor - Water Deprived Test - Food Deprived	Donor - Water Deprived Test - Water Deprived

- During Phases 1 and 3 both odor-donor and test subjects received their eight daily trials in a positively correlated sequence (RRNNRRNN).
- During Phase 2 both odor-donor and test subjects received their eight daily trials in a reverse sequence (NNRRNNRR).

Experimental Design - Eslinger & Travis-Neideffer, Note 2

	Phase 1	Phase 2
CI	Donor - Water Deprived Test - Water Deprived	Donor - Water Deprived Test - Food Deprived
IC	Donor - Food Deprived Test - Water Deprived	Donor - Food Deprived Test - Food Deprived

- During both phases all subjects were given eight daily trials with RRNN and NNRR sequences being alternated every two days (i.e., two days of RRNN were followed by two days of NNRR, etc.).
- The R-N schedule was positively correlated for all donor-test pairs on each day.

(Note 2) conducted a two-phase study utilizing two groups of startbox-placed odor-donor subjects (one food-deprived, one water-deprived). Unlike the Davis et al. (1974, 1976) studies, the R-N events between donor and run subjects remained positively correlated throughout the experiment. Hence, only deprivation states were incongruent in appropriate phases. During Phase 1, the congruent groups consisted of water-deprived odor-donor subjects and

water-deprived run subjects. The incongruent groups consisted of food-deprived odor-donor subjects and water-deprived run subjects. In Phase 2 the run subjects were shifted to the opposite deprivation state resulting in the congruent groups becoming incongruent and the incongruent groups becoming congruent. The findings of this study indicate that *only* when subjects are initially trained under congruent states (i.e., odor-donors and run subjects are both water-deprived) can they establish appropriate patterned responding which is maintained when the deprivation states are shifted to incongruent states. The prior congruent training somehow enabled the subjects to successfully discriminate R and N odors when the deprivation states differed. Thus, even though R and N odors may differ to some extent as a function of deprivation state, the specific deprivation conditions do not appear to pose *absolute* limits on the discriminative use of these odors.

In view of these data, the present studies were designed to further investigate the apparent limits on the discriminative use of odor cues that may be imposed by different deprivation states. As four separate experiments will be reported, the theoretical basis and rationale for each one will be presented separately.

EXPERIMENT 1

Data from the previous motivational specificity studies (Davis, et al. 1974, 1976; Eslinger & Travis-Neideffer, Note 2) are not without potential interpretation problems. In particular, when the rats in these studies were tested under different deprivation states, they also were receiving qualitatively and/or quantitatively different reinforcers. Hence, the lack of patterning displayed under these conditions could be attributed to either: 1) deprivation-state differences, or 2) reinforcer differences. Addressing this interpretation problem, Davis, Weaver, Nash, and Spence (1983), administered two different reinforcers to rats experiencing the same deprivation state. Data from this research suggested that food-deprived rats exuded a common odor under quinine (Q) and nonreward (N) reinforcement conditions. In this experiment two groups of animals receiving a DA schedule of R-N and R-Q, respectively, were trained. Specifically, the squad consisted of seven animals receiving a R-N schedule of reinforcement (Group R-N), that were immediately followed by seven animals receiving a R-Q schedule of reinforcement (Group R-Q). Under these conditions the first animal in Group R-Q displayed strong DA responding suggesting that odors exuded under Q and N conditions are the same or are at least very similar.

The purpose of Experiment 1 was to investigate the other side of this interpretation problem by evaluating the effects of administering the *same* reinforcer to rats experiencing *different* deprivation conditions. Throughout experimental testing all subjects received a 32% sucrose-water reward solution under conditions of either food-deprivation or water-deprivation. In support of the use of this reinforcer, previous studies (Burns, DeHart, & McRae, 1980; Burns, Dupree, & Lorig, 1978) have demonstrated that sucrose-water is an effective reinforcer for food-deprived rats.

As Davis et al. (1981) demonstrated the effective use of one large squad composed of two distinct groups for the study of odor processes, this procedure was utilized during Phase 1 testing. Two subgroups, one food-deprived (FD) and one water-deprived (WD), constituted each squad. In one squad the FD animals preceded the WD animals, while in the second squad the WD animals preceded the FD animals. Phase 2 further investigated the effects of odors exuded under different deprivation conditions. On each day of Phase 2, the last subject in each of the second subgroups was rotated to occupy the first position of his respective *subgroup*. Based upon the previous use of this rotation technique (Prytula et al. 1981), it might be predicted that if common, usable odors were being produced by the first four animals, then each rotated subject should be able to maintain appropriate responding when moved to immediately follow these first four (different deprivation state) subjects.

Phase 3 testing regrouped the squads so that all FD subjects and all WD subjects were run as separate squads. This group rearrangement was implemented to allow an evaluation of any carryover effects from the previous incompatible deprivation testing conditions (Phases 1 and 2) into the compatible deprivaiton conditions of Phase 3.

Method.

Subjects. Sixteen, 90-day-old albino rats purchased from the Holtzman Company, Madison, Wisconsin, served as subjects. One week prior to pretraining the animals were randomly assigned to either a FD or WD condition (n = 8). Food-deprived subjects were placed on a food-deprivation regimen that maintained them at 85% of their free-feeding body weight while the water-deprived subjects were maintained on a 23-hour water-deprivation schedule with food freely available. Subjects experiencing these conditions were further assigned to subgroups of four subjects each: two WD (Subgroups WDA and WDB) and two FD (Subgroups FDA and FDB).

All animals were housed in individual cages and received their respective regimen following the daily experimental session. The deprivation schedules imposed at this time were maintained throughout the duration of experimental testing.

Apparatus. The apparatus consisted of a single straight runway (11.4 cm wide × 12.7 cm high) having a gray startbox (28.1 cm), black run section (91.4 cm), and black goalbox (30.5 cm). Guillotine doors separated the startbox and goalbox from the run section. Start, run, and goal latencies, produced by the activation of a microswitch located on the start door and the interruption of a series of photoelectric cells (located 15.2, 92.4, and 116.8 cm, respectively, beyond the start door) were recorded on all trials. A plastic receptacle mounted into the end wall of the goalbox was modified to allow the external attachment of a plastic water bottle. The drinking spout of the water bottle extended into the receptacle, thus allowing the subject easy access but preventing water from dripping onto the goalbox floor. A thin sheet of transparent plastic covered the top of the runway to prevent odors from dissipating. As this apparatus was employed in all experiments to be reported, only specific modifications will be reported in subsequent sections.

Procedure. A four-day pretraining phase immediately preceded experimental testing. All days of pretraining consisted of handling and taming, and habituation to the 32% sucrose-water reward solution in the home cage. On Day 3 each subject received a 5-min exploration period in the unbaited apparatus. The fourth pretraining day was the same as the third, with the exception that the apparatus was baited and all photoelectric equipment was operative. The specific squad and/or subgroup compositions and experimental design for this and all other experiments to be presented are delineated in Table 3.

TABLE 3

Experimental Design - Experiment 1

Phase 1 - All subjects received daily double-alternation (RRNNRRNN) training in the straight runway for 18 days (144 trials).

	SQUAD 1		SQUAD 2	
Subgroup A	S 1	FD	S 1	WD
	2	FD	2	WD
	3	FD	3	WD
	4	FD	4	WD
Subgroup B	S 5	WD	S 5	FD
	6	WD	6	FD
	7	WD	7	FD
	8	WD	8	FD

TABLE 3 (con't.)

Experimental Design - Experiment 1 (con't.)

- Each squad received all daily trials before the next squad received its daily session.
- Trial 1 was administered to all subjects within a squad before Trial 2 was administered, etc. The apparatus was swabbed and aired after the completion of each trial for all animals in a squad.
- The order for running squads alternated daily.
- Subgroup A always preceded Subgroup B. Within each squad the subjects were run in a fixed (1-8) order on each day.
- An R event consisted of 30-sec access to a 32% sucrose-water solution.
- An N event consisted of 30-sec confinement to an empty goalbox.

Phase 2 - All subjects received daily double-alternation training in the straight runway for 3 days (24 trials).

SQUAD 1			SQUAD 2		
Subgroup A	S 1	FD	Subgroup A	S 1	WD
	2	FD		2	WD
	3	FD		3	WD
	4	FD		4	WD

- Subjects within the A subgroups were run in a fixed (1-4) order on all days of Phase 2.
- On each day of Phase 2 the last subject (Position 8) within each B subgroup was rotated to the first position (Position 5) within his respective subgroup.

Day 1

SQUAD 1			SQUAD 2		
Subgroup B	S 8	WD	Subgroup B	S 8	FD
	5	WD		5	FD
	6	WD		6	FD
	7	WD		7	FD

Day 2

SQUAD 1			SQUAD 2		
Subgroup B	S 7	WD	Subgroup B	S 7	FD
	8	WD		8	FD
	5	WD		5	FD
	6	WD		6	FD

Day 3

SQUAD 1			SQUAD 2		
Subgroup B	S 6	WD	Subgroup B	S 6	FD
	7	WD		7	FD
	8	WD		8	FD
	5	WD		5	FD

- Trial administration procedures, R and N events, and order for running subgroups and squads were the same as those employed in Phase 1.

TABLE 3 (con't.)

Experimental Design - Experiment 2 (con't.)

Phase 3 - All subjects received daily double-alternation training in the straight runway for 3 days (24 trials).

SQUAD 1			SQUAD 2		
Subgroup B	S 6	FD	Subgroup B	S 6	WD
	7	FD		7	WD
	8	FD		8	WD
	5	FD		5	WD
Subgroup A	S 1	FD	Subgroup A	S 1	WD
	2	FD		2	WD
	3	FD		3	WD
	4	FD		4	WD

- Subgroup B always preceded Subgroup A. Within each squad the subjects were run in a fixed (6-7-8-5-1-2-3-4) order on each day.
- Trial administration procedures, R and N events, and order for running squads were the same as those employed in Phases 1 and 2.

Experimental Design - Experiment 2

Phase 1 - All subjects received daily double-alternation training in the straight runway for 12 days (96 trials).

Group WD1: Ss 1-7
Group WD2: Ss 8-14
Group FD1: Ss 15-21
Group FD2: Ss 22-28

Phase 2 - All subjects received daily double-alternation training in the straight runway for 4 days (32 trials).

SQUAD 1 - (n = 2)			SQUAD 2 - (n = 2)		
Subgroup A	S 1	WD	Subgroup A	S 1	FD
Subgroup B	S 1	FD	Subgroup B	S 1	WD
SQUAD 3 - (n = 4)			**SQUAD 4 - (n = 4)**		
Subgroup A	S 1	WD	Subgroup A	S 1	FD
	2	WD		2	FD
Subgroup B	S 1	FD	Subgroup B	S 1	WD
	2	FD		2	WD
SQUAD 5 - (n = 6)			**SQUAD 6 - (n = 6)**		
Subgroup A	S 1	WD	Subgroup A	S 1	FD
	2	WD		2	FD
	3	WD		3	FD
Subgroup B	S 1	FD	Subgroup B	S 1	WD
	2	FD		2	WD
	3	FD		3	WD

- Each group (Phase 1) or squad (Phase 2) received all daily trials before the next group/squad was run.
- Trial 1 was administered to all subjects within a group or squad before Trial 2 was administered, etc. The apparatus was swabbed and aired after the completion of each trial for all animals in a group or squad.
- The order for running groups/squads was randomized daily.

TABLE 3 (con't.)

Experimental Design - Experiment 3 (con't.)

- During Phase 2 Subgroup A always preceded Subgroup B. Within each subgroup the subjects were run in the same fixed sequence on all days. (Note: the fixed sequence was also employed during Phase 1.)
- An R event consisted of 1 ml of a 32% sucrose-milk solution.
- An N event consisted of 30-sec confinement to the empty goalbox.

Experimental Design - Experiment 3

	Phase 1	Phase 2	Phase 3
Group WD (n = 7)	WD/RND	WD/FXD	WD/RND
Group FD (n = 7)	FD/RND	FD/FXD	FD/RND

- All subjects received daily double-alternation training in the straight runway for 14 days (112 trials) during Phase 1, 8 days (64 trials) during Phase 2, and 2 days (16 trials) during Phase 3.
- Each group received all daily trials before the next group received its daily session.
- Trial 1 was administered to all subjects within a group before Trial 2 was administered, etc. The apparatus was swabbed and aired after the completion of each trial for all animals in a group.
- An R event for Group WD consisted of 30-sec access to plain tap water while an R event for Group FD consisted of 12, 45-mg Noyes pellets.
- An N event for both groups consisted of 30-sec confinement to the empty goalbox.

Experimental Design - Experiment 4

	Phase 1	Phase 2	Phase 3
Group F-F-F (n = 6)	WD/FXD	FD/FXD	WD/FXD
Group R-F-F (n = 6)	WD/RND	FD/FXD	WD/FXD
Group F-R-R (n = 6)	WD/FXD	FD/RND	WD/RND

- All subjects received daily double-alternation training in the straight runway for 13 days (104 trials) during Phase 1, 17 days (136 trials) during Phase 2, and 8 days (64 trials) during Phase 3.
- Trial administration and cleaning procedures were the same as those employed in Experiment 3.
- The order for running groups was cyclic over a three-day period.
- During Phases 1 and 3 (WD) an R event consisted of 15-sec access to plain tap water. During Phase 2 (FD) an R event consisted of 12, 45-mg Noyes pellets.
- An N event consisted of 15-sec confinement to the empty goalbox.

Prior to Phase 1 testing, the subgroups were combined to form two larger squads: Squad 1 - Subgroups A (FD) and B (WD) and Squad 2 - Subgroups A (WD) and B (FD). As can be seen from Table 3, in Squad 1 four FD animals preceded four WD animals, while in Squad 2 four WD animals preceded four FD animals. During Phase 1 (18 days, 144 trials), the subjects within each squad were tested in a fixed (Position 1 - 8) running order (FXD) on all days.

On each day of Phase 2 (3 days, 24 trials), the animal in Position 8 (the last animal) was rotated to Position 5, thus allowing an animal that normally followed three animals of the same deprivation state to follow four animals of the opposite deprivation state. None of the subjects in the first A subgroups were rotated during this phase.

Phase 3 (3 days, 24 trials) involved: 1) a reversal of subgroup ordering within each squad (i.e., the B subgroups preceded the A subgroups in both squads), and 2) switching the second subgroup from one squad to the other squad. In other words, Squad 1 now consisted of both FD subgroups with Subgroup B preceding Subgroup A, while Squad 2 consisted of both WD subgroups with Subgroup B preceding Subgroup A. The FXD running order was employed with the sequence for the first subgroup in each squad being the same as that which was in effect on the last day of Phase 2.

During all three phases of the experiment, each rat received its eight daily trials in a DA (RRNNRRNN) sequence. On each trial, the appropriate subject was removed from the home cage and placed in the startbox. Following a 3-sec confinement, the start door was raised and the subject was allowed to traverse the runway. The R and N events consisted of 30-sec access to a full water bottle containing 32% sucrose-water and 30-sec confinement to an empty goalbox, respectively. An empty water bottle was in place on N trials. All daily trials were administered to the first squad before the second squad was run. All animals within a particular squad received Trial 1 before Trial 2 was administered, and so forth. The order for running squads was alternated daily. The entire apparatus was swabbed with a water-dampened sponge and aired for 5-min after the completion of each trial for each squad. The swabbing procedure was carried out twice with two separate sponges to assure that no sucrose odor or residue was present on the next trial.

Results and Discussion

General Statistical Procedures. As the same data-reduction techniques were employed for all experiments, they will be discussed briefly at this point. For purposes of clarity these procedures are further delineated in Table 4. The eight daily latencies

TABLE 4

Data-Reduction Procedures

1. All latencies from the daily eight-trial sequence are reciprocated to yield speed scores.
2. The speed scores are then multiplied by the appropriate metric constant to yield speed scores in meters per second.
3. The eight daily speeds for each subject are then reduced to four representative scores thusly:

$$\frac{R+R}{2} \quad \frac{N+N}{2} \quad \frac{R+R}{2} \quad \frac{N+N}{2}$$

$$\downarrow \qquad \downarrow \qquad \downarrow \qquad \downarrow$$

$$R_1 \qquad N_1 \qquad R_2 \qquad N_2$$

4. These four composite scores are then used for graphing and analysis purposes.

for each subject were reciprocated and multiplied by the appropriate metric constant to yield speed scores (meter/sec.). Prior to analysis and graphing, the speed scores for the daily eight-trial double-alternation sequence were combined as follows: the first two trials were averaged to yield an R_1 composite score, the next two trials were averaged to yield an N_1 composite score, and so forth. Hence, the daily double-alternation performance was reduced to four scores for each subject. These scores were, in turn, used for graphing and analysis purposes.

Experiment 1 Results.

Visual inspection of Figures 1 and 2 indicates that both of the B subgroups displayed appropriate double-alternation responding in the goal measure during Phase 1, while the A subgroups failed to establish such appropriate responding. As will be elaborated, these results would appear to add further support to the contention that absolute limits are not imposed on the discriminative use of odor cues under specific deprivation conditions.

An analysis of variance incorporating two between-groups factors, Deprivation Condition (Water-Deprived vs Food-Deprived) and Position Within The Squad (Subgroup A vs Subgroup B), and

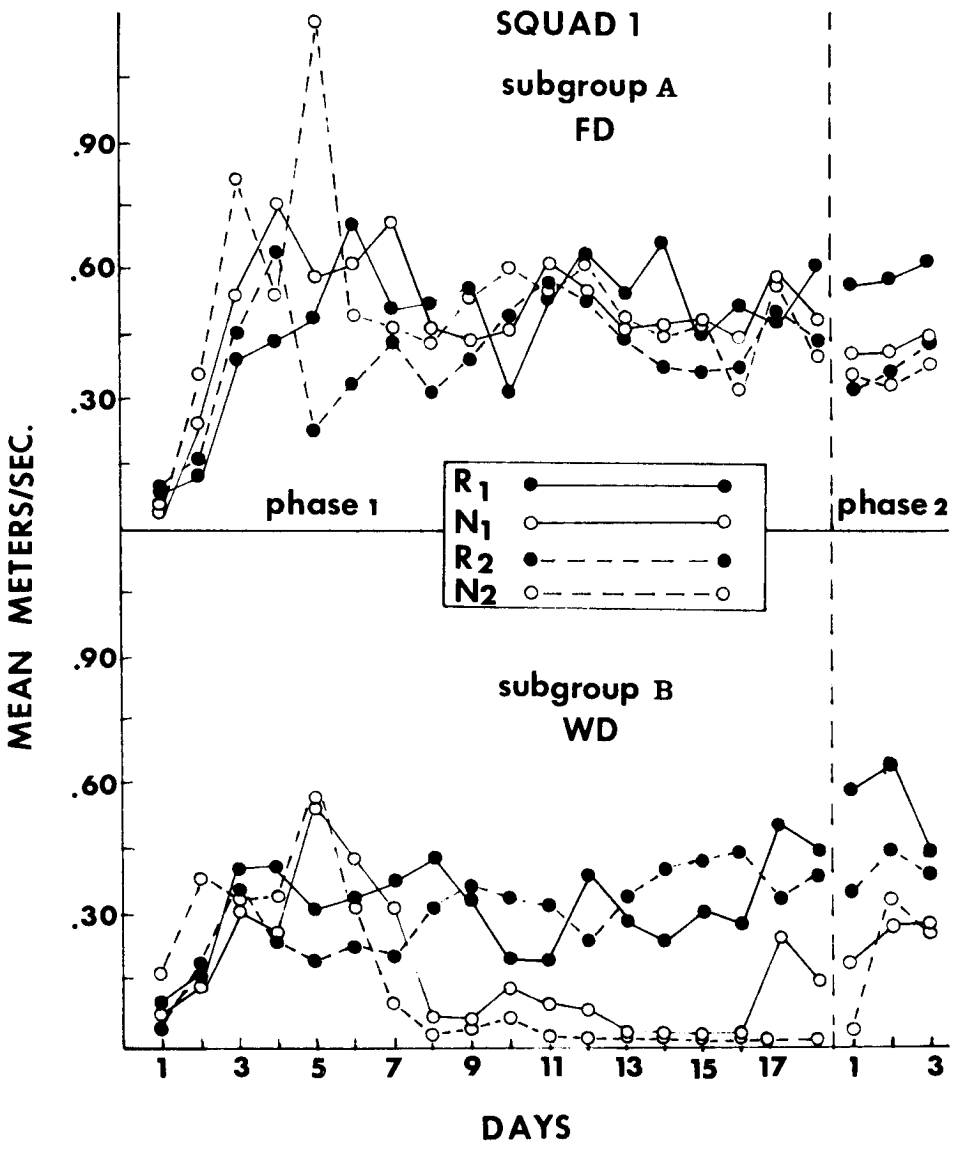


Figure 1 - Mean Goal Speeds for Squad 1, Subgroups A and B, During Phases 1 and 2 of Experiment 1.

two within-groups factors (R vs N, and Days) were performed on the speed scores from the last eight days of Phase 1 (the point at which appropriate patterning appeared to have been established by both of the B subgroups). The results of this analysis yielded significance for the Deprivation Condition by Position Within The Squad, $F(1,12) = 5.21$, $p < .05$, and Position Within The Squad by R/N, $F(1,12) = 7.56$, $p < .05$, interaction effects. The Newman-Keuls procedure was used to probe these significant interactions. The results of these tests indicated that Subgroup B in Squad 1 ran

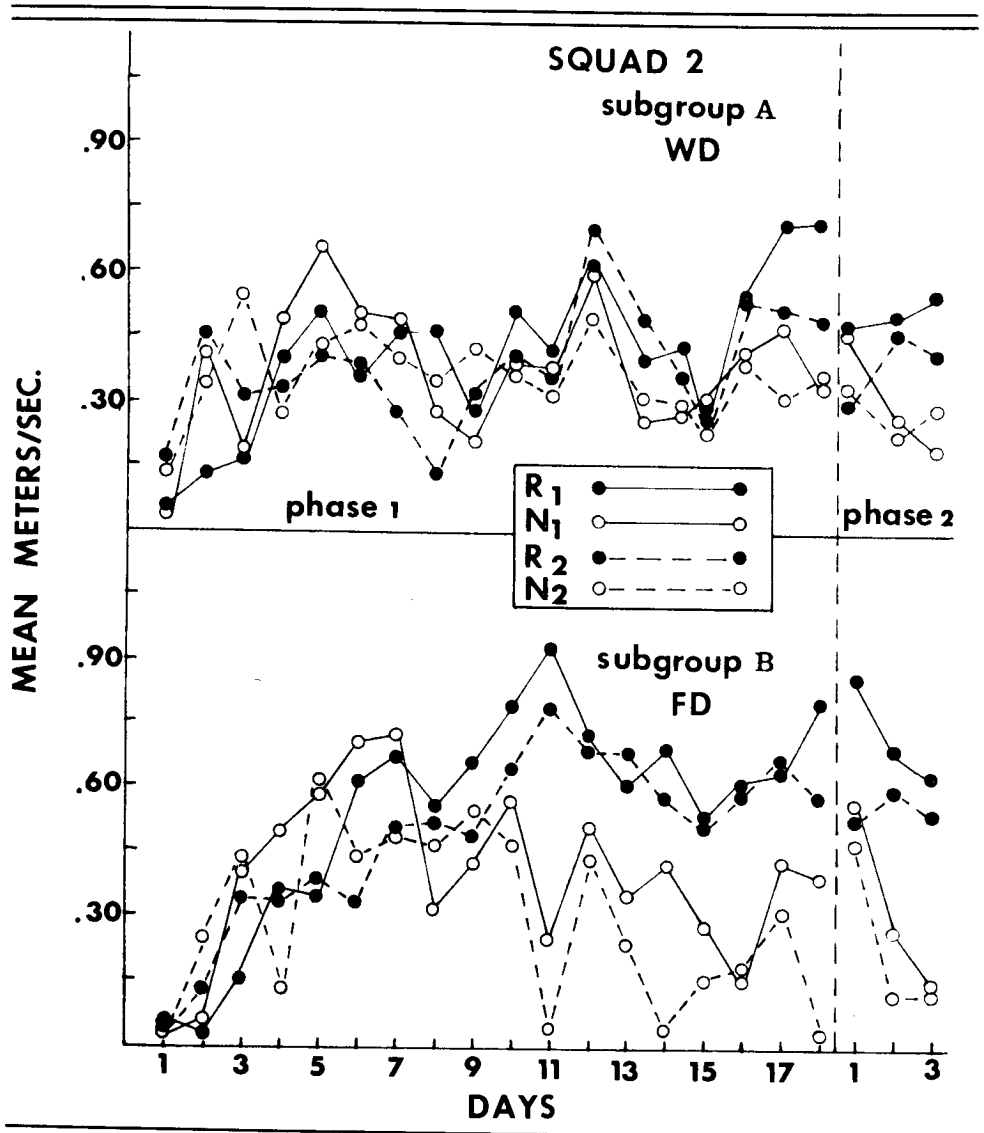


Figure 2 - Mean Goal Speeds for Squad 2, Subgroups A and B, During Phases 1 and 2 of Experiment 1.

significantly ($p < .05$) slower than the other three subgroups, and that significant ($p < .05$) R vs N differences where shown only by the two B subgroups. The significantly slower speeds shown by the B subgroup in Squad 1 would appear to be attributable to the development of appropriate patterend responding by these animals.

These data might be interrupted as suggesting that Subgroup A in both squads was not exuding any discernible odor cues that could be utilized by the following, opposite-deprivation B subgroups. Given this view, it would further be assumed that the

patterning displayed by Subgroup B in both squads resulted from an accumulation of their own (within-subgroup) odor cues. However, a closer examination of the Phase 1 data reveals that some individual animals within *both* of the A subgroups had developed appropriate patterned responding. Unfortunately, this responding was not sufficient and did not occur in enough animals to be reflected in group means. Visual inspection of the data also indicated that the first animal in the FD Subgroup B (which followed the WD Subgroup A) displayed strong patterned responding. This finding is not predictable if one assumes that different deprivation states produce different odors.

As Prytula et al. (1981) have suggested that larger squads produce greater odor-buildup, it might alternately be argued that odor cues accumulated across all subjects within each squad. In particular, the A subgroups (*S*s 1-4) were run under theoretically low odor-buildup conditions, while the B subgroups (*S*s 5-8) were tested under theoretically higher odor-buildup conditions. Based upon this contention, Subgroup A in both squads might not be expected to display patterned responding due to weaker odor cues. However, the odors exuded by these subgroups would, theoretically, accumulate and be utilized by the subsequent animals in Subgroup B of both squads. Assuming that low odor-buildup conditions (4 *S*s) do not allow odors to accumulate sufficiently for the development of patterned responding, it would appear reasonable to suggest that B subgroups, in turn, did not establish patterned responding solely on the basis of their *own* within-subgroup odor cues. A more plausible explanation would be that these subgroups developed double-alternation responding due to odors that had, in fact, accumulated over all eight subjects within each squad.

As depicted in Figures 1 and 2, the Phase 2 rotation of subjects from Position 8 to Position 5 within the B subgroups resulted in some disruption of the previously established patterned responding. (As the daily subject-rotation procedure resulted in a daily change in the subject ordering within each of the B subgroups, statistical analyses were not performed on the data from Phase 2.) However, Figure 3 readily indicates that this disruption was not attributable to the performance of the rotated subjects, i.e., *each* rotated subject displayed appropriate DA responding during Phase 2. Thus, the disruption resulted from fluctuations in the performance of animals that followed the rotated subject. These results suggest that individual animal odors may play *some* role in the runway behavior of the rat. However, it is just as clear that the

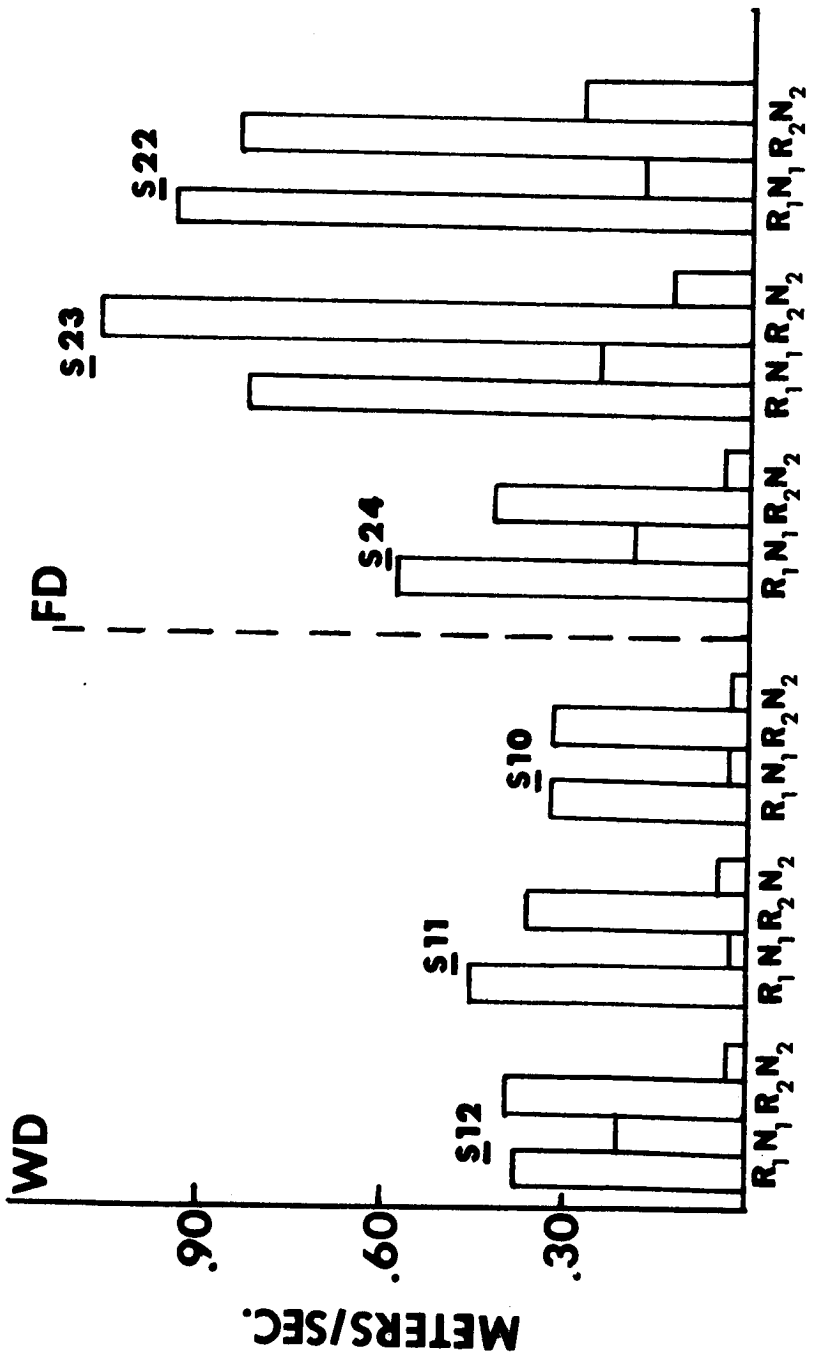


Figure 3 - Mean Goal Speeds for Rotated Subjects During Phase 2 of Experiment 1.

maintenance of patterning by the rotated subjects also is supportive of odor commonality across deprivation state.

Phase 3 further investigated the lack of patterned responding displayed by Subgroup A in both squads. If this failure to establish patterning was a result of low odor-buildup conditions, then placing these subgroups in the higher odor-buildup positions (i.e., second subgroup in the squad) should facilitate the development of DA responding. Figure 4 graphically supports this contention. In particular both of the A subgroups displayed patterned responding after only three days of training.

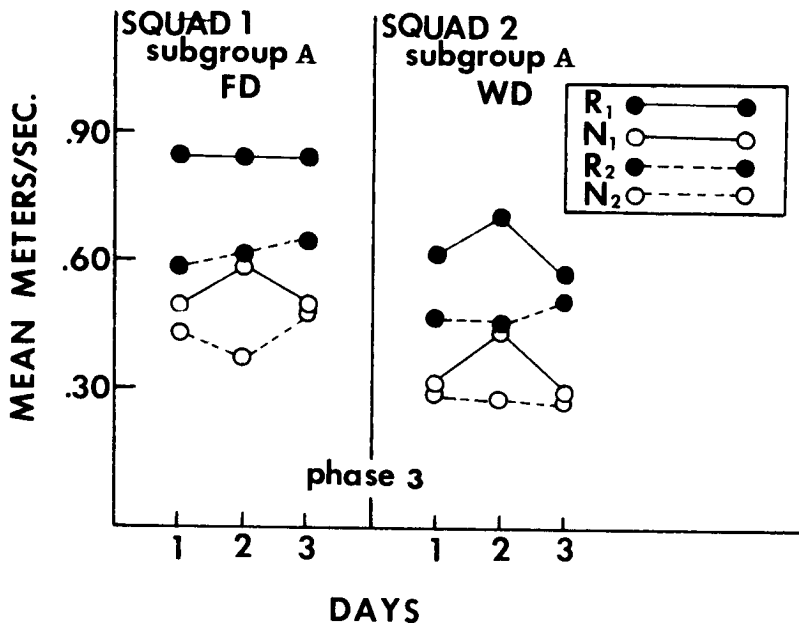


Figure 4 - Mean Goal Speeds for Squad 1, Subgroup A and Squad 2, Subgroup A During Phase 3 of Experiment 1.

A three-factor split-plot factorial analysis of variance incorporating Groups (Subgroup A-WD vs Subgroup A-FD) as a between-subjects factor, and R vs N and Days as within-groups factors was performed on the speed data of the two A subgroups for the three days of Phase 3. The results of this analysis yielded significance for the Groups, $F(1,6) = 6.16$, $p < .05$, and R vs N, $F(1,6) = 7.87$, $p < .05$, factors. Thus, it is clear that even though both A subgroups displayed appropriate patterned responding on all days of Phase 3, the FD subjects were approaching the goal significantly faster than the WD subjects.

The data from Experiment 1 give rise to two points of interest. First, it would appear that individual animal odors may play a role in the runway performance of rat subjects. As noted, this was clearly demonstrated through the effects of the rotation technique of Phase 2. Second, and perhaps of potentially greater interest, is the fact that the training procedure utilized when rats are experiencing different deprivation conditions may affect the discriminative use of odor cues. In the present experiment demonstrating commonality of odors, independent groups of test animals were used, whereas the odor-donor technique was employed in the studies demonstrating motivational specificity. In particular, the previous studies (Davis et al., 1974, 1976; Eslinger & Travis-Neideffer, Note 2) utilized a startbox-placed odor-donor technique. If odors exuded by the odor donors were the same as, or similar to, those exuded by the run subjects (i.e., same deprivation states), patterning was developed in all runway segments (Davis et al., 1974, 1976). If the odors were dissimilar (i.e., different states), then patterning developed only in the goal area where the run animals encountered odor cues exuded by previous run animals experiencing the same deprivation state (Davis et al., 1974, 1976). These results certainly suggest that odors exuded under different states may be dissimilar. However, Eslinger and Travis-Neidiffer (Note 2) have established patterned responding in *all* segments of the runway utilizing the odor-donor technique, but this was accomplished *only* after the run subjects were previously trained with odor-donors experiencing the *same* deprivation condition. The Eslinger and Travis-Neideffer, (Note 2) results lead to the assumption that there may be some common element between odors exuded under different deprivation states. As already noted, the Phase 1 and Phase 2 data of the present experiment are supportive of such a "common-element" view.

EXPERIMENT 2

The purpose of experiment 2 was to further investigate: 1) the effect(s) of individual animal odors on the development of patterned responding, and 2) the effects of previous runway training on the utilization of odors as discriminative cues under different deprivation states. As in Experiment 1, all subjects received a common reinforcer while selected groups experienced different deprivation conditions. However, the reinforcer employed in Experiment 2 was a 32% sucrose-milk solution. The basis for the change in reinforcers from Experiment 1 to Experiment 2 resulted from visual inspection of Figures 1, 2, and 4. A comparison of the A

subgroups (see Figures 1 and 2) suggests that patterned responding may have begun to develop on the last two days of Phase 2 for the WD Subgroup A but not for the FD Subgroup A. In turn, as depicted in Figure 4, the Phase 3 patterning displayed by the WD Subgroup A appears to be stronger (i.e., greater R-N differences) than that shown by the FD Subgroup A. In light of these observations it might be argued that the sucrose-water mixture may not have been as reinforcing for the FD subjects as it was for the WD subjects. Therefore, a potentially more substantial reinforcer, sucrose-milk, was employed during Experiment 2.

Experiment 2 employed four groups that consisted of seven naive subjects each. This number of groups and subjects was needed to conduct Phase 2. It also provided a within-experiment replication for the randomized-running-order (RND) condition employed in Phase 1. Phase 1 addressed the effects of individual animal odors on the development of patterned responding. It was predicted that if individual animal odors do play a role in runway performance, then patterned responding might be precluded or at least slow to develop under the RND condition. If individual odors do not play a role, then patterning should be established just as readily under the RND condition as under the more traditionally used FXD condition.

During Phase 2, 24 of the subjects were randomly assigned according to deprivation state, to one of six squads. Each squad was composed of two subgroups having different deprivation states. The subgroups within each squad contained an equal number (i.e., 1, 2, or 3) of WD and FD animals. This particular squad composition allowed an evaluation of: 1) the odors exuded by initial subjects tested under each type of deprivation and 2) the utilization of these odors by subsequent animals tested under the different deprivation state.

As the results of Phase 2 testing might well be influenced by Phase 1 training, Phase 2 should also provide additional information regarding the effects of previous runway training on the discriminative use of odor cues produced under different deprivation states. Given that a daily RND sequence was used in Phase 1, and a daily FXD sequence was used in Phase 2, several predictions might be entertained. First, as noted above, it might be assumed that the RND procedure might, in some way, preclude odor production and utilization during Phase 1 training. Hence, several days of training may be required in Phase 2 before the subjects would be able to effectively utilize odor cues. On the other hand, if the RND

procedure results only in the masking of N and R odors by individual animal odors, then some learning about such N and R odors might take place during Phase 1 training. Under this condition, the utilization of N and R odors would become manifested more completely only under the FXD condition of Phase 2. Third, it might be argued that patterned responding would not be displayed during either phase. This view might assume that randomization would preclude odor production during Phase 1, while the small squad size would preclude odor utilization during Phase 2. However, with several days of training, patterned responding might be predicted for the second subgroups (n = 3) in Squads 5 and 6 during Phase 2 training. These results would be expected if odors exuded under different deprivation states are similar and accumulate across subjects (see Experiment 1).

Method

Subjects. Twenty-eight, 90-day-old, naive, male Holtzman rats served as subjects. One week prior to experimental testing the animals were randomly assigned to either a FD or WD condition (n = 14). Subjects in these groups were further assigned to one of four equal groups (n = 7): two food-deprived (FD1 and FD2) and two water-deprived (WD1 and WD2). Respective feeding regimens for these groups were the same as those delineated in Experiment 1. These schedules were maintained throughout the duration of experimental testing.

Apparatus. The runway apparatus was modified by removing the water bottle and attaching a ½-tsp. metal measuring spoon (goalcup) to the end wall of the goalbox.

Procedure. The five days preceding Phase 1 constituted pretraining. Rats were handled and tamed (Days 1-5) and habituated to the 32% sucrose-milk reward solution in the home cage (Days 3-5). On Days 4 and 5 each subject was allowed to explore the baited apparatus for a 5-min period. Photoelectrical equipment was operative only on Day 5.

As can be seen in Table 3, Experiment 2 employed four groups of animals (n = 7): FD1, FD2, WD1, and WD2. During Phase 1 (12 days, 96 trials) the order for running subjects within all groups was randomized (RND) daily. To accomplish this, on each day of Phase 1 a new randomized running sequence was assigned to each group. This sequence was then held constant throughout the eight daily trials. Hence, subjects did not precede or follow the same subject on all days of experimental testing. The trial-sequencing (i.e., RRN-

NRRNN) and trial-administration procedures employed in Experiment 2 were the same as described in Experiment 1. On an R event, 1 ml of the sucrose-milk reward was present in the goalcup. On R trials, subjects were removed from the goalbox after consuming the reward. An N event consisted of a 30-sec confinement to an empty goalbox. The empty ½-tsp was in place during N trials. All daily trials were administered to an entire group before another group was run. The order for running individual groups was randomized daily. After the completion of each trial for each group, the runway cleaning procedures of Experiment 1 were employed.

Prior to Phase 2 (4 days, 32 trials) testing, one animal from each group was randomly eliminated. The remaining 24 subjects were then randomly distributed, according to deprivation state, across three squads (Squad 1, $n = 2$; Squad 2, $n = 4$, and Squad 3, $n = 6$) consisting of two subgroups (SGA and SGB) each. Although these squads did not consist of an equal number of subjects, an equal number of subjects *were* contained in the two subgroups within a particular squad (i.e., 1, 2, or 3 WD and FD animals). This arrangement allowed squads to be counterbalanced with regard to the ordering of deprivation states. Animals within each squad were tested in the same FXD running order on all days of Phase 2 while the order for running squads was randomized daily.

Results and Discussion

The results of Phase 1 lend further support for the individual animal odor hypothesis proposed in Experiment 1. Visual inspection of Figures 5 and 6 indicates that none of the four groups, FD1, FD2, WD1, or WD2, established reliable patterned responding under the daily RND conditions.

Prior to overall statistical analysis, separate analyses of variance were performed on the speed data from Days 7-12 for Group WD1 vs WD2, and FD1 vs FD2. As these analyses failed to yield any significant effects, Groups WD1 and WD2, and FD1 and FD2 were pooled for further analysis. A subsequent analysis incorporated one between-groups factor, Deprivation Condition (Water-Deprived vs Food-Deprived), and two within-groups factors (R vs N, and Days) was performed over the speed scores from Days 7-12. The results of this analysis also failed to yield any significant effects and corroborated the visual impression described above.

It should be noted than when food-deprived subjects receiving food pellets (see Davis & Prytula, 1979; Ludvigson & Sytsma, 1967; Prytula, Davis & Fanning, 1981) and water-deprived subjects

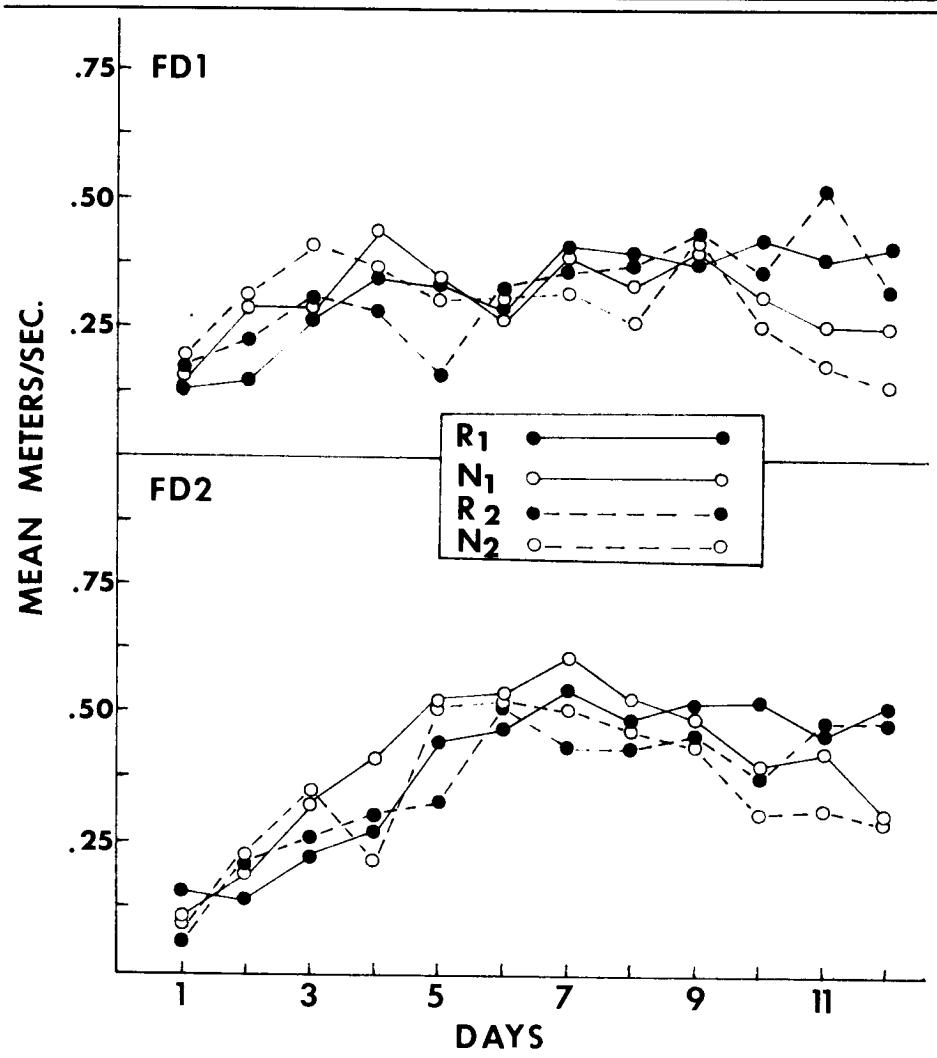


Figure 5 - Mean Goal Speeds for Groups FD1 and FD2 During Phase 1 of Experiment 2.

receiving sucrose reinforcement (see Davis, Burns, Howard, & Voorhees, 1982) are tested under a daily, FXD running order, appropriate patterned responding is typically displayed around Day 7. As no patterned responding was displayed by any of the four groups during the 12 days of Phase 1 training, these results strongly suggest that individual animal odors may play a significant role in determining the development of appropriate DA responding.

Although patterned responding was not evident for Groups FD1, FD2, WD1, and WD2 during Phase 1, the rather *rapid* development of patterned responding in Phase 2 suggests that the Phase 1 randomization procedure did not preclude odor produc-

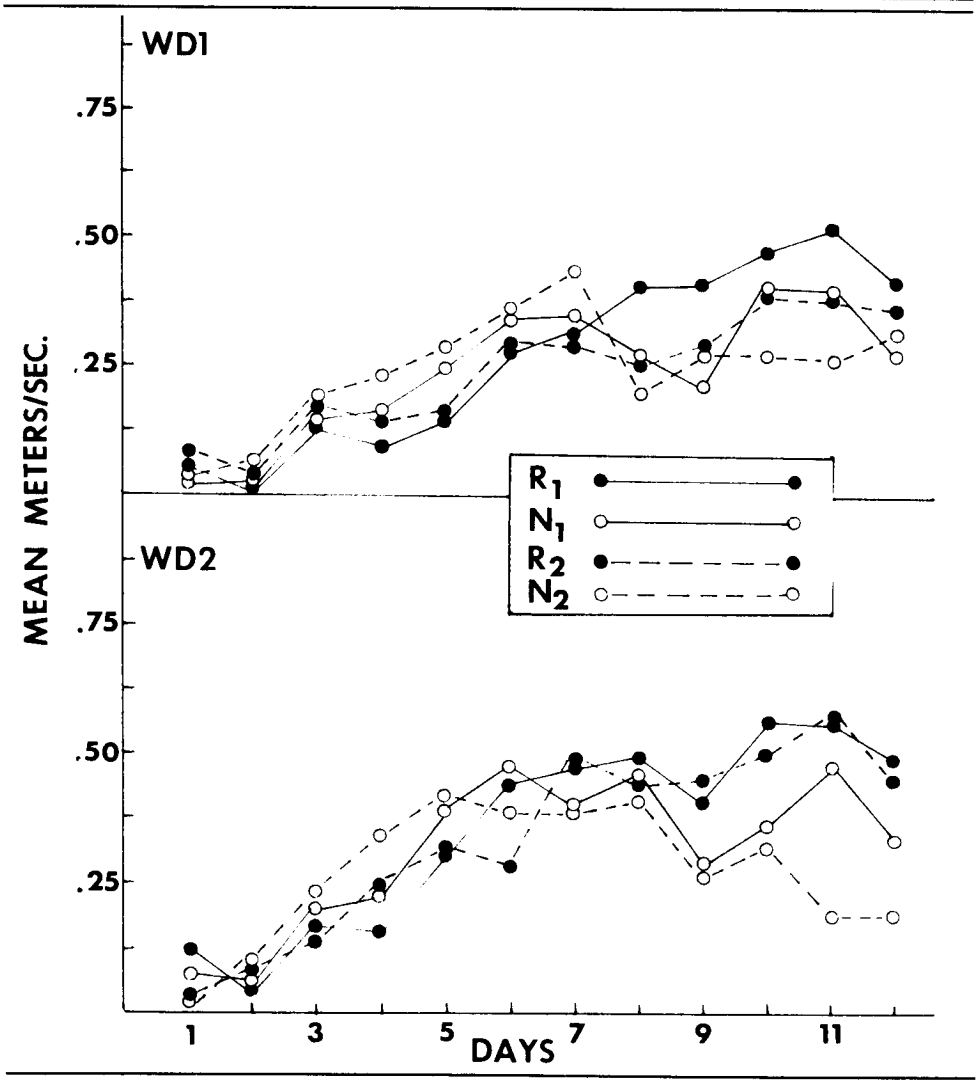


Figure 6 - Mean Goal Speeds for Groups WD1 and WD2 During Phase 1 of Experiment 2.

tion, but rather masked them. As can be seen from Figure 7, appropriate patterned responding was displayed by SGA in Squads 4 and 5 and SGB in Squads 1, 2, 3, 4, 5, and 6 within only four days of runway training under the daily, FXD sequence. Further inspection of Figure 7 reveals that nondifferential responding was displayed by SGA in Squads 1, 2, 3, and 6.

A separate analysis of variance incorporating one between-groups factor (SGA vs SGB) and two within-groups factors (R vs N, and Days) was performed on the speed scores for all days of Phase 2 for Squads 3-6. As SGA and SGB in Squads 1 and 2 contained only one subject each and, therefore, precluded the calculation of any

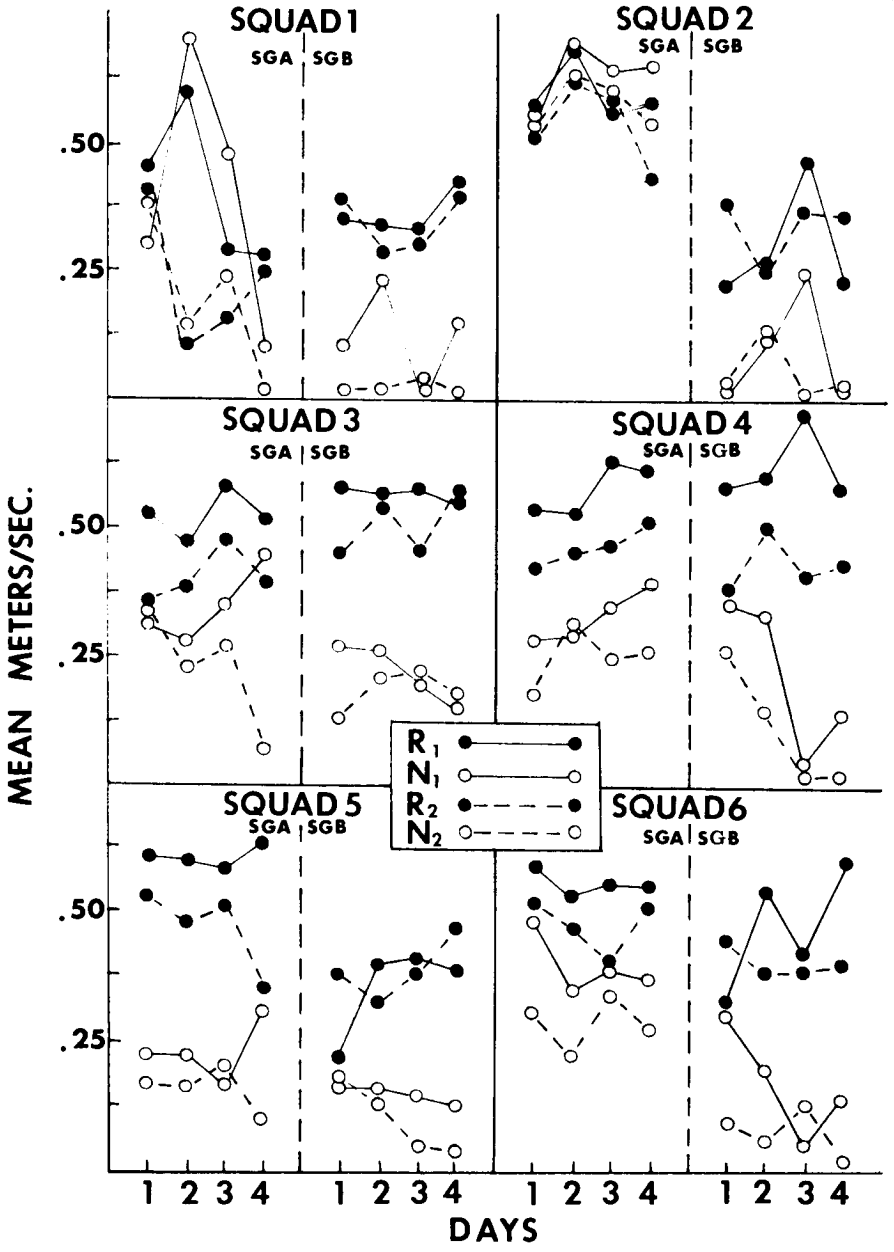


Figure 7 - Mean Goal Speeds for Squads 1-6, Subgroups A and B, During Phase 2 of Experiment 2.

within-group variability, statistical analyses were not performed on these squads. The results of the analyses of Squads 3-6 indicated that significant R vs N effects were developed in all cases. More specifically, the Squad 3 analysis yielded significance for the SGA/SGB by R/N interaction, $F(1,23) = 4.37$, $p < .05$. Subsequent examination of this interaction (Newman-Keuls procedure) indicated that significant ($p < .05$) R vs N differences were shown on-

ly by SGB in squad 3. As only the R vs N main effect was shown to be significant, $F(1,23) = 8.68$, $p < .01$, in the Squad 4 analysis, it can be concluded that both SGA and SGB had developed appropriate patterned responding during Phase 2. The Squad 4 results were mirrored by the results of the Squad 5 speeds, i.e., only the R vs N effect yielded significance, $F(1,37) = 9.07$, $p < .01$. However, the SGA/SGB by R/N interaction, as with Squad 3, was found to be significant, $F(1,37) = 5.39$, $p < .05$, in the Squad 6 analysis. Again, significant ($p < .05$) R vs N differences were shown only by SGB.

The lack of patterning displayed by SGA ($n = 1$) in Squads 1 and 2 is to be expected. These results are consistent with data reported by previous studies (Prytula et al., 1980; Prytula et al., 1981) which indicate that the first animal in a group does not display differential responding due to being tested in a clean, odor-free apparatus.

If one assumes odor commonality across deprivation states, then only SGB in Squads 1, 2, 3, and 4 were tested under theoretically low odor-buildup conditions. Within Squads 5 and 6, each SGB consisted of three subjects and followed SGA which also consisted of three subjects. Hence, SGB subjects in Squads 5 and 6 were tested under theoretically higher odor-buildup conditions than the other subgroups. This should allow for the sufficient accumulation of odors for the development of patterned responding. The results indicate that this is exactly what happened. Likewise, although run under theoretically low odor-buildup conditions, SGB in Squads 1, 2, 3, and 4 also displayed patterned responding. It is of particular interest to note that the SGB animals in Squads 1, 2, 3, and 6 were able to establish appropriate patterned responding even though the preceding SGA animals displayed no such behavior. The patterned responding shown by SGA in Squads 4 and 5 suggests the importance that the strength of R and N odors from individual animals may play. These results are in accord with those reported in Phase 1 of Experiment 1 and further suggest that odors are being produced by the initial animals experiencing one deprivation state and are being utilized by the terminal animals (SGB) experiencing a different deprivation state. The argument for odor similarity is further strengthened by the patterned behavior displayed by SGB ($n = 1$) in Squads 1 and 2.

In summary, three salient points are suggested by the results of Experiment 2. First, given that none of the four groups displayed patterned responding after 12 days of Phase 1 training (RND condition), it appears that individual animal odors do play a role in the

development of odor-based DA responding. Second, the rapidity with which the subgroups developed patterned responding during Phase 2 (FXD condition) certainly supports the contention that previous runway training, even under randomized conditions, enables subjects to obtain information about R and N odors. Third, and possibly of greater importance, is the fact that SGB in all six squads established patterned responding in only four days (Phase 2) when following animals of a different deprivation state. This finding certainly lends further support for the contention that odors exuded under different deprivation states may be similar and that learning about R and N odors may occur under the RND condition.

EXPERIMENT 3

Experiment 3 was specifically designed to further investigate the runway performance of animals tested under the daily, within-groups randomized (RND) sequence. Visual inspection of the Phase 1 data of Experiment 2 (Figures 5 and 6) for Groups FD1, FD2, WD1, and WD2 suggested that patterning may have been emerging for these animals. As the possibility of this patterned responding was most pronounced on the last day of Phase 1 training (Day 12), it might be that extension of RND runway training to 14 days would allow subjects to more completely develop odor-based DA responding. Hence, Phase 1 of Experiment 3 tested two groups, FD and WD, with extended training under the same RND procedure employed in Phase 1 of Experiment 2. The only exception was that each group was administered a reinforcer that more directly corresponded to its deprivation state (i.e., FD animals received food pellets and WD animals received water). As the main thrust of Experiment 3 was to specifically evaluate the RND procedure, the use of the more traditional and/or appropriate reinforcer was implemented in order to make tentative comparisons with previously reported data.

During Phase 2 of Experiment 3 both Groups FD and WD were shifted to the FXD sequence. If patterned responding does occur during Phase 1 RND training, then it should continue undisrupted under the Phase 2, FXD training. This view assumes that subjects can eventually discriminate among N, R, and individual animal odors under the RND condition if acquisition training is extended, and continue this discrimination undisrupted when the FXD conditions are imposed. On the other hand, if patterned responding is not established under the RND condition of Phase 1, then addi-

tional information can be obtained concerning the length of time required for these groups to develop patterned responding under the FXD condition of Phase 2. Assuming that previous RND training allows subjects to learn something about the discriminatory use of N and R odors (Experiment 2), then patterned responding might be expected to manifest itself somewhat more rapidly during Phase 2 (FXD) even if it is not shown in Phase 1. Phase 3 constituted a reversal phase during which Groups FD and WD were returned to the Phase 1 RND condition. Previous positive data gathered under the FXD condition (e.g., Ludvigson & Sytsma, 1967) prompts the assumption that both groups will display DA responding during Phase 2, regardless of the RND technique employed in Phase 1. Hence, it might be further predicted that once the animals have learned to utilize N and R odors as discriminatory cues they should continue to disregard individual animal odors and maintain patterned responding.

Method

Subjects. Fourteen, 120-day-old, naive, Holtzman rats served as subjects. One week prior to pretraining the animals were randomly assigned to FD and WD groups ($n = 7$). Subjects in Groups FD were maintained on a food-deprivation regimen that kept them at 85% of their free-feeding body weight. Group WD animals were maintained on 23-hr water deprivation.

Apparatus. As Group FD received food-pellet reward and Group WD received water reward, respectively, on R trials, the receptacle mounted on the end wall of the goalbox was modified accordingly to accept both food pellets and a plastic water bottle.

Procedure. The five days preceding Phase 1 constituted pretraining. All days of pretraining consisted of handling and taming, and habituation to the 45-mg Noyes reward pellets in the home cage for Group FD. The WD subjects received their regular daily access to water in the home cage at this time. On Day 3 each subject received a 5-min exploration period in the unbaited apparatus. On Days 4 and 5, the apparatus was baited with the appropriate reward and all photoelectric equipment was operative.

During Phase 1 (14 days, 112 trials) the order for running subjects *within* each group (FD and WD) was *randomized* daily. Phase 2 (8 days, 64 trials) employed the FXD sequence. During this phase all subjects were run in the order which was in effect for the respective group on the last day of Phase 1. On each day of Phase 3

(2 days, 16 trials) the subjects within each group were again run in the RND sequence. (Please refer to Table 3 for a complete delineation of the experimental design employed in Experiment 3.)

In all three phases, trial-administration and runway cleaning procedures were the same as those employed in Experiments 1 and 2. The order for running groups was alternated daily. An R event for Group WD consisted of 15-sec access to a full water bottle, while Group FD received 12, 45-mg Noyes pellets on R trials. Group FD subjects were removed after consuming the reward pellets. On an N event all subjects received a 15-sec confinement period in the empty goalbox. An empty water bottle was in place during N-trial confinement for Group WD subjects.

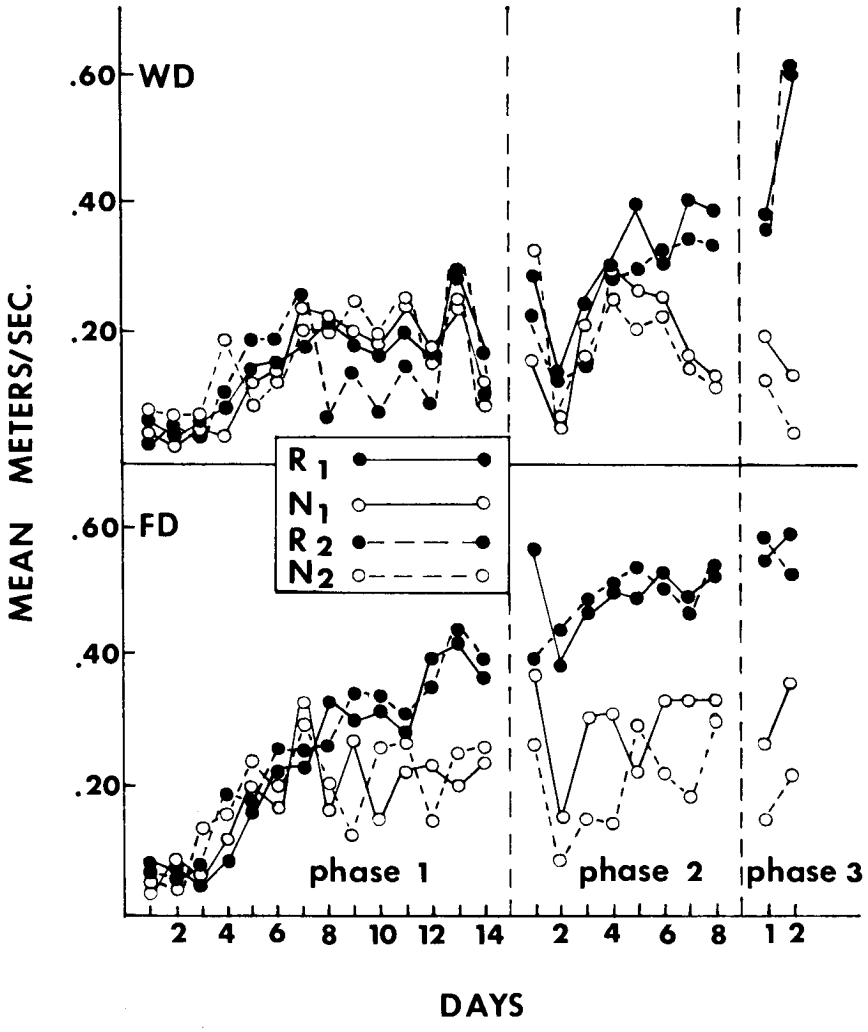


Figure 8 - Mean Goal Speeds for Groups WD and FD During Phases 1, 2, and 3 of Experiment 3.

Results and Discussion

Visual inspection of Figure 8 indicates that Group WD did not develop appropriate patterned responding during Phase 1 under the RND sequence. In contrast, Group FD had established patterned responding by Day 12 of Phase 1. An analysis of variance incorporating one between-groups factor, Deprivation Condition (Water-Deprived vs Food-Deprived) and two between-groups factors, R vs N and Days, was performed on the speed data from the last three days of Phase 1 (the point at which appropriate patterning appeared to have been established by Group FD). The results of this analysis yielded significance for the Deprivation Condition by R/N interaction, $F(1,12) = 8.29$, $p < .05$, and the Deprivation Condition by Days interaction, $F(2,24) = 4.30$, $p < .05$. Subsequent Newman-Keuls tests indicated that significant ($p < .05$) R vs N differences were shown on Days 12-14 only by Group FD. Further, it was found that Group FD approached the goal significantly ($p < .05$) faster than Group WD on Days 12 and 14.

During Phase 2, when tested under the FXD sequence, patterned responding was maintained by Group FD and established by Group WD on Day 7. Further, this patterning persisted into Phase 3, when the RND condition was reinstated, for both Groups FD and WD. These visual impressions and conclusions were supported by statistical analyses, similar to the one conducted on the Phase 1 data, of the Phase 2 and Phase 3 speeds. More specifically, the Phase 2 analysis indicated that the Deprivation Condition by R/N by Days interaction was significant, $F(2,24) = 6.23$, $p < .01$. Subsequent analysis of this interaction (Newman-Keuls tests) indicated that Group FD displayed significant patterned responding (R speeds faster than N speeds) on Days 1 ($p < .05$) and 2-8 ($p < .01$), while Group WD displayed such appropriate responding only on Days 7 and 8 ($p < .01$). Further, it also was found that Group FD approached the goal significantly ($p < .05$) faster than Group WD on Days 1, 2, 3, 7, and 8. In accord with the last point raised above, the Phase 3 analysis yielded significance only for the R vs N main effect, $F(1,12) = 12.78$ $p < .01$.

The fact that Group FD did establish patterned responding during Phase 1, by Day 12, suggests that FD subjects can eventually discriminate among N, R, and individual animal odors when trained under the RND condition. However, it should be recalled that FD rats run in a FXD sequence and receiving pellet reinforcement typically display strong patterning after approximately seven days of training (see Davis & Prytula, 1979; Ludvigson & Sytsma, 1967;

Prytula et al., 1981). In view of this retarded development of patterning shown by Group FD under RND conditions, and the complete lack of patterning shown by Group WD in Phase 1, it would appear that individual natural animal odors may serve to mask or obscure R and N odors under the RND condition. As noted, when tested under the FXD sequence during Phase 2, both groups displayed patterned responding. In light of these results, it is proposed that once the individual animal odors are fixed by having each subject follow the same animal on all trials, there are no longer any novel animal odor(s) that compete(s) with the R and N odors. Thus, those R and N odors that are present can now be more effectively utilized as discriminative cues.

That Group WD failed to establish patterned responding during Phase 1 (RND), also might suggest that N and R odors exuded by WD subjects are less salient than N and R odors exuded by FD subjects. Thus, it might be suggested that the lack of Phase 1 (RND sequence) patterning displayed by Group WD was a result of natural animal odors over-shadowing these presumably less intense water-related R and N odors. However, as suggested by Phase 2, running the WD subjects under the FXD condition allows the less intense R and N odors to be used more effectively as discriminative cues. As appealing as this interpretation might be, it should be mentioned that the development of patterning by WD animals may not be influenced by such natural animal odors. If the odors exuded under this deprivation state are less salient and/or intense such retarded patterning may simply indicate that patterning takes longer to develop under this deprivation state.

That no disruption was evidenced Day 1 of Phase 3, when the RND sequence was reinstated, was not completely unexpected. Recall that Group FD had previously established patterned responding under the RND sequence in Phase 1. Similarly, Group WD also continued to display patterned responding during the Phase 3 reversal to the RND sequence. These results are in accord with a previous drug study (Davis et al., 1981) which suggests that once patterning has been established, it is relatively resistant to disruption.

EXPERIMENT 4

Experiment 4 was a three-phase study designed to further investigate: 1) the saliency of N and R odor cues exuded by FD and WD subjects receiving corresponding reinforcers (i.e., FD subjects received food pellets and WD subjects received water) and 2) the similarity of these odor cues between deprivation states when *both*

the within-day running sequence (FXD and RND) and deprivation state (FD and WD) were manipulated within and between groups. During each of the three phases either the WD or the FD condition was held constant across all subjects while the FXD an RND running order conditions differed among groups.

During Phase 1 the WD condition was held constant for all subjects. The FXD running-order sequence was employed for Groups F-F-F and F-R-R while the RND running-order sequence was employed for Group R-F-F. As the conditions employed for Group R-F-F are identical to those employed for Group WD during Phase 1 of Experiment 3, it might be predicted that Group R-F-F would fail to establish patterned responding during Phase 1. Predictions regarding the Phase 1 Performance of Group F-F-F and F-R-R are less clear. Given the FXD sequence of trial administration, one might argue convincingly for the development of patterning. It will be recalled that patterning was established under this condition in Phase 2 of Experiment 3. However, this patterning was established following 14 days of RND training. On the other hand, as only six animals will be used per group, it could be argued that a sufficient amount of the potentially less intense water-deprivation odors will not be accumulated to support appropriate patterned responding.

During Phase 2 the FD condition was held constant for all subjects. The FXD running-order sequence was employed for Groups F-F-F and R-F-F while the RND running-order sequence was employed for Group F-R-R. Regardless of whether or not any group establishes patterned responding during Phase 1, *all three* groups would be expected to display patterning at some time during Phase 2. As Phase 2 employs the FXD/FD conditions for Groups F-F-F and R-F-F, these subjects might be expected to establish patterned responding around Day 7 (see Davis & Prytula, 1979; Ludvigson & Sytsma, 1967; Prytula et al., 1982). Likewise, the results of Experiment 3 indicated that naive FD subjects (receiving a food reinforcer) tested under the RND condition developed patterned responding. Hence, it would be predicted that Group F-R-R will also display patterned responding, albeit delayed due to the RND training condition.

During Phase 3, the WD condition was reinstated for all subjects. Additionally, the Phase 2 running-order conditions remained in effect for each group during Phase 3. As all three groups should develop patterned responding during Phase 2, Phase 3 will allow an evaluation of the similarity of odor cues exuded under the different deprivation state conditions. If Phase 2 patterning is maintained in

Phase 3, then an even stronger case can be made for odor-cue similarity across deprivation conditions. On the other hand, disruption in responding would be attributable to deprivation-induced changes in the nature of the R and N odors that are exuded.

Method

Subjects. Eighteen, 110-day-old, naive, male Holtzman rats were randomly distributed across three groups (n = 6): F-F-F, F-R-R, and R-F-F. One week prior to pretraining all animals were placed on a 23-hr water deprivation regimen with food available on a free-feeding basis. This schedule remained in effect until the end of Phase 1 training. Two days prior to Phase 2 testing all subjects were shifted to a food-deprivation regimen that maintained them at 85% of their free-feeding body weight. Water was now available on an *ad libitum* basis. At the end of Phase 2 and 2 days prior to Phase 3 training, all subjects were returned to the water-deprivation schedule employed during Phase 1. Hence, a two-day interim existed between Phases 1 and 2, and Phases 2 and 3. On all days of experimental testing all animals received their respective feeding/water regimen following the daily experimental session.

Apparatus. As all groups received a water reinforcer during Phases 1 and 3 and a food reinforcer during Phase 2, the runway apparatus was modified to allow the attachment of a water bottle and the delivery of food pellets.

Procedure. A one-week pretraining phase immediately preceded Phase 1 of experimental testing. On all days of pretraining, all animals were handled and tamed and administered their regular daily access to water in the home cage. On Days 6 and 7 each subject received a 5-min exploration period in a baited (water bottle present) apparatus with all photoelectric equipment operative. During the interim between Phases 1 and 2, the subjects were habituated to the 45-mg Noyes reward pellets in the home cage.

During Phase 1 (13 days, 104 trials) the order for running subjects within Group R-F-F was randomized daily (please refer to Table 3). Subjects within Groups F-F-F and F-R-R were run in a fixed order (1-6) on all days.

During Phase 2 (17 days, 136 trials) the running order for subjects in Group F-F-F remained constant while Groups R-F-F and F-R-R were shifted to the opposite running-order condition. Thus, the order for running subjects within Group F-R-R was randomized daily while subjects within Group R-F-F were run in a fixed order (i.e., the order which was in effect on the last day of Phase 1).

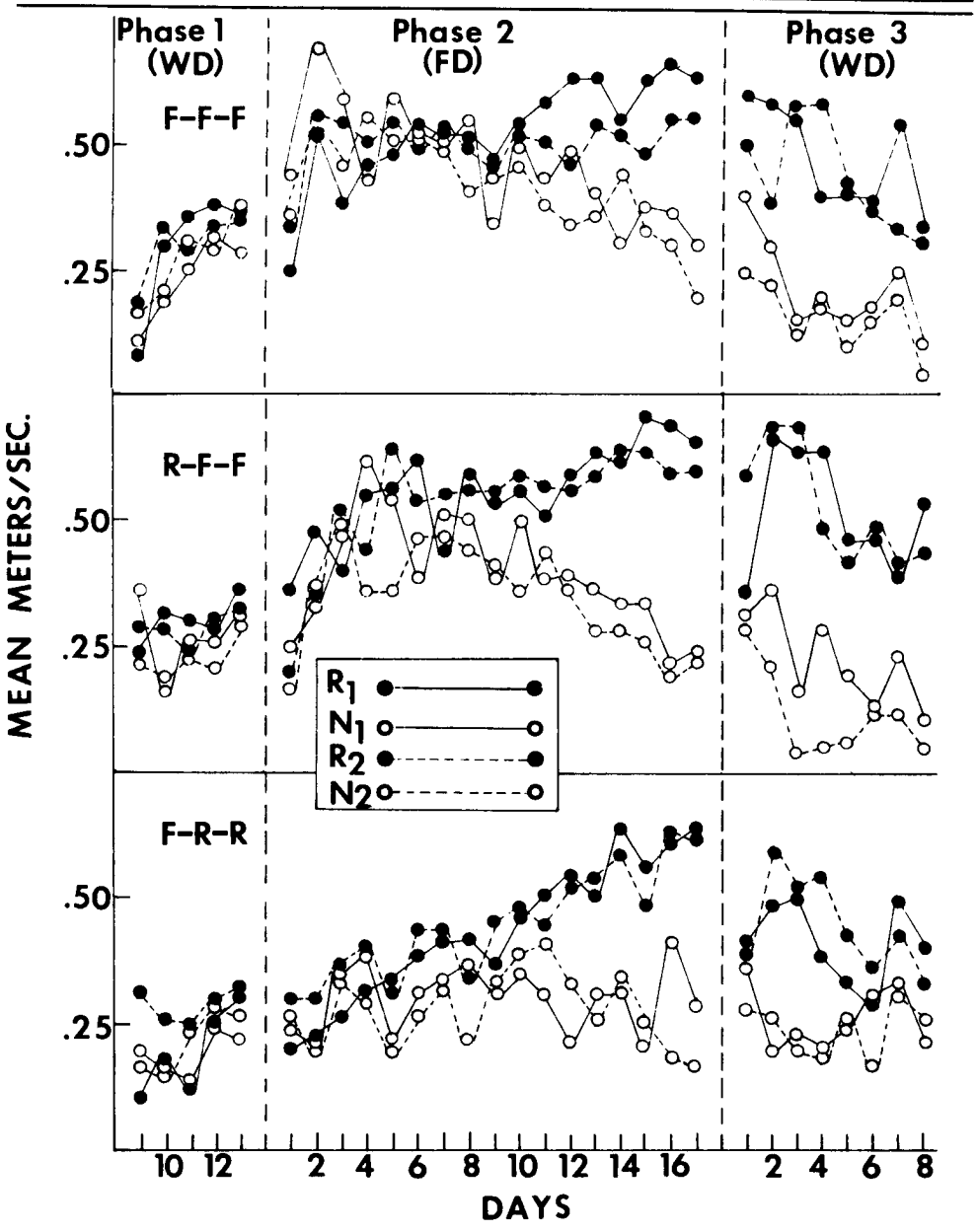


Figure 9 - Mean Goal Speeds for Groups F-F-F, R-F-F, and F-R-R During Phases 1, 2, and 3 of Experiment 4.

During Phase 3 (8 days, 64 trials) all groups were tested under the same running-order conditions employed in Phase 2. Throughout all three phases of Experiment 4, the order for running groups was randomized daily.

In all three phases, trial administration and runway cleaning procedures were the same as those employed in the previous experiments. During Phase 1 and 3 an R event consisted of 30-sec ac-

cess to a full water bottle. An N event consisted of 30-sec confinement in the goalbox with an empty water bottle in place. During Phase 2, 12 45-mg Noyes pellets were present on R trials. Subjects were removed upon consumption of the pellets or after 30-sec. On N trials animals received 30-sec confinement to an empty goalbox.

Results and Discussion

Visual inspection of Figure 9 indicates that during Phase 1, when tested under the WD condition, *no* group displayed patterned responding. In support of this visual impression, an analysis of variance performed on the speed scores from the last 5 days of Phase 1 failed to yield any significant effects.

In contrast, switching subjects to the FD condition during Phase 2 resulted in the development of patterned responding by all groups by approximately Day 12. An analysis of variance performed on the goal-measure speed scores from the last seven days of Phase 2 (the point at which appropriate patterned responding appeared to have been developed by all groups) yielded significance only for the R vs N factor, $F(1,15) = 11.46$, $p < .01$. This finding corroborates the graphical impression (see Figure 9) that appropriate responding had been established by all groups under the FD condition of Phase 2.

Although reinstating the WD condition in Phase 3 resulted in a slight disruption in performance on Day 1, patterned responding was reestablished by all groups on Day 2. As can be seen in Figure 9, this patterning continued for Groups F-F-F and R-F-F (FXD condition), but underwent further disruption in Group F-R-R (RND condition) on Days 6-8. An analysis of variance of the Phase 3 speed data yielded significance for the R vs N, $F(1,15) = 6.36$, $p < .05$, and Groups by R/N by Days, $F(14,105) = 2.13$, $p < .05$, factors. Newman-Keuls tests indicated that R speeds were significantly ($p < .05$) faster than N speeds on all days of Phase 3 for Groups F-F-F and R-F-F. On the other hand, R speeds were significantly ($p < .05$) faster than N speeds for Group F-R-R only on Days 2-4 of Phase 2 (i.e., nonsignificant differences were shown on Days 1, 5, 6, 7, and 8).

As noted, the nondifferential responding displayed by Group R-F-F in Phase 1 was expected (see the comparable performance of Group WD in Phase 1 of Experiment 3). Thus it would appear that less salient odor may be exuded by water-deprived animals, especially those trained under the RND condition. If one accepts the premise that a group of six animals is not sufficiently large to allow water-deprivation-based odor cues to accumulate, then the

lack of Phase 1 patterning shown by Groups F-F-F and F-R-R would also be supportive of the contention that these odors are less salient. However, such an interpretation leaves unanswered why the WD animals in Experiment 3 did display patterning. A viable explanation would appear to be one that stresses differences in prior experience.

As predicted, all groups developed appropriate odor-based patterning during Phase 2. Compared to previous studies (e.g., Davis & Prytula, 1979; Prytula et al., 1982) which reported well-established patterning by Day 7, Phase 2 patterning in the present experiment was delayed until Day 12. This finding might also reflect the influence of the use of six, as opposed to seven, animals per group and the corresponding lack of odor accumulation.

The results of Phase 3 indicate that all three groups displayed some disruption on Day 1 when the WD condition was reinstated. This disruption could be attributable to the one-day interim that existed between Phases 2 and 3, as well as the shift in deprivation and odor conditions. Despite these disruptions, these data are in accord with the Phase 2-Phase 3 shift results of Experiment 3 and the previous drug study (Davis et al., 1981), in suggesting that once patterning is established, it is *relatively* resistant to a variety of experimental manipulations.

GENERAL DISCUSSION

To reiterate, the present series of studies was designed to further investigate the contention of strict motivational specificity of conspecific odor cues. Several parameters which appear to interact with and/or influence the utilization of R and N odors for both FD and WD animals were manipulated.

Taken collectively, the data from the present studies seriously question the view that completely different odors are exuded under different deprivation states. For example, in Experiment 1 it was clearly demonstrated that a small subgroup of rats trained under one deprivation state developed patterning when they immediately followed another small subgroup trained under a different deprivation state. As patterning is typically not shown by such a small number of animals, it is proposed that odors from the first subgroup accumulated and were subsequently utilized by animals in the second, motivationally different, subgroup. This contention is further supported by the fact that the first small subgroups failed to establish patterned responding but the first animal in each of the

second subgroups did display appropriate patterning. Further, when the last subject in each of the second subgroups was rotated to the first position in his respective subgroup (Experiment 1, Phase 2) patterning was maintained by these rotated subjects. This result indicates that the rotated subjects were capable of using odors from the motivationally different animals that now preceded them. Similar results were obtained when all subjects received a sucrose-milk reward and the squad size was as small as two animals (Experiment 2, Phase 2). That subjects receiving deprivation-state-related reinforcers displayed minimal disruption when shifted from water- to food-deprivation (Experiment 4, Phase 3), strongly suggests that a *common* reinforcer is not a necessary factor for odors to be effectively utilized across deprivation states.

A second major point that the present data hightlight is that natural animal odors may serve to mask or obscure R and N odors. The finding that *both* food- and water-deprived subjects failed to develop patterned responding when tested under the RND running sequence (Experiment 2, Phase 1) would certainly appear to be supportive of this view. In short, it is proposed that subjects experiencing runway training in a FXD sequence are confronted with an invariant accumulation of natural animal odors. Under this training sequence, the accumulation of these natural odors remains constant (i.e., predictable) on all trials thus allowing R and N odors to become more salient and potentially utilized earlier in training. Conversely, subjects tested under an RND sequence are confronted with a changing accumulation of natural animal odors on each day of runway training. Such fluctuations, presumably, would make any R and N odors that are present less discriminable (i.e., salient). In support of this contention it will be recalled that food-deprived animals did ultimately develop patterning under the RND sequence, but only after extended training (see, Experiment 1, Phase 3).

The fact that FD subjects did eventually display patterned responding when tested under the RND sequence and WD subjects failed to establish such patterning under *both* the RND (Experiments 3 and 4, Phase 1) and the FXD sequences (Experiment 4, Phase 1) prompts a consideration of a third finding from the present studies. Namely, that odors exuded by water-deprived subjects are less intense and/or salient than those exuded by food-deprived subjects. Although the odor-intensity interpretation is quite plausible, the fact remains that water-deprived subjects did establish patterned responding when tested under the FXD sequence of Phase 2 in

Experiment 3. In attempting to resolve this discrepancy, it should be mentioned that two procedural differences existed between Experiment 3, Phase 2 and Experiment 4, Phase 1. Specifically, the subjects in Experiment 3 (Phase 2) had experienced, albeit under the RND condition, 14 days of previous runway training. Second, this group consisted of seven subjects whereas the groups in Experiment 4 contained only six animals. Thus, it would appear reasonable to suggest that 14 days of RND training by groups of seven animals is sufficient to somehow sensitize the subjects to R and N odors such that they are effectively used as discriminative cues under the FXD schedule which was subsequently imposed. Also supportive of this interpretation is the finding that water-deprived animals receiving sucrose-milk reward established patterning under the FXD sequence *following* RND training. Patterning was *not* displayed under the RND sequence by these animals.

Undoubtedly, there are still a number of unanswered questions with regard to the production and utilization of odor cues. However, it is clear that research in the area of odor control of animal maze performance has gone far beyond the simple conceptualization of *just* reward and nonreward odor cues. We must now contend with considerations of the daily within-group running sequence, the influence of natural animal odors, the deprivation state employed, the effects of previous runway training, and the specific type of reinforcer employed, to name just a few parameters—let alone their possible interactions. What is quite clear is the fact that such odors may be powerful determinants of animal maze performance. Certainly, if psychology is to continue in its traditional use of the white rat as a subject of study, then such odors must be given the utmost consideration.

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