AN ABSTRACT OF THE THESIS OF

Brenda J. Anderson _____ for the __Master of Science__

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Title: __Odor-Mediated Runway Performance Following__

__Extended Training and Gradual Changes in__

__Reinforcement Magnitude__

Abstract approved: _Stephen F. Davis_

Stephen F. Davis

Many researchers in the area of odor-mediated runway performance have suggested that frustration (as spoken of by Amsel, 1958, 1962) may be the mechanism whereby nonreward odors are produced. The present research was designed to test this idea. Three groups of rats received a daily 8-trial double-alternation (DA) schedule of reward and nonreward in a straight runway during a three-phase experiment. Only subjects receiving large (12 pellet) rewards developed appropriate DA patterning during Phase 1 (12 days). During Phase 2 (33 days) one group continued to receive large reward training, while a second group underwent gradual reward reduction, and a third group experienced gradual reward increase. Appropriate patterning was maintained throughout the entire phase by the group continued on large reward, and until the final block of trials (small-reward level) by the gradual-decrease animals. Patterning was established by the gradual-increase animals. During Phase 3 (6 days) all

groups received 1 pellet on reward trials. Although R trials speeds for all groups on all days were faster than N trial speeds, they were not significantly faster on all days.

The results indicate that frustration is not the underlying mechanism of odor production. Frustration has been shown to decrease after 240 trials. In the present study Group E continued to maintain patterning as long as 360 trials. When reward size was decreased abruptly (a condition which should result in frustration) Group E continued to respond appropriately in the run section. Thus, reward odors were present during frustrative conditions. Because Group I was trained on a 1 pellet reward schedule they should not have experienced frustration. However, they developed patterning during Phase 2. Two predictions could be made based on frustration for Group D's behavior. However, neither prediction can account for the behavior of subjects in Group D.

ODOR-MEDIATED RUNWAY PERFORMANCE

FOLLOWING EXTENDED TRAINING AND

AND GRADUAL CHANGES IN REINFORCEMENT MAGNITUDE

A Thesis

Presented to

the Division of Psychology and Special Education

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Thesis
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My parents and brother must be thanked also for their patience, encouragement, and loans. Special appreciation must be extended to them for their forgiveness of my decision to be a profession. . .

Stephen F. Davis
Approved for the Major Department

. . .loan], and their forgiveness for the times I spent running rats and attending conventions instead of going home for. . .

The one person that I would like to thank the most however, is the ever-present Dr. Stephen F. Davis. Appreciation is extended for his patience, knowledge, attitude, and enthusiasm.

Harold E. Durst
Approved for the Graduate Council

. . .for the many opportunities he has given me cannot be. . .

447389

expressed.   At this time, however, it is most   appropriate
to commend and thank him for his prompt proofreading.   The
completion of this project would not have been possible
without his invaluable assistance.

CONTENTS

LIST OF FIGURES

INTRODUCTION

Odor based responding by rats was first demonstrated by Ludvigson and Sytsma in 1967. Rats under a double-alternation schedule, receiving two reward (R) trials followed by two nonreward (N) trials, ran fast on the R trials and slow on the N trials when odor cues were maximized, but not when they were minimized. Seago, Ludvigson and Remley (1970) confirmed the "odor hypothesis" by demonstrating that anosmic rats (i.e., rats whose olfactory bulbs had been removed) could not learn to run fast on R trials and slow on N trials under a double-alternation (DA) schedule.

For over 15 years a group of researchers dealing in animal behavior has observed rats "communicating" with each other in this manner. In that animals have been known to use odors for communication, this is not surprising. For example, the case of sexual pheromones and odors for territorial marking are frequently encountered topics in the literature. However, the odors under present consideration are unusual in that they are the result of the receipt of R or N in conditions where rewards have previously been experienced. Thus, the presence and utilization of such odors has important implications for learning research in which mazes are used, as well as open-field foraging behavior, because such odors could

potentially serve as discriminative cues and influence instrumental responding.

Basically, what has been observed is appropriate responding when conditions in the runway are enclosed and not cleaned or aired out between subjects. Each subject that runs leaves an odor according to the goal conditions, i.e., R or N. These odors build up or accumulate as additional animals are tested, and act as "informants" to the subsequent rats. For instance, if we have a group of seven rats which are run in a fixed order or sequence in an enclosed runway, the last subject(s) should be able to anticipate the type of trial (R vs. N) from these odors. The extant data corroborate this prediction. Typically when rats are put under these conditions, it will take approximately seven days for them to learn to respond in a discriminative manner to R and N odors. Over the first seven days all speeds increase, then with the onset of discrimination N speeds decrease while R speeds remain fast and stable.

Collerain and Ludvigson (1972) have attempted to account for the production of N odors by linking them to frustration theory (Amsel, 1958, 1962). Frustration theory predicts that an emotional state, frustration, will be aroused when nonreward is experienced in a situation where reward has previously been given. Nonreward odors are only elicited in environments in which rewards have been received previously, thus appearing to be the result of

frustration. Several studies (Davis, Nash, Young, Weaver, Anderson, and Buchanan, 1984; Mellgren, Fouts, and Martin, 1973) have shown that nonreward odors are aversive and hence, possibly due to frustration which is generally conceptualized as an aversive motivational state (e.g., Amsel, 1958, 1962; Amsel & Roussel, 1952). In general, these studies refer to N odors as "frustrative nonreward odors" and suggest that this paradigm could be used to investigate further Amsel's frustration theory. More specifically, Collerain and Ludvigson (1972) trained naive rats to choose between two arms of a T-maze. One arm had either an R or N odor while the other had no odor. Subjects avoided the arms with N odors, thus allowing the inference that N odors are aversive. In a second experiment rats chose between an arm with no odors and an arm with odors from naive rats which had experienced nonreward conditions. Because the experimental subjects in the second experiment did not avoid the neutral placement odors (naive rats experiencing no reward), Collerain and Ludvigson (1972) argued that N odors are the result of frustration. However, the fact that frustration, as spoken of in Amsel's (1958, 1962) theory, and N odors appear to occur in the same conditions is not proof that they are interconnected.

To further emphasize the aversive qualities of N odors, Collerain (1978) and Collerain and Ludvigson (1977) demonstrated an enhancement of hurdle jumping by rats when N odors were present. Rats exposed to nonreward odors

escaped across a 1" high hurdle significantly faster than subjects exposed to neutral odors or no odors in the runway (Collerain and Ludvigson, 1977). Further, rats will escape faster as the result of nonreward odors from rats who had received as few as four previously reinforced trials (Collerain, 1978). As well, the number of trials previously reinforced affected the rate of hurdle-jump escape speeds Thus, odors from nonreward trials administered after six rewarded trials will result in faster escape speeds than odors from nonreward trials after four rewarded trials. Hence, Collerain suggested that hurdle-jump escape speeds could be used to measure levels of frustration.

In opposition to a strict frustration-theory interpretation, Davis, Whiteside, Bramlett, and Petersen (1981) found that rats did not pattern under conditions of double alternating 12 pellet large reward vs. 1 pellet small reward trials, (i.e., 12-12-1-1-12-12-1-1) when the 1 pellet reward was present as the subject entered the goalbox. Patterning appeared only when a nonreward confinement period was experienced before the presentation of the 1 pellet reward. Thus, subjects only exuded odors when they entered an empty goalbox. From this we see that N odors may not always be emitted under frustrating conditions. Davis, Burns, Howard, and Voorhees (1982) also found the confinement period to be necessary for elicitation of N odors when sucrose solutions were used as rewards.

In a somewhat different, but related view, Gonzalez,
Gleitman, and Bitterman (1962) reported that reducing
reward from 32 to 2 pellets at the rate of 2 pellets per
day eliminated the depression or negative contrast effect
that is typically seen when there is an abrupt downward
shift in reinforcement magnitude (e.g., Crespi, 1942; Davis
& North, 1967; Dilollo, 1964; Dilollo & Lumsden, 1962;
Zeaman, 1949). As the elicitation of frustration has been
employed (e.g., Davis & North, 1967) to account for the
negative contrast effect and the data reported by Gonzalez
et al. (1962) suggest that a gradual reduction in
reinforcement magnitude attenuates frustration, then we may
argue that gradually changing the magnitude of reward on
reward trials in a DA schedule of reward and nonreward
trials would not result in the elicitation of frustration
and its theoretically attendant odors. Hence, one question
of the present experiment was, "If a gradual reduction in
reward size reduces the negative contrast effect typically
seen with a downward shift in reinforcement, thus reducing
frustration, will rat subjects continue to pattern, i.e.,
run fast on R trials and slow on N trials, after a gradual
change in reward size?" This question should directly
address the relationship between frustration and N odors.

It has been shown (e.g. Amsel & Ward, 1965; Daly,
1974; Terrace, 1972) that following extended discrimination
training the aversiveness of the small or N stimulus
decreases. These findings have been taken as reflecting a

reduction in frustration due to a decrease in the generalization of the expectancy of reward from the large-reward alternative to the small-reward alternative. Hence, after sufficient training the animals no longer expect large rewards on every trial. If frustration were responsible, via the elicitation of odor cues, for the establishment of odor-based patterning, then one would expect to see some merging of R and N speeds as training progressed following the establishment of the R vs. N discrimination. We must also ask then, if a group of rats would maintain patterning on a 12-12-0-0-12-12-0-0 (DA) reward schedule over a lengthy period of time.

To answer these questions three groups were formed. Group E (extended training) was given a 12-12-0-0-12-12-0-0 R-N schedule throughout Phases 1 and 2 which consisted of over 350 trials. The purpose of this group was to see if patterning would decrease after extended training due to a decrease in the amount of "frustration" (in terms of Amsel's Frustration Theory).

To answer the question, "Will gradual changes in reward sizes, hence lowered frustration, result in decreased patterning?" two groups, D and I, were formed. Group D was trained on a 12-12-0-0-12-12-0-0 reward schedule. During Phase 2 subjects received 1 less pellet on each R trial every three days. Thus, at the beginning of Phase 2 Group D (decreasing) received 11 pellets on R trials for 3 days, then 10 pellets on R trials for 3 days, then 9 pellets on R trials for 3 days, and so on until they

received 1 pellet on R trials for the last 3 days of Phase 2. On the other hand, Group I (increasing) was trained on a 1-1-0-0-1-1-0-0 R-N schedule during Phase 1. At the beginning of Phase 2 subjects received 2 pellets on R trials for 3 days, then 3 pellets on R trials for 3 days and so on until they received a 12-12-0-0-12-12-0-0 R-N schedule for the last 3 days of Phase 2.

Phase 3 was designed to answer the following question, "Will odor-based patterning be maintained and/or developed under conditions of 1-pellet reward contrasted with non-reward?" Because of the small difference between goal conditions, maintenance of patterning in this phase would be unexpected if frustration is responsible for nonreward odors. In support, Davis, Weaver, and Janzen (1982) reported that animals failed to show odor-based double-alternation patterning when initially trained under those parameters. Phases 1 and 2 provided an ideal opportunity to test the 1-1-0-0-1-1-0-0 condition.

CHAPTER 2

METHOD

Subjects

Twenty-one, ninety-day-old, male Holtzman rats served as subjects. All animals were individually caged with water continuously available.

Apparatus

A single straight runway divided into start, run and goal sections served as the experimental apparatus. Plexiglas guillotine doors separated the startbox and goalbox from the run section. A microswitch located on the startbox door and three photoelectric beams located 30.48, 91.44, and 60.96 cm beyond the start door, respectively, selectively started and stopped three electronic digital timers to yield start, run, and goal latencies. Thus, the start measure extended from the start door to the first beam, the run measure extended from the first beam to the second beam, and the goal measure extended from the second beam to the third beam located in the goalbox. A plastic receptical recessed into the end wall of the goalbox served as the goal cup. To prevent odor dissipation the apparatus was covered by 1/4" Plexiglas lids.

Procedure

Two weeks prior to the start of experimental training all subjects were placed on a food-deprivation regimen and

maintained at 85% of their free-feeding body weight for the duration of the experiment. All animals were fed following the completion of each daily session.

A five-day pretraining phase immediately preceded the start of Phase 1. During pretraining all subjects were handled and tamed, habituated to the 45-mg Noyes pellets in the home cage, and given a 5 minute exploration in the apparatus. On the last day of pretraining the subjects were randomly distributed across three equal ($\underline{n}$=7) groups: E, I, and D. A permanent running-order number (1-7) was randomly assigned to the subjects within each group.

During all phases of the experiment, all subjects received their eight daily trials in a DA sequence. On each trial, the designated subject was removed from the home cage and placed into the startbox. Following a 3-second confinement, the start door was raised and the subject was allowed to traverse the runway. All daily trials were administered to a particular group before the other groups received their daily session. The entire apparatus was swabbed with a water-dampened sponge and allowed to air dry for 5 minutes after the completion of each trial for each group and between groups.

During Phase 1 (12 days, 96 trials) subjects in Group E and D received 12, 45-mg pellets on R trials, while subjects in Group I received 1, 45-mg pellet on R trials. Phase 2 was 33 days (264 trials) long. During this phase Group E continued to receive 12 pellets on R trials. However, the R-trial reinforcement magnitude was gradually

increased by one pellet every three days for Group I and gradually decreased by one pellet every three days for Group D. Thus, prior to Phase 3 the groups had had extended training under a variety of conditions.

During Phase 3 all procedures stayed the same, however, Groups E and I began receiving 1 pellet on reward trials, while Group D continued to receive 1 pellet on reward trials. The speed scores for the daily DA sequence were combined as follows: the first two trials were averaged to yield an R1 composite score, the next two trials were averaged to yield an N1 composite score, and so forth. Hence, the daily eight-trial sequence was reduced to four scores for each measure for each subject. A separate analysis of variance incorporating one between subjects factor, Groups (E, D, & I), and two within subjects factors, Type of Trial (R1, N1, R2, & N2) and Days/Blocks, was performed on the start, run and goal speed data, respectively, for each phase. The four composite speed scores were averaged over three-day blocks for Phase 1 and Phase 2. These three-day averages, in turn, were subjected to the analysis of variance procedure. An alpha level of .05 was used to determine significance in all cases.

Phase 1

Mean start, run, and goal speeds for Groups E, D, and for Phases 1 and 2 are shown in Figures 1 - 3, respectively. It can be seen from Figure 3 that appropriate double-alternation patterning was established

CHAPTER 3

RESULTS

The eight daily start, run, and goal latencies for each subject were reciprocated and multiplied by the appropriate metric constant to yield start, run, and goal speeds in meters per second. Prior to analysis and graphing, the speed scores for the daily DA sequence were combined as follows: the first two trials were averaged to yield an R1 composite score, the next two trials were averaged to yield an N1 composite score, and so forth. Hence, the daily eight-trial sequence was reduced to four scores for each measure for each subject. A separate analysis of variance incorporating one between subjects factor, Groups (E, D, & I), and two within subjects factors, Type of Trial (R1, N1, R2, & N2) and Days/Blocks, was performed on the start, run and goal speed data, respectively, for each phase. The four composite speed scores were averaged over three-day blocks for Phase 1 and Phase 2. These three-day averages, in turn, were subjected to the analysis of variance procedure. An alpha level of .05 was used to determine significance in all cases.

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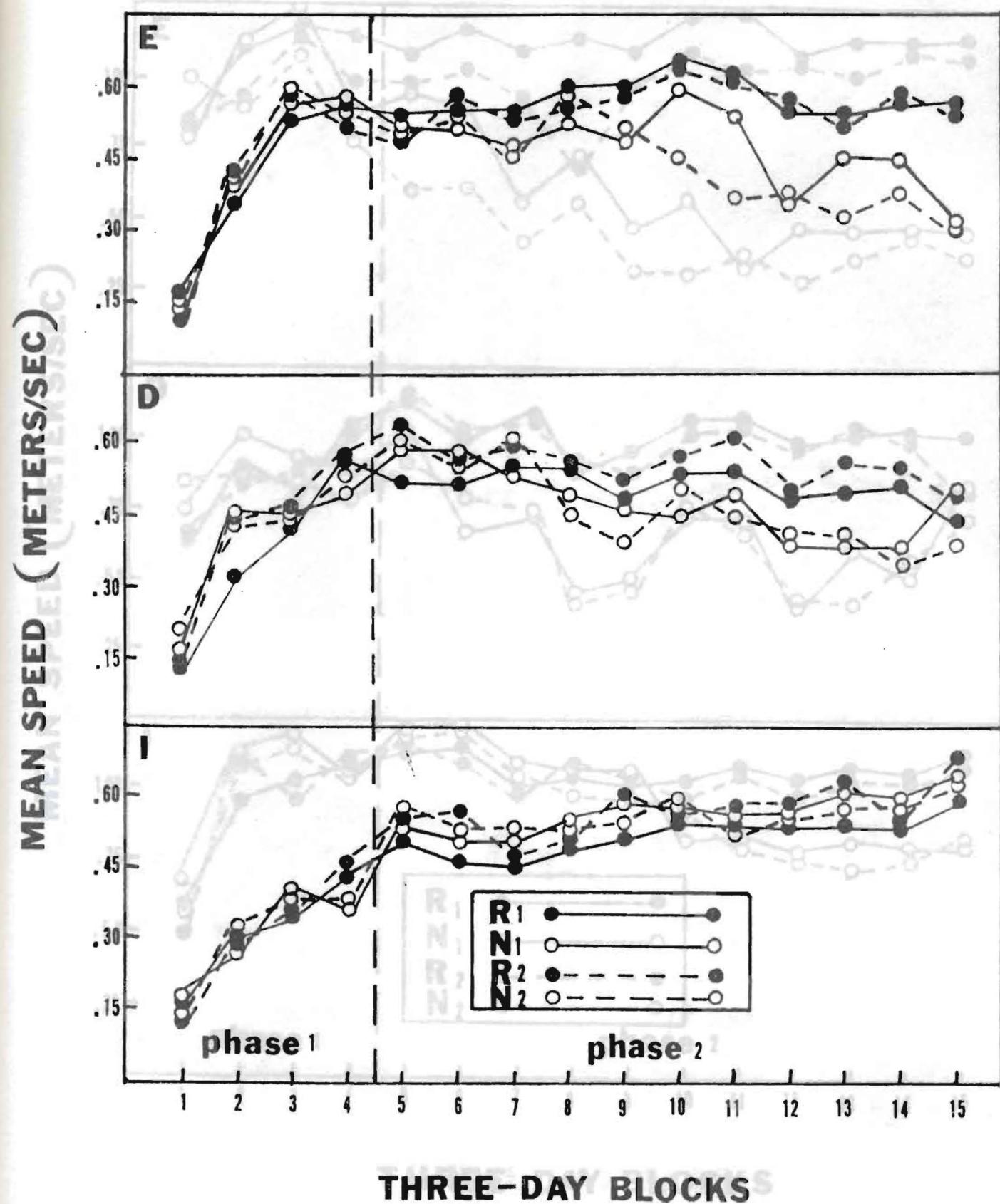
Figure 1 - Mean Start Speeds for Groups E, D, and I for blocks of three dyas during Phases 1 and 2.
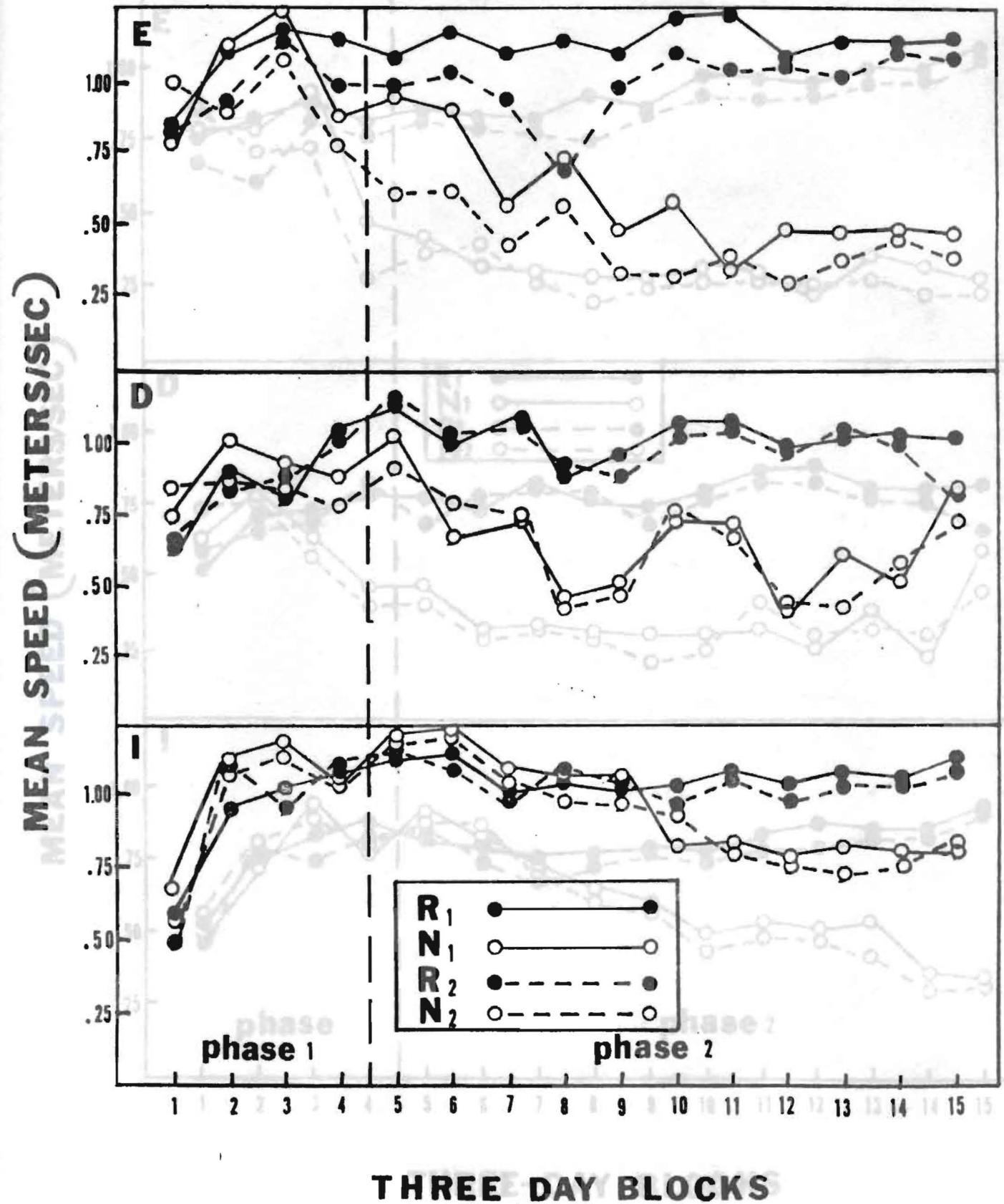
Figure 2 - Mean Run Speeds for Groups E, D, and I for blocks of three days during Phases 1 and 2.

MEAN SPEED (METERS/SEC)

E

1.00
.75
.50
.25

D

R1
N1
R2
N2

1.00
.75
.50
.25

I

1.00
.75
.50
.25

phase 1   phase 2

1   2   3   4   5   6   7   8   9   10   11   12   13   14   15
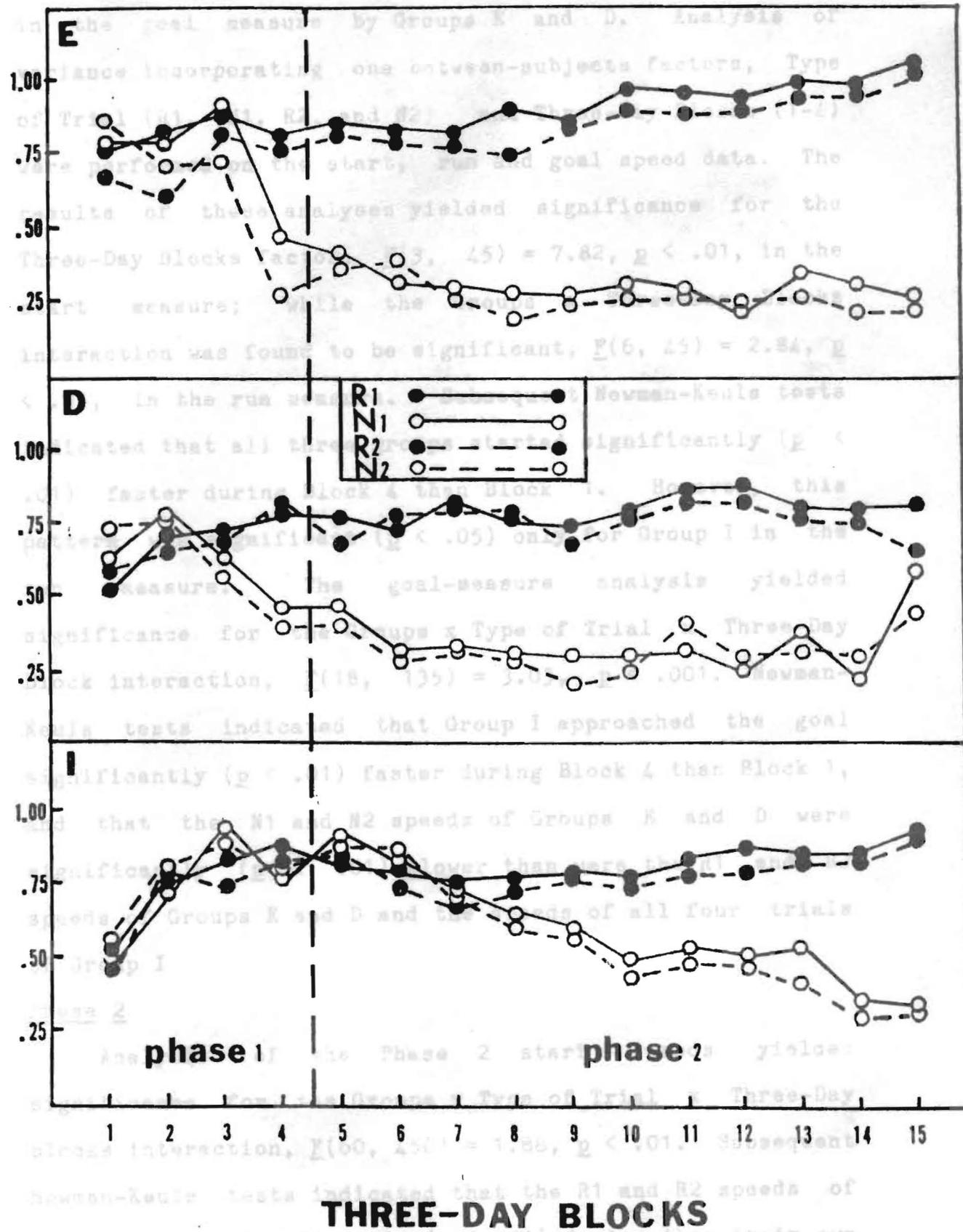
THREE-DAY BLOCKS

Figure 3 - Mean Goal Speeds for Groups E, D, and I for blocks of three days during Phases 1 and 2.

in the goal measure by Groups E and D. Analysis of variance incorporating one between-subjects factors, Type of Trial (R1, N1, R2, and N2) and Three-Day Blocks (1-4) were performed on the start, run and goal speed data. The results of these analyses yielded significance for the Three-Day Blocks factor, $F(3, 45) = 7.82$, $p < .01$, in the start measure; while the Groups x Three-Day Blocks interaction was found to be significant, $F(6, 45) = 2.84$, $p < .05$, in the run measure. Subsequent Newman-Keuls tests indicated that all three groups started significantly ($p < .01$) faster during Block 4 than Block 1. However, this pattern was significant ($p < .05$) only for Group I in the run measure. The goal-measure analysis yielded significance for the Groups x Type of Trial x Three-Day Block interaction, $F(18, 135) = 3.03$, $p < .001$. Newman-Keuls tests indicated that Group I approached the goal significantly ($p < .01$) faster during Block 4 than Block 1, and that the N1 and N2 speeds of Groups E and D were significantly ($p < .01$) slower than were the R1 and R2 speeds of Groups E and D and the speeds of all four trials of Group I.

Phase 2

Analysis of the Phase 2 start speeds yielded significance for the Groups x Type of Trial x Three-Day Blocks interaction, $F(60, 450) = 1.88$, $p < .01$. Subsequent Newman-Keuls tests indicated that the R1 and R2 speeds of Groups E were significantly ($p < .01$) faster than their own N2 speeds during Blocks 10-15 and their own N1 speeds

during Blocks 12 and 15. These results corroborate the graphical impression (see, Figure 1) that some degree of significant DA patterning had been established during the later stages of training in the start measure by Group E.

Run-speed analysis also yielded significance for the Groups x Type of Trial x Three-Day Blocks interaction, $F(60, 450) = 2.97$, $p < .001$. Supportive of the graphical impression (see, Figure 2) that all three groups developed significant run-measure patterning, subsequent Newman-Keuls tests yielded the following significant results. Both R speeds were significantly ($p < .01$) faster than both N speeds as follows: Group E during Blocks 7, 9-15; Group D during Blocks 6-14; Group I during Blocks 11-15. Further, it was found that the R1, R2, and N1 speeds of Group E were significantly ($p < .01$) faster than their N2 speeds during Blocks 5-6, and that the R2 speeds of this group were significantly ($p < .01$) faster than their R1, N1, and N2 speeds during Block 8.

Significant Type of Trial, $F(3, 45) = 7.36$, $p < .001$, and Groups x Type of Trial x Three-Day Blocks interaction, $F(60, 450) = 1.57$, $p < .025$, effects were shown by the goal-measure analysis. Newman-Keuls tests indicated that both R speeds were significantly faster than both N speeds as follows: Group E during Blocks 5-15; Group D during Blocks 5-14; Group I during 9-15. All differences were reliable at the .01 level except Block 5 for Group D, and Block 9 for Group I which were reliable at the .05 level.

Certainly these statistical results mirror the presence of strong DA patterning shown in Figure 3.

Phase 3

Analysis of Phase 3 start speeds yielded significance for the Groups x Type of Trial x Days interaction, $\underline{F}(30, 225) = 2$, $\underline{p}<.05$. Subsequent Newman-Keuls tests yielded failure of patterning by all three groups. (See Figure 4 on the following page.) It should be noted, however, that despite a lack of significance both R trial speeds were faster than both N trial speeds for on all six days for Group E.

Run speed analysis yielded significance for the Type of Trial x Days interaction, $\underline{F}(15, 225) = 2.179$, $\underline{p} < .05$. Subsequent Newman-Keuls tests yielded the following results. Both R speeds were significantly ($\underline{p}<.05$) faster than both N speeds on Days 1-6 for Group E and Day 1 for Group D. Further, it was found that R1 speeds were significantly ($\underline{p}<.05$) faster than N1 and N2 speeds on Day 3 for Group D, and on Days 2, 3, 4, and 5 for Group I, and R1, R2, and N2 speeds were significantly ($\underline{p}<.05$) faster than N1 speeds on Day 1 for Group I.

Goal speeds analysis yielded a significant Groups x Type of Trial x Days interaction, $\underline{F}(30, 225) = 2.24$, $\underline{p} < .001$. Subsequent Newman-Keuls tests yielded significantly ($p<.05$) faster R1 and R2 scores for Days 1, 3, and 4 for Group D, and Day 4 for Group E. Also, it was shown that R1, R2 and N1 scores were significantly ($\underline{p}<.05$) faster for Group D on Day 2, and for Group I on Day 5. Further, R1
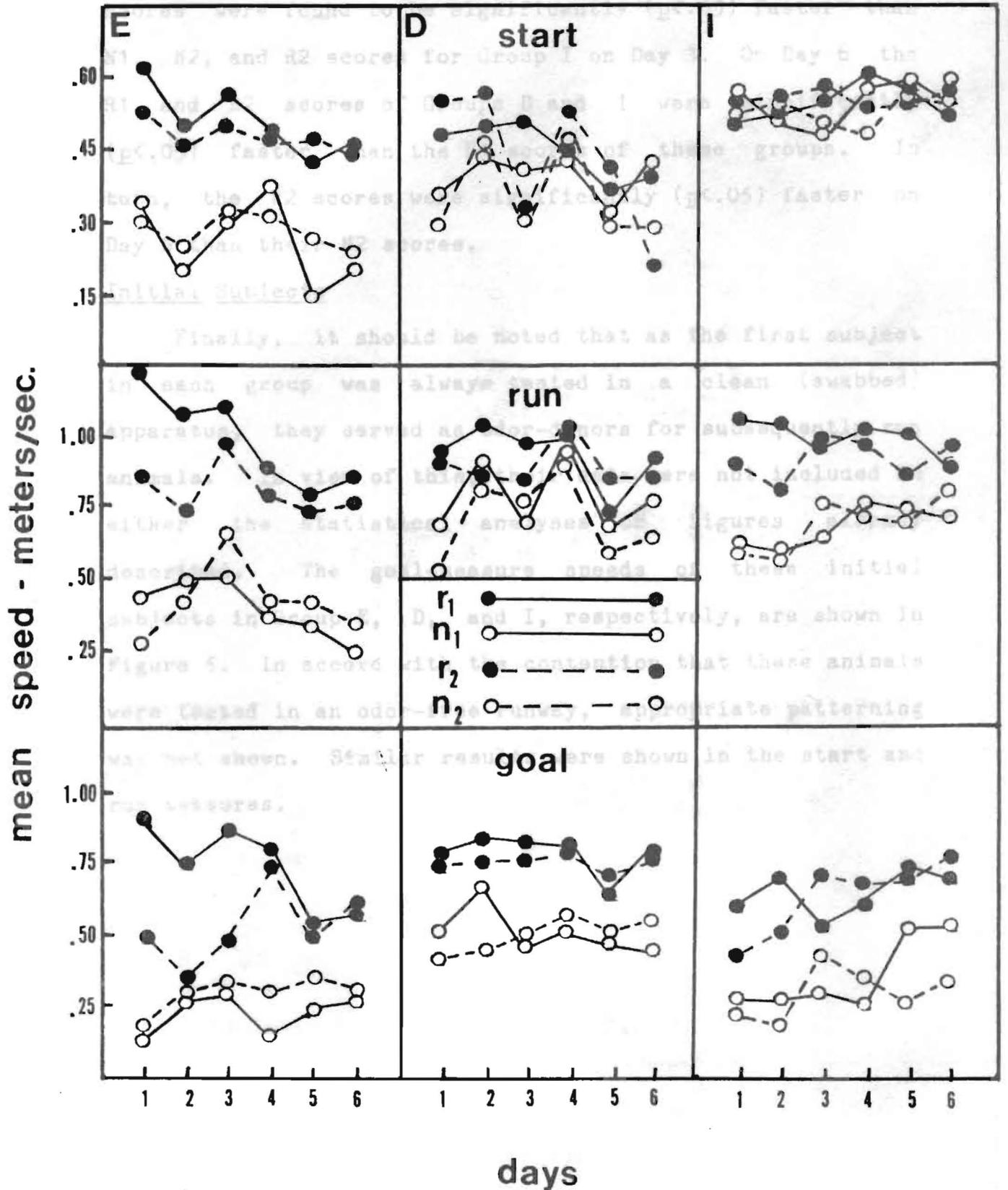
Figure 4 – Mean Start, Run and Goal Speeds for Groups E, D, and I for each day of Phase 3.

scores were found to be significantly ($p<.05$) faster than N1, N2, and R2 scores for Group I on Day 3. On Day 6 the R1 and R2 scores of Groups D and I were significantly ($p<.05$) faster than the N1 scores of these groups. In turn, the R2 scores were significantly ($p<.05$) faster on Day 6 than their N2 scores.

Initial Subjects

Finally, it should be noted that as the first subject in each group was always tested in a clean (swabbed) apparatus, they served as odor-donors for subsequently run animals. In view of this, their data were not included in either the statistical analyses or figures already described. The goal-measure speeds of these initial subjects in Group E, D, and I, respectively, are shown in Figure 5. In accord with the contention that these animals were tested in an odor-free runway, appropriate patterning was not shown. Similar results were shown in the start and run measures.

THREE-DAY BLOCKS

Figure 5 - Mean Goal Speeds of the Initial Subjects in Groups E, D, and I for blocks of three days during Phases 1 and 2.

DISCUSSION

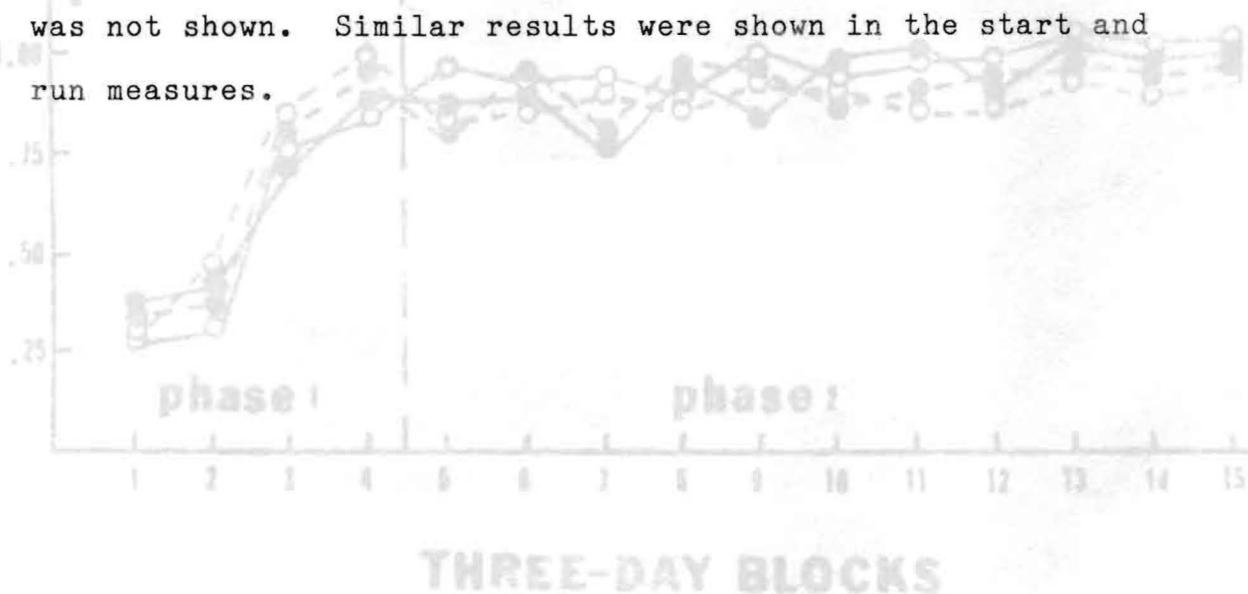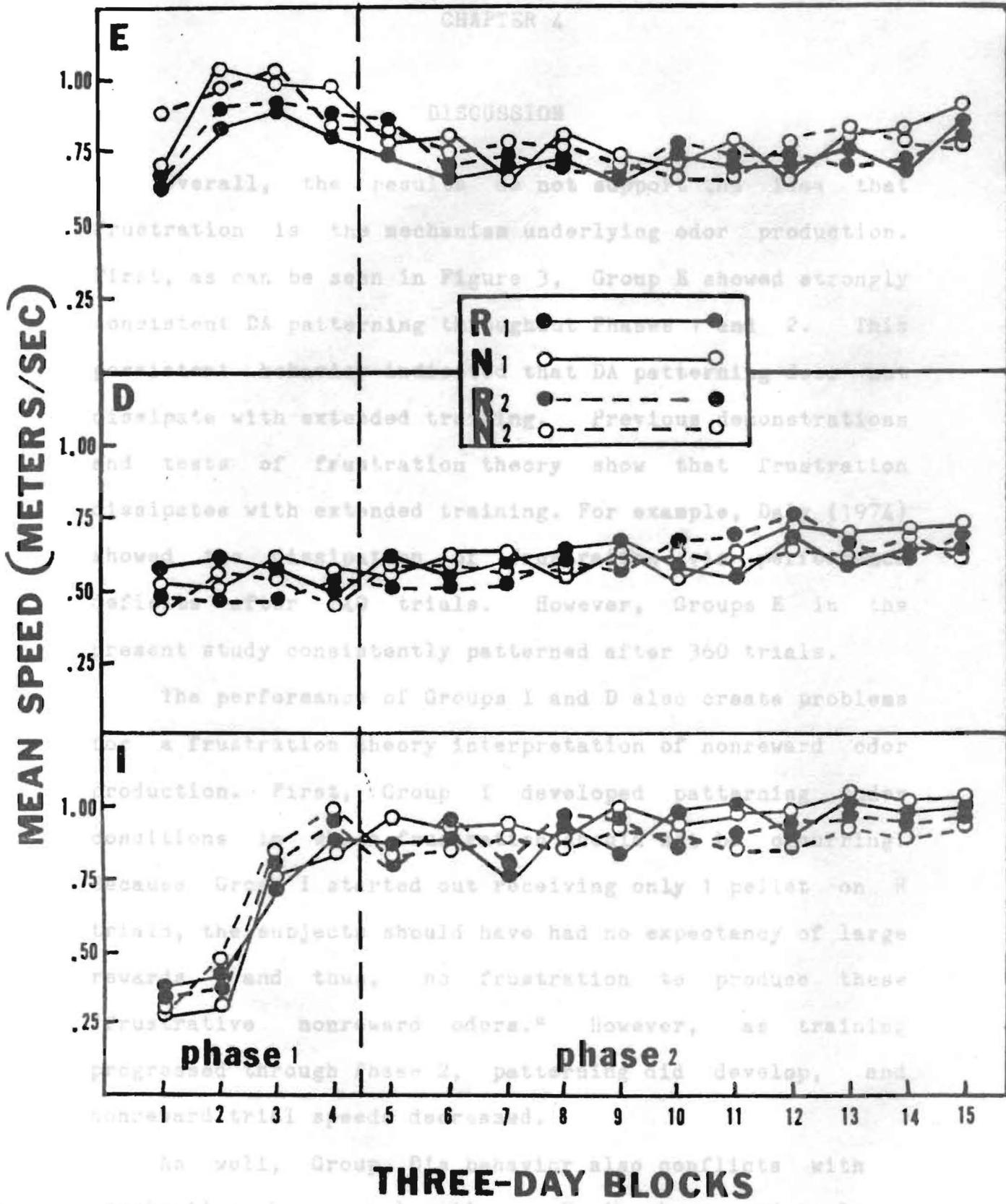Overall, the results do not support the idea that frustration is the mechanism underlying odor production. First, as can be seen in Figure 3, Group E showed strongly consistent DA patterning throughout Phases 1 and 2. This persistent behavior indicated that DA patterning does not dissipate with extended training. Previous demonstrations and tests of frustration theory show that frustration dissipates with extended training. For example, Daly (1974) showed the dissipation of frustration via performance deficits after 240 trials. However, Groups E in the present study consistently patterned after 360 trials.

The performance of Groups I and D also create problems for a frustration theory interpretation of nonreward odor production. First, Group I developed patterning under conditions in which frustration should not be occurring. Because Group I started out receiving only 1 pellet on R trials, the subjects should have had no expectancy of large rewards, and thus, no frustration to produce these "frustrative nonreward odors." However, as training progressed through Phase 2, patterning did develop, and nonreward trial speeds decreased.

As well, Group D's behavior also conflicts with a frustration theory explanation. Having been used to large reward from the beginning, one would expect Group D to

increase frustration on R trials as reward size decreased. However, despite a reduction in reward size we continue to see fast running speeds on R trials in the goal section. Only on the last day of Phase 2 did patterning dissipate in the goal measure. On the last day, frustration should have occurred on all trials as the result of the small reward (1 pellet). Hence, we would expect reward trial speeds to decrease and the nonreward trial speeds to remain consistent with past speeds. However, on the last day R trial speeds for Group D did not differ significantly from previous days (see Figure 3).

Another prediction is possible for Group D's behavior. From this standpoint we would predict a decrease in frustration because of the progressive, but not abrupt, decreasing differences in the magnitude of reward throughout Phase 2. Because of the continual decrease in the contrast between reward and nonreward, we would expect a decrease in frustration and thus, a gradual convergence of R and N speeds. However, we see a convergence only on the last day of Phase 2 for this Group.

In Phase 3 Group E displayed stronger patterning in the start, run and goal measures than the other two groups. Group E ran faster on R than on N trials on all six days in the start and run section. However, only in the run section of the runway were the R trial speeds significantly faster. Goal speeds for R and N trials were not significantly different on all six days. It could be that these subjects were experienceing frustration in the goal section due to

the downward shift in reinforcement magnitude. Slowing goal speeds would then be the result of competing goal responses. Subjects may have been avoiding frustration in the goal section while still continuing to approach the goal section because of the presence of reward odors. This suggests that frustration may act independently of odors.

It could be argued that frustration was not occurring in Phase 2 for Group D because of the gradual (versus abrupt) shift in reinforcement magnitude. Thus, it is interesting to look at how the subjects in Group E responded when they received an abrupt shift from 12 pellets on reward trials (received during Phases 1 and 2) to 1 pellet on reward trials (first day of Phase 3). Because of this abrupt change in reinforcement magnitude, one would expect R trial speeds to decrease as a result of frustration, and converge with N trial speeds. Although there is a tendency for R2 trial speeds to decrease in the goal section, R1 speeds were consistent with the goal speeds seen in Phase 2. As well, there was a significant difference between both R trial speeds and N trial speeds. Further, the significant patterning that occurred in the run section on the first day of Phase 2 refutes frustration as the mechanism of odor production.

Although R trial speeds do not drastically decrease on the first day of Phase 3, R1 and R2 speeds show a marked decrease on the last 2 days of Phase 3. It should be re-emphasized that if frustration were playing a role one

would expect the decrease to appear at the height of frustration, at the beginning of Phase 3 when no large reward trials have been encountered. Frustration should then decrease across these "extinction" trials. As the expectation of large rewards fades, R trial speeds (or all speeds) should increase.

One would think that reward and nonreward odors have some adaptive value, as do most other behaviors in an organism's repetoire. Thus, looking at theories of odor production in this light may be useful. There is some evidence that odor production does occur in the natural environment. Davis, Gustavson, Zirnstein and Anderson (1984) have reported that wood rats (<u>Neotoma floridana osagensis</u>) do produce odors of reward and nonreward in the runway. Hence, it is possible that these odors are used while rats forage. If this were true one should look at odor production in terms of what would be most adaptive.

Many researchers have recently become concerned with the concept of optimal foraging (Mellgren, 1982; Mellgren, Misasi, & Brown, 1984; Baum, 1983). Optimal foraging theory is based on the idea that animals maximize energy gain during foraging. Thus, rats weigh the costs and benefits of staying at a patch or moving to another patch. Variables that may be taken into consideration, via unknown proximate mechanisms, include patch density, travel time, energy spent searching in a patch, and probability of being captured by a predator. Hence odor production may serve as one of the proximate mechanisms for optimal foraging.

Assume if you will, that a rat has encountered an empty patch, which previously had food. The rat may leave a signal that food is no longer present. After many visits to the now empty patch, expectations of food will be replaced with expectations of no food. However, it would be more adaptive to continue to leaving signals even after expectations of food no longer occur.

Because rats have been observed sampling patches that previously have had little food (Mellgren, Misasi, & Brown, 1984), nonreward odors may serve to signal how much time should be spent sampling one of these patches, or possibly whether or not to sample a patch at all. The aversive quality of nonreward odors would appear to be very useful if this were so. Because of these possibilities, and to further understand the production of odors, future studies of odor production should be incorporated within the study of foraging behavior.

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27

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