

**RUNWAY PERFORMANCE OF NORMAL, SHAM,
AND ANDROMEDIC RATS AS A FUNCTION OF
MAGNITUDE OF REWARD AND MAGNITUDE
SHIFT**



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RUNWAY PERFORMANCE OF NORMAL, SHAM, AND ANOSMIC RATS
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AND MAGNITUDE SHIFT

An Abstract
Presented to
the Graduate Council of
Austin Peay State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Arts
in Psychology

by
Wyatt Eugene Harper III
August 1974

ABSTRACT

A two-phase experiment was designed to yield information concerning the effects of reward magnitude and magnitude shifts on the runway performance of normal, sham-operated, and anosmic rat subjects. During the first phase three squads of normal, sham, and anosmic rats were further divided into three equal subgroups which received single pellet large, multiple-pellet large, and small reward respectively for 51 trials. A second phase (30 trials) during which all subjects received small reward immediately followed Phase I.

Analysis of variance was performed on the speed data to determine significant results. Reward magnitude effects were shown only by the normal and sham subjects during Phase I. These effects persisted throughout the entire 51-trial phase. Normal and sham subjects shifted from large to small reward during Phase II exhibited significant depression effects (i.e., their performance fell below that of appropriate small reward control groups). Although magnitude effects did not develop during Phase I in the case of anosmic subjects, primarily due to the fact that the receipt of large reward, especially single-pellet-large reward, appeared to be an aversive event for the anosmic subjects. However, the shift from multiple-pellet large and single-pellet large reward conditions to small reward resulted in performance decrements in all three measures for the anosmic subjects, thus

indicating that the shift from large to small reward appeared to be even more aversive than the receipt of large reward. Large fluctuations in performance appeared in the goal measure for both normal and sham small-reward subjects during Phase II while anosmic small reward performance remained stable during this phase. These fluctuations are tentatively attributed to the presence of frustrating odor cues which may have also heightened the "depression effects" displayed by the normal and sham subjects shifted from large to small reward during Phase II.

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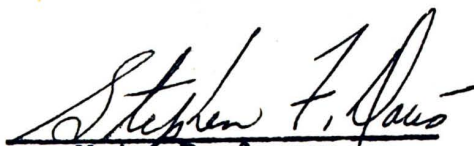
A Thesis
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August 1974

To the Graduate Council:

I am submitting herewith a Thesis written by Wyatt Eugene Harper III entitled "Runway Performance of Normal, Sham, and Anosmic Rats as a Function of Magnitude of Reward and Magnitude Shift." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Psychology.

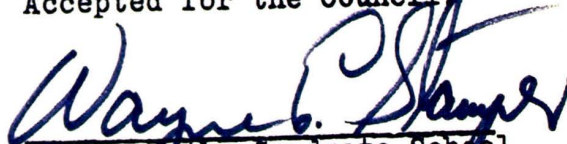

Major Professor

We have read this thesis and recommend its acceptance:


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ACKNOWLEDGEMENTS

The author wishes to express sincere appreciation to Dr. Stephen F. Davis, Assistant Professor of Psychology, Austin Peay State University, who suggested the problem. With untiring patience he aided and counseled the author during the course of the study.

Appreciation is also extended to Dr. John D. Seago, Assistant Professor of Psychology, Concord College, Athens, West Virginia, for his aid in performing the surgery necessary to the study.

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CHAPTER I

INTRODUCTION

Much literature in the area of animal learning has been concerned with the problem of the effect of reinforcement magnitude. The assumption generated by this research (e.g., Hull, 1943; Spence, 1956; and Capaldi, 1967) has been that there is a positive relationship between reinforcer magnitude and performance (i.e., the larger the reward magnitude, the better the performance or faster the acquisition of an instrumental response).

Crespi (1942), presented the results of three experiments in which positive relationships between reinforcer magnitude and running speed in a straight runway were found. Runway training was given to various groups of rats, with the number of incentive units given as reward varied in logarithmic steps. Asymptotic running speeds were an approximate logarithmic function of the number of incentive units. However, it should be noted that the number of training trials utilized by Crespi (1942) was small, never exceeding 25. Zeaman (1949) reported corroborative evidence. The weight of single-incentive units was varied and the positive relationship obtained, but it is again worthy of note that less than 20 acquisition trials were used in the study. In addition, studies reported by Reynolds and Pavlik (1960) and Pavlik and Reynolds (1963) also using

the straight-runway apparatus and rat subjects yielded similar findings. These studies employed 72 and 80 acquisition trials respectively. Other supportive runway studies (e.g., Armus, 1959; D'Amato, 1955; Grindley, 1929; Lawrence and Miller, 1947; Metzger, Cotton, and Lewis, 1957) could be mentioned.

Conversely, McCain and his collaborators (1969, 1970, 1971) have seriously challenged the effectiveness of reward magnitude. The data reported by McCain have consistently indicated the presence of a performance difference due to reward magnitude early in training, however the difference dissipated. As training progressed virtually no differences were shown between large and small reward subjects after approximately 50 trials. Additional support for McCain's (1969, 1970, 1971) position against the effectiveness of reward magnitude has been reported by Black (1969). The studies reviewed and reported by Black (1969) supported the position that reward magnitude was initially effective, but that this effectiveness diminished with training. Black (1969) also indicated that under some conditions small reward may eventuate in faster speeds than large reward.

Using a spaced-trials procedure (one trial per day) to avoid problems of satiation (a criticism of the McCain data) and single vs. multiple-pellet, small and large rewards, Campbell, Batsche and Batsche (1972) have also reported initial superiority for large reward subjects.

This study incorporated four groups of rat subjects. One group designated small-single (S-1) received one 97 mg. Noyes pellet in the goal box. The groups designated small-multiple received two 45 mg. Noyes pellets in the goal box. The large-reward groups received either one 1 mg. Noyes pellet or twenty-two 45 mg. Noyes pellets. They also reported that this superiority dissipated after approximately 60 trials.

On the other hand, several recent studies have been supportive of the traditional assumption of the effectiveness of reward magnitude. For example, Wike and Chen (1970) reported that subjects receiving large reward (11 pellets) showed faster starting and running speeds than did two groups, one a drive-satiation control of small reward (1 pellet) subjects. These differences appeared early in training and persisted throughout the course of the experiment (84 trials). To account for the discrepancy between their data and that reported by McCain (1969, 1970, 1971), Wike and Chen (1970) suggested that the differences may have been due to the use of multiple-pellet large reward in their experiment and single-pellet large reward in the studies reported by McCain. However, a report by Daly (1972) has questioned the generality of this interpretation. Daly (1972) reported finding reward magnitude effects in two separate experiments each using 60 acquisition trials, and single-pellet large, multiple small pellet, and single small pellet groups.

Three groups of rats were given either one 500 mg. pellet, twenty-five 20 mg. pellets or one 20 mg. pellet. The multiple small pellet group ran faster than the single large pellet reward group and at asymptote they ran faster than the single small reward group. Finally, a recent study by Marrero, Davis and Seago (1973) utilizing single-pellet large vs. single-pellet small reward magnitudes has indicated that magnitude effects developed, and persisted throughout the course of 50 acquisition trials, in start, run, and goal measures.

In an attempt to determine the effects of surgical anosmia on runway behavior, the Marrero, Davis and Seago (1973) study also employed two groups, (large and small reward), of anosmic subjects, although rats rendered surgically anosmic have been the focus of a number of recent studies, the behavioral effects of anosmia still remain unclear and somewhat elusive. For example, the Marrero, Davis and Seago (1973) study indicated that the performance of the large-reward anosmic subjects was somewhat inferior (significantly so in the start measure) to that of the small-reward anosmic subjects. Conversely, Seago, Ludvigson and Remley (1970) reported that anosmic rats trained under a double-alternation pattern of reward-nonreward ran faster than did normal rats, particularly in the goal section of the apparatus. In addition these investigators reported that several of the anosmic subjects were quite vicious.

Other investigations have pointed to the apparent inferiority of anosmic rats in various tasks. Early studies (Lindley, 1930; Honzik, 1936) investigating complex maze learning ability of anosmic and normal rats indicated that anosmic subjects made consistently more errors than did normal subjects. More recently, Phillips (1969) found that a group of anosmic rats failed to display learning set formation in a visual discrimination problem. Sieck (1970) reported difficulty in handling anosmic rats and his data reflected better performance of anosmics in an active avoidance task but decreased learning ability in a passive avoidance task. He speculated that the olfactory system was important in maintaining a balance between activating and directing mechanisms in the rat brain. Marks, Remley, Seago and Hastings (1970) have reported somewhat different results. They reported that in both active and avoidance tasks control rats were superior to anosmics, while in an operant task anosmics maintained a higher rate of bar pressing than did controls.

The above mentioned studies suggest that ablation of the rat's olfactory lobes influences behavior in subtle and varied ways. A full delineation of the behavioral effects of anosmia, especially as they pertain to runway behavior has recently become increasingly important. Ludvigson and Sytsma (1967) published a study which indicated that rats were capable of learning a double-

alternation schedule of reward-nonreward under odor-maximizing conditions but unable to do so under odor-minimizing conditions. Previous data had indicated that the rat could not learn this pattern. Odor cues have since been implicated as possible determining factors in other animal learning situations (e.g., disruption of extinction performance, Wasserman and Jensen, 1969; and latent extinction, Pratt and Ludvigson, 1970). Consequently, numerous methods have been employed to control subject-generated olfactory cues. The control procedures have included: swabbing the apparatus with water or a disinfectant solution (Davis and Ludvigson, 1969); spraying the apparatus with an aerosol deodorant (Davis and Ludvigson, 1969); utilizing removable paper floors (Means, Hardy, Gabriel and Uphold, 1971); and exhausting the runway air (Phillips and Bloom, 1971). The most effective odor control procedure would appear to be the utilization of anosmic subjects. However, before the unconditional use of anosmic subjects is effected a more thorough understanding of the effects of anosmia on runway behavior is needed.

The present experiment was designed to yield additional information on the effects of reward magnitude and reduction of reward magnitude on the runway performance of normal, sham-operated, and surgically anosmic subjects.

Dating from the research of Crespi (1942) it has been consistently demonstrated (Zeaman, 1949; Ehrenfreund and

Badia, 1962; DiLollo and Lumsden, 1962; DiLollo, 1964) that an abrupt shift from large to small reward has produced a performance decrement on the part of shifted subjects. Quite often the performance of the shifted subjects has fallen significantly below that of a small reward control group (i.e., a "depression effect"). Odor cues have been implicated by Davis and Ludvigson (1969) as possibly contributing to the magnitude of the depression effect. The present study with its inclusion of anosmic subjects and an incentive reduction phase would appear to offer an excellent opportunity to assess the influence of olfactory cues on the depression effect.

During the first phase of the experiment, a factorial design employing three levels of reward magnitude (small, single-pellet large, and multiple pellet large) and three olfactory states (normal, sham operated, and surgically anosmic) was used. During the second phase of the study all subjects received additional trials with the small reward magnitude. This phase was an incentive reduction phase for the subjects initially trained on single-pellet large and multiple pellet large reward.

CHAPTER II

METHOD

Subjects

Eighty-one male albino rats purchased from the Sprague-Dawley Co., Madison, Wisconsin, were used as subjects. Twenty-seven of the subjects were rendered surgically anosmic in the following manner. First, the subjects were anesthetized with sodium pentobarbital. Then, utilizing a stereotaxic instrument, trephine openings were placed on each side of the sagittal suture above the olfactory bulb. The olfactory bulbs and connecting tracts were removed from each subject with an aspirator. Twenty-seven additional animals, (sham-operated subjects), received identical surgical treatment with the exception that their olfactory bulbs and tracts were not removed. A third set of 27 animals (normal subjects) were not subjected to surgical procedures. All subjects were approximately 120 days old at the beginning of the experiment. The subjects were housed in individual cages with water always available. Two weeks preceding the experiment the subjects were placed on food deprivation and maintained at 85 per cent ad lib body weight during the experiment. All subjects were fed at the completion of each day's session.

Apparatus

The apparatus consisted of a single straight, 11.43 cm. wide, 12.70 cm. high, runway made from 12.7 mm. thick pine lumber. The runway was divided into a 38.10 cm. gray start box, a 91.44 cm. black run section, and a 30.48 cm. black goal box. The start and goal boxes were separated from the run section by guillotine doors. Raising the start door activated a Standard Electric Timer (start time). Passing through a photoelectric beam located 15.24 cm. beyond the start door stopped the first timer and activated a second timer (run time). Breaking a second beam, located 76.20 cm. beyond the first beam, stopped the second timer and started the third timer (goal time). Breaking a third beam, located 5.08 cm. in front of the goal cup, stopped the third timer. The plastic goal cup, recessed into the back wall of the goal box, was 4 cm. high, 4 cm. wide, and 3.40 cm. deep. Hardware-cloth tops covered by a thin sheet of transparent plastic covered the entire apparatus.

Procedure

The normal, sham, and anosmic squads were randomly divided into three equal subgroups: 11L (multiple pellet large reward), 1L (single pellet large reward), and S (small reward). At the inception of deprivation all subjects received 5 days of pretraining prior to the beginning of the first phase of the experiment. During this period all subjects were handled and tamed (Days 1-2); allowed to

individually explore the runway (Days 3-5); and pellet habituated in the home cage (Days 1-5). A 51-trial-acquisition phase (Phase I) followed the pretraining period. During this phase Group 11L received 11, 45 mg. Noyes pellets per trial, while Group 1L received one 500 mg. Noyes pellet, and Group S received one 45 mg. Noyes pellet per trial. Phase II (30 trials) immediately followed Phase I. During this phase all subjects received one 45 mg. Noyes pellet per trial. This phase constituted an incentive reduction phase for Groups 1L and 11L. The experimental design is presented in Table 1.

Trials were administered at the rate of 3 per day during the experiment with the sham, normal and anosmic subjects being run as three separate squads. Both the order for running squads and the order for running subjects within a squad were randomized daily. All members of a squad received their 3 daily trials before the next squad was run. The intertrial interval was approximately 10 minutes during both phases of the experiment.

Following the general testing procedure, each of the 54 anosmic and sham subjects was sacrificed using an overdose of sodium pentobarbital; the animals were then perfused with normal saline and a 10 per cent neutral buffered Formalin solution. The entire brain was then removed and stored in the Formalin solution. Visual inspection of the brains revealed that the olfactory bulbs and tract had been successfully removed from all of the anosmic animals.

CHAPTER III

RESULTS

Analysis of variance was performed on the speed data from the last 5 days of Phase I since this appeared to be the point in training at which reward magnitude effects had developed most strongly. Speeds during Phase I and II for the various reward conditions within the normal, sham, and anosmic squads are presented in Figures 1-9. An alpha level of .05 was used in all tests of significance. For purposes of clarity and brevity specific F values and probability statements have been omitted from the body of the text. F values and probability statements may be found in Table 2 through 7.

The results of the Phase I analysis indicated that the reward magnitude factor was significant in the start and goal measures. Newman-Keuls procedure was used to further investigate these significant effects. In the start measure Group 11L did not differ significantly from Group 1L, however, both groups started faster than Group S ($p < .05$). In the goal measure it was found that Group 11L was approaching the goal faster than Group 1L. Both of these groups were approaching the goal faster than Group S.

The Reward Magnitude by Olfactory State interaction was significant in the start and run measures. It is noteworthy that this interaction approached significance

in the goal measure also. Simple main effects analyses were employed to further investigate these significant interactions. Both start and run measures yielded significant reward magnitude differences in the normal, sham and anosmic squads. Newman-Keuls tests were again used to further investigate these significant differences. For the normal and sham squads the results were identical in the start and run sections. Group 1L ran faster than Group 11L ($p < .01$) which ran faster than Group S ($p < .01$). In the anosmic squad, however, the start measure performance of Group 11L surpassed both Groups 1L and S ($p < .01$) which did not differ significantly. In the run measure Group 11L ran faster than Group S, ($p < .01$), and Group S ran faster than Group 1L ($p < .01$).

It is evident from the results of Phase II (see Figures 1-9) that the shift from large to small reward had pronounced behavioral effects in all three measures. Analysis of variance performed on the Phase II data yielded the following results. The Trials factor, Incentive Reduction by Trials interaction, Olfactory State by Trials interaction, and Olfactory State by Incentive Reduction by Trials interaction were significant for the start measure. Further inspection of the Incentive Reduction by Trials interaction via simple main effects analyses and Newman-Keuls tests statistically supported the graphical impressions that during the early portions of Phase II the subjects shifted

from 11L and 1L to small reward were both starting significantly ($p < .01$) faster than the small reward control (Group S) subjects. As Phase II progressed this superiority decreased and reversed such that no significant differences existed by Day 5. However by the end of the Phase the Group S subjects were starting significantly ($p < .01$) faster than the subjects that had experienced incentive reduction. Sham, normal, and anosmic subjects did not differ initially in starting speeds, however, as Phase II progressed the performance of both sham and normal subjects fell significantly below that of the anosmic subjects.

The results of the Phase II run and goal speed analyses were similar. Incentive Reduction, Olfactory State, Trials, Incentive Reduction by Trials interaction, Olfactory State by Trials interaction and the Incentive Reduction by Olfactory State by Trials interaction were significant. The subsequently performed Newman-Keuls tests indicated that:

(1) the small reward (Group S) subjects were running and approaching the goal significantly faster ($p < .01$) than the subjects (Groups 11L and 1L) that had experienced incentive reduction, and (2) the anosmic subjects were running and approaching the goal significantly faster ($p < .01$) than the normal and sham subjects. Further investigation of the significant Incentive Reduction by Olfactory State by Trials interactions upheld the graphical impressions that significant differences between the 11L, 1L, and S subjects within the

three olfactory states were often influenced by large variations in the performance of Group S within both the sham and normal squads.

CHAPTER IV

DISCUSSION

The data of the present study yielded several findings which merit consideration. First, in the case of normal and sham subjects the traditional assumption concerning the effectiveness of reward magnitude was supported in that the performance of both the 11L and 1L subjects in these squads was superior to that of the respective small reward (Group S) subjects during Phase I. These results, especially those of the goal measure, are consistent with Daly (1972) who reported superior performance for single-pellet and multiple-pellet large reward subjects relative to a small reward control group, and further, that the subjects receiving the multiple pellet large reward approached the goal significantly faster than the subjects receiving the single-large pellet reward. Although, consistent with respect to showing magnitude effects in the start and run measures, the present study and that of Daly (1972) differ in another way. The present study, unlike that of Daly (1972), indicated that normal and sham subjects receiving the one large pellet reward (1L subjects) were starting and running faster than those subjects receiving multiple-pellet reward (i.e., 11L subjects). This discrepancy may be due to differences between the multiple-pellet rewards used in the two studies. In Daly's (1972) study multiple-pellet large reward subjects

received 25, 20 mg. pellets, whereas the multiple-pellet subjects in the present study received 11, 45 mg. pellets.

Obviously, the Phase I data for the normal and sham subjects in the present study are inconsistent with the data reported by McCain and his collaborators (1969, 1970, 1971). In the present study, as noted above, magnitude effects developed and persisted throughout the course of the 51-trial acquisition phase. Of course these magnitude effects were obtained with reciprocated latencies (i.e., a speed measure) being used as the dependent variable. It is interesting to note, however, that identical conclusions were reached when the data of the present study were reanalyzed using median latency, the measure consistently reported by McCain, as the dependent variable.

On the other hand, the Phase I performance of the anosmic subjects presents a different picture. During this Phase the performance of the 11L and S anosmic subjects was very similar and superior (significantly so in the run measure) to that of the 1L anosmic subjects. This finding corroborates the data reported by Marrero, Davis, and Seago (1973). These investigators reported that the performance of anosmic subjects receiving a single-pellet large (1, 300 mg.) reward was depressed below that of small (1, 45 mg.) reward anosmic subjects. Taken together, the results of the Marrero, Davis, and Seago (1973) study and those of the present study would indicate that the receipt of a single-

pellet large reward is an aversive event to the anosmic subject.

Turning to the Phase II data it is clear that depression effects were shown by the normal and sham 11L and 1L subjects shifted to small reward. That is, the performance of these subjects which was superior to that of the small reward control subjects during Phase I, fell significantly below that of the respective small reward subjects when their reward was reduced (i.e., Phase II). However, the performance of the 11L and 1L anosmic subjects was not superior, as noted above, to that of the small reward anosmic subjects during Phase I, thus depression effects, in the strict sense of the term, did not develop during Phase II. However, the shift from multiple-pellet large and single-pellet large reward conditions of Phase I to small reward during Phase II did result in performance decrements in all three measures for the shifted anosmic subjects. This finding viewed in conjunction with the Phase I data suggests that although the receipt of a single-pellet large reward may be a somewhat aversive condition for anosmic subjects, a shift from large to small reward is even more aversive.

The present study also helps to elucidate the role of olfactory cues as possible determinants of the depression effect. Davis and Ludvigson (1969) suggested that the presence of frustrative odors produced by incentive reduction might well be enhancing the depression effect. However, due

to the fact that these investigators did not utilize a "no-odor" condition, they were unable to indicate whether or not depression effects would occur in the absence of odor cues. Strictly speaking, the data from the present study indicate that in the absence of odor cues depression effects do not occur. However, the data clearly indicate that performance decrements do occur when anosmic subjects (i.e., a "no-odor" condition) are shifted from large to small reward. It should also be noted that the performance of the anosmic small reward control group (Group S) remained quite stable during Phase II while the performance of the normal and sham small reward (Group S) subjects was relatively unstable during this Phase. As can be seen from Figures 7-9 large fluctuations, especially in the goal measure, where frustrative odor cues would be expected to be maximal, were shown by both the normal and sham small reward (Group S) subjects. Obviously, it is quite possible that the depression effects shown by the normal and sham shifted subjects were heightened by odor cues. The Davis and Ludvigson (1969) study supports this conclusion.

In view of the depressed performance of the large reward (11L and 1L) anosmic subjects during Phase I, their gradual decline when shifted to small reward (Phase II), and the lack of large performance fluctuations on the part of the small reward anosmic subjects, another aspect of the present data deserves mention. It appears that removal of

the olfactory sense from the rat serves to negate, at least partially, motivational factors. As can be seen from Figures 7-8 pronounced and abrupt performance decrements were shown in the goal measure by the second day of Phase II by the normal and sham subjects experiencing incentive reduction. As already noted, the performance of these subjects gradually declined during the incentive reduction phase. The same trends also appeared in the start and run measure. A conditioning theory, such as classic frustration theory (Amsel, 1958), reliably predicts the behavior of the shifted normal and sham subjects during Phase II. The largest and most pronounced decrements occurred during the early stages of Phase II in the goal measure (where frustration would, theoretically, develop quickly and be maximal), later, and to a lesser extent in the run and start measures due to generalization of conditioned frustration. On the other hand, the gradual decline on the part of the shifted anosmic subjects would not be predicted by frustration theory. As previously noted, the data of the present study strongly suggest that incentive motivation was lower for the 11L and 1L anosmic subjects during Phase I. Hence it might be argued that shift from large to small reward was less frustrating for the anosmic subjects. In any event it would appear that that it is necessary to include motivational and/or emotional factors to account for the data of the anosmic subjects in the present study.

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APPENDIX A: FIGURES

Fig.1 - Mean Start Speed (meters per second)
for the Normal Subjects during
Phase I and II

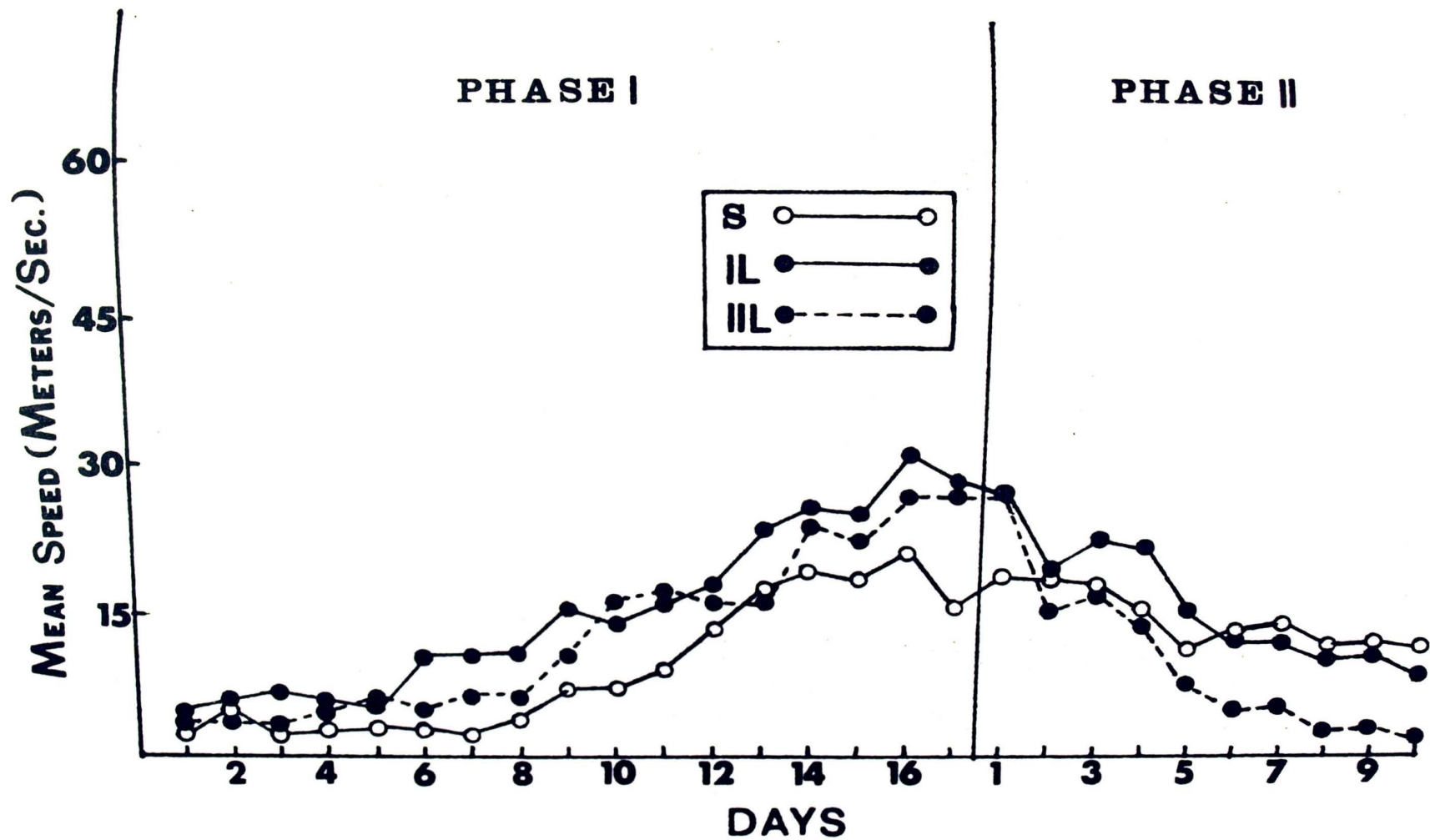


Fig.2 - Mean Start Speed (meters per second)
for the Sham Subjects during
Phase I and II

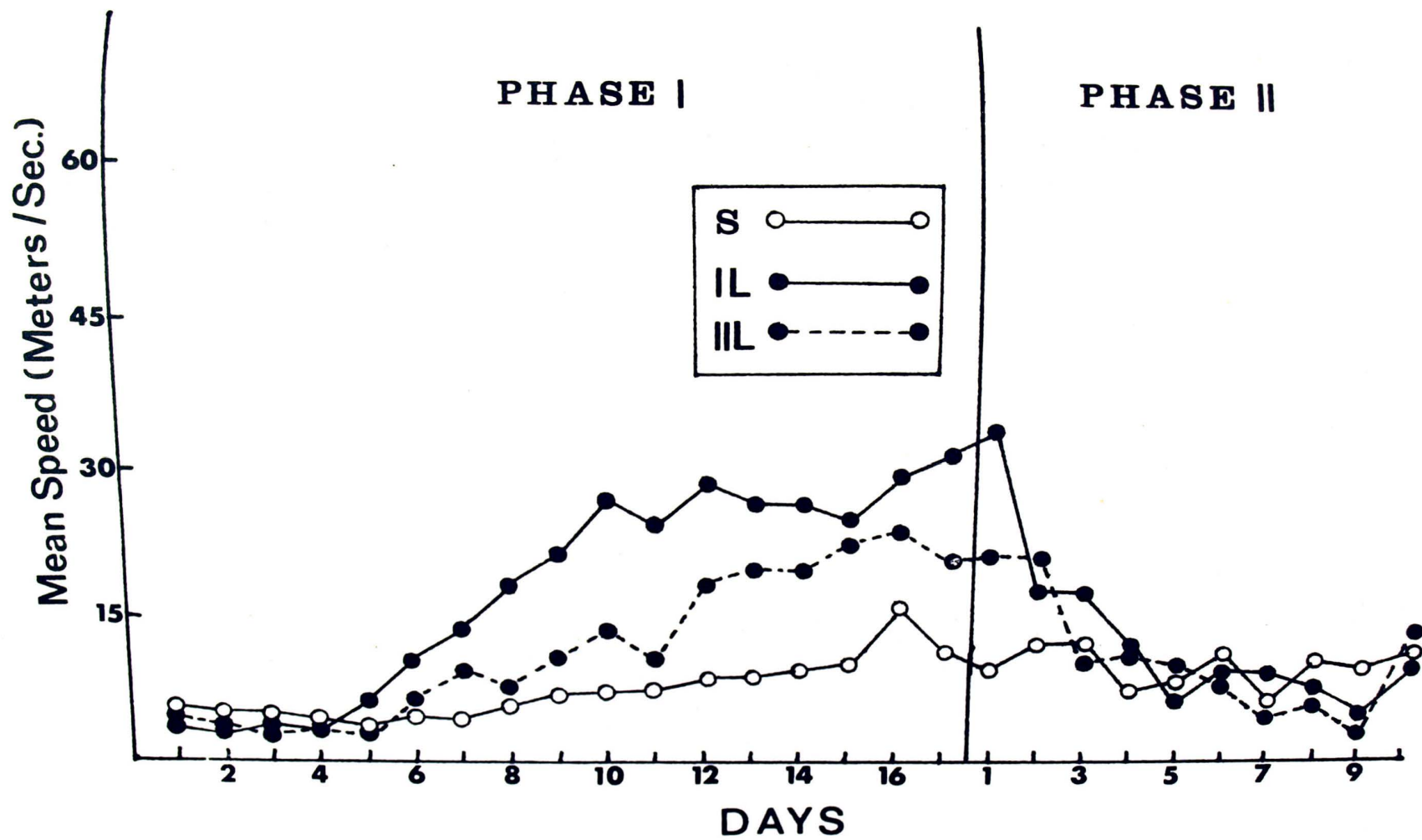


Fig.3 - Mean Start Speed (meters per second)
for the Anosmic Subjects during
Phase I and II

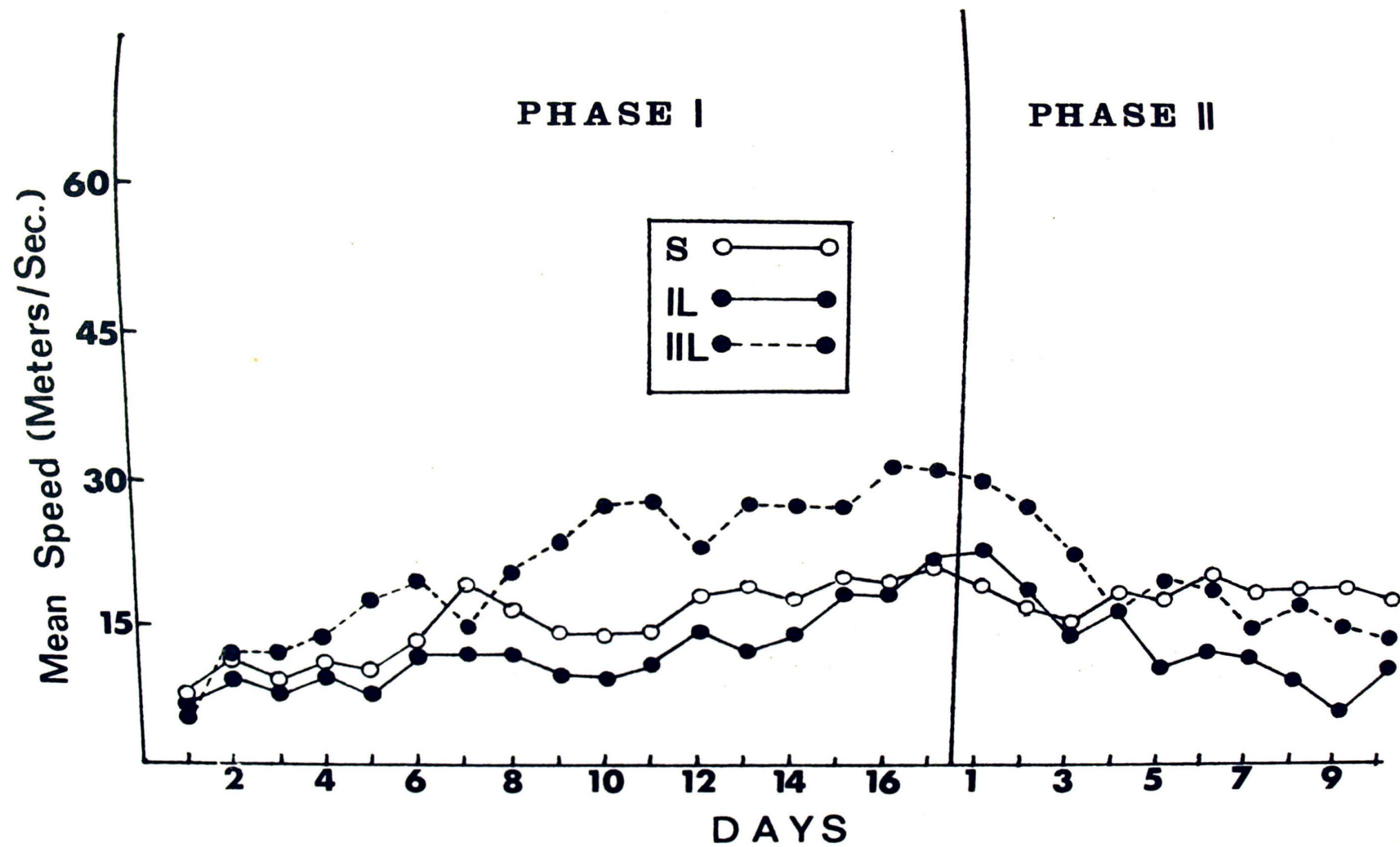


Fig.4 - Mean Run Speed (meters per second)
for the Normal Subjects during
Phase I and II

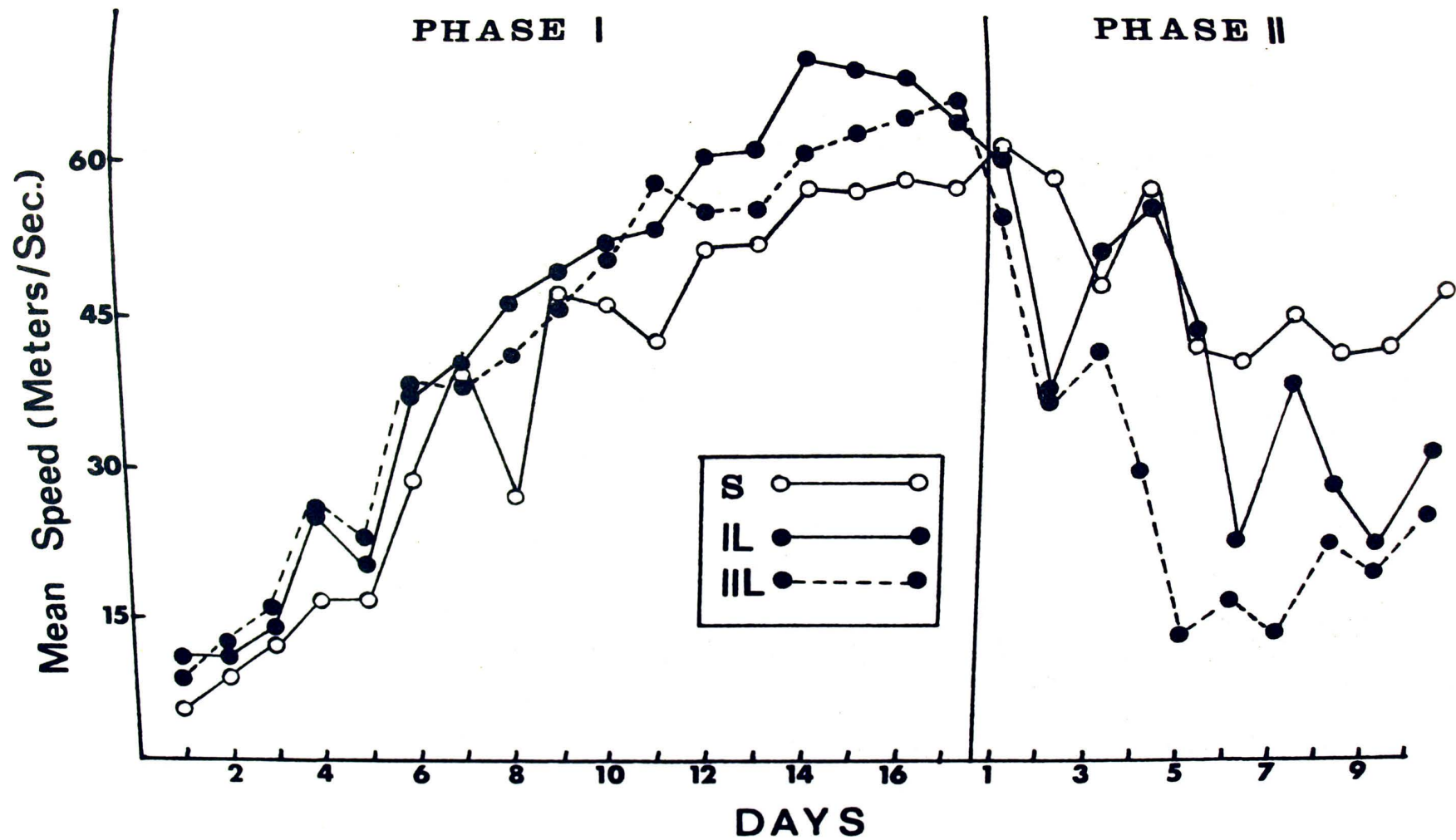


Fig.5 - Mean Run Speed (meters per second)
for the Sham Subjects during
Phase I and II

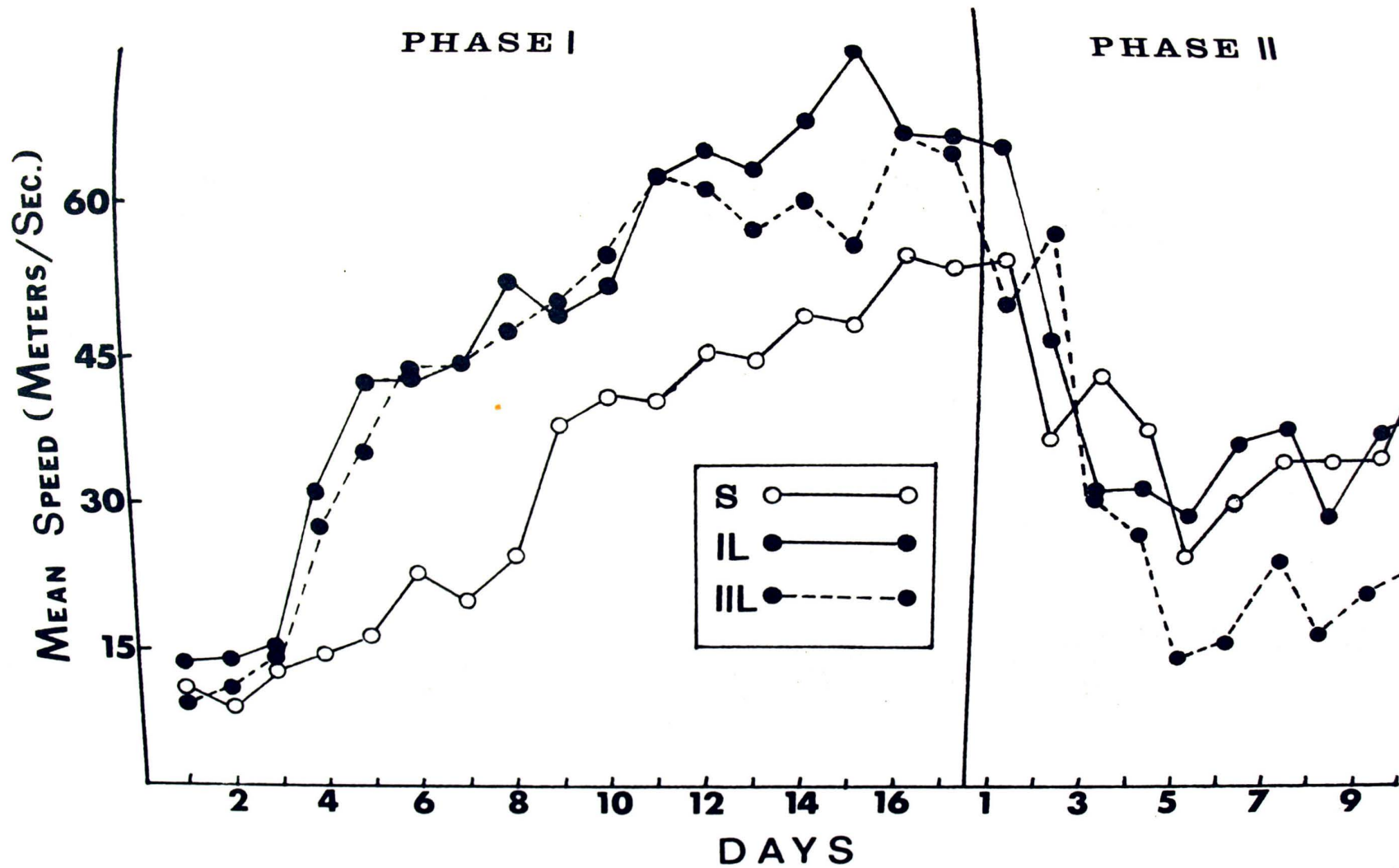


Fig.6 - Mean Run Speed (meters per second)
for the Anosmic Subjects during
Phase I and II

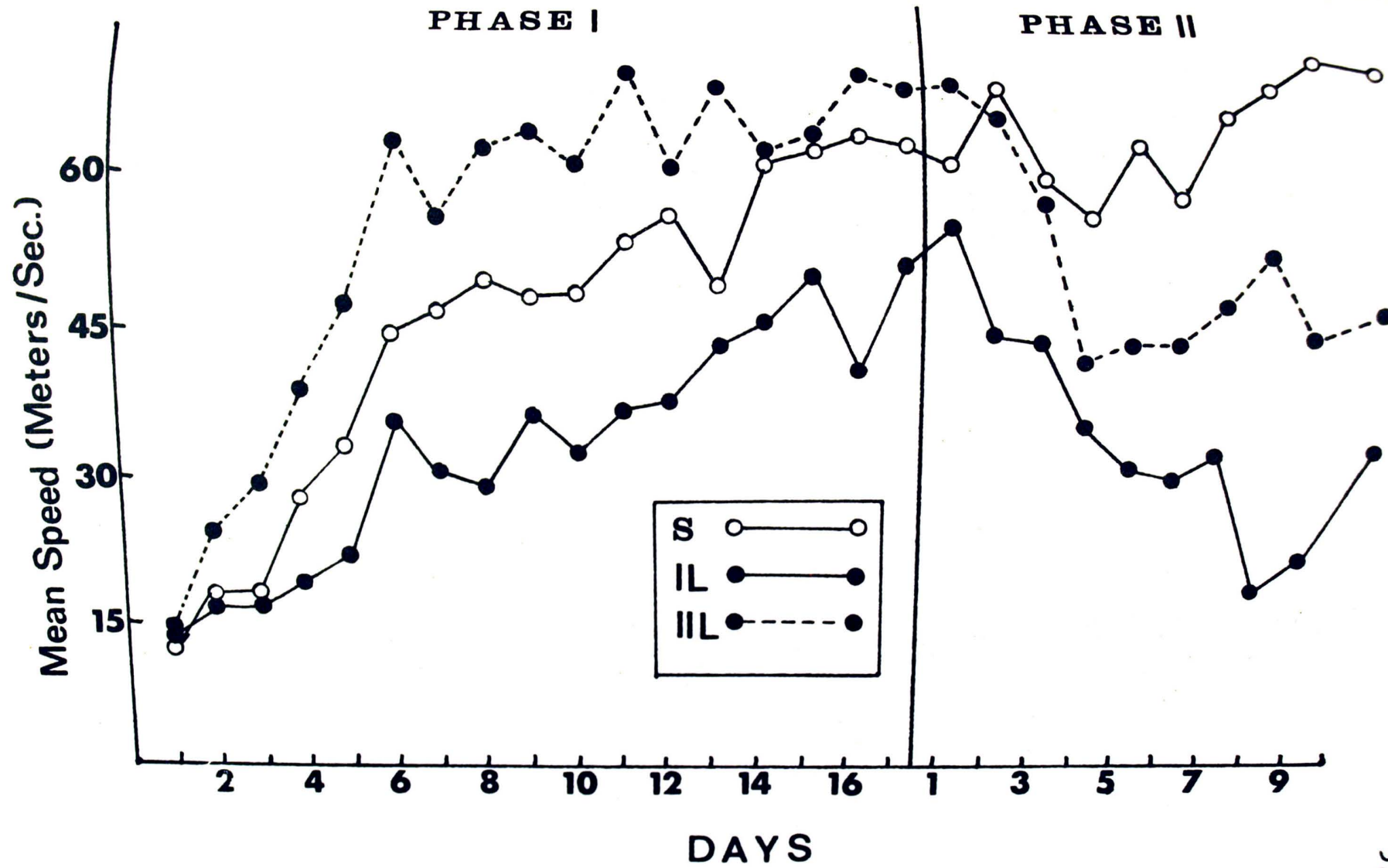


Fig.7 - Mean Goal Speed (meters per second)
for the Normal Subjects during
Phase I and II

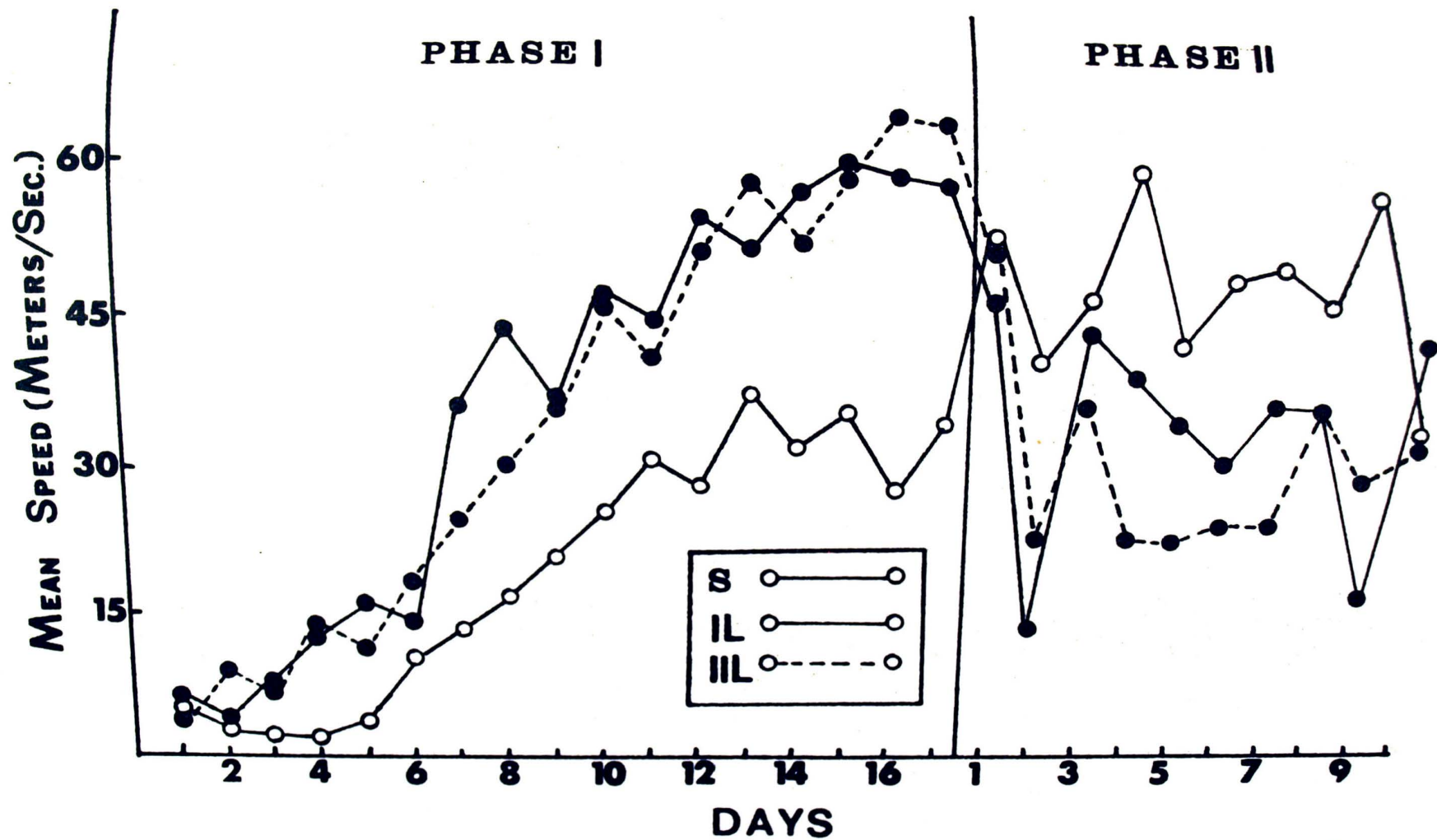


Fig.8 - Mean Goal Speed (meters per second)
for the Sham Subjects during
Phase I and II

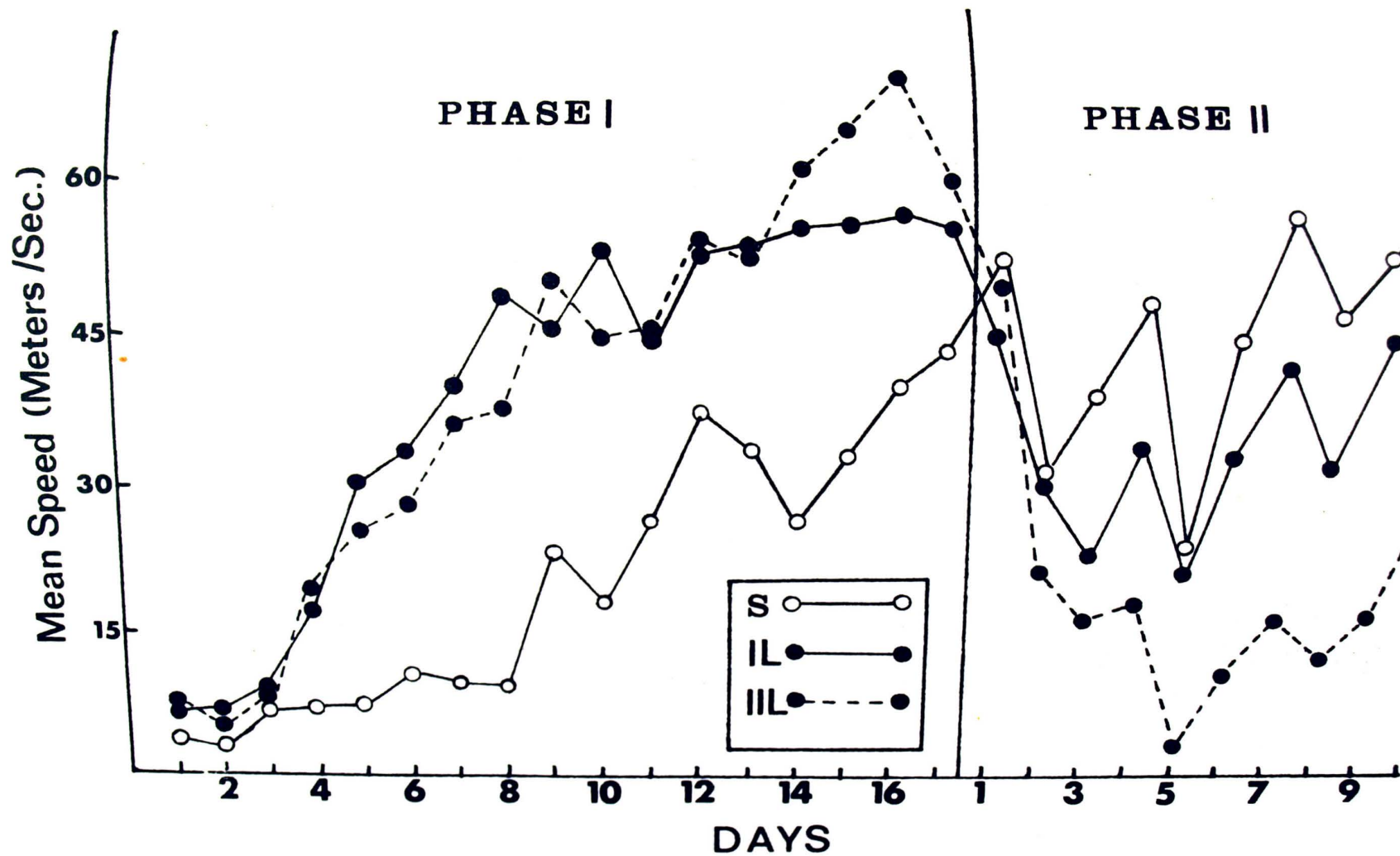
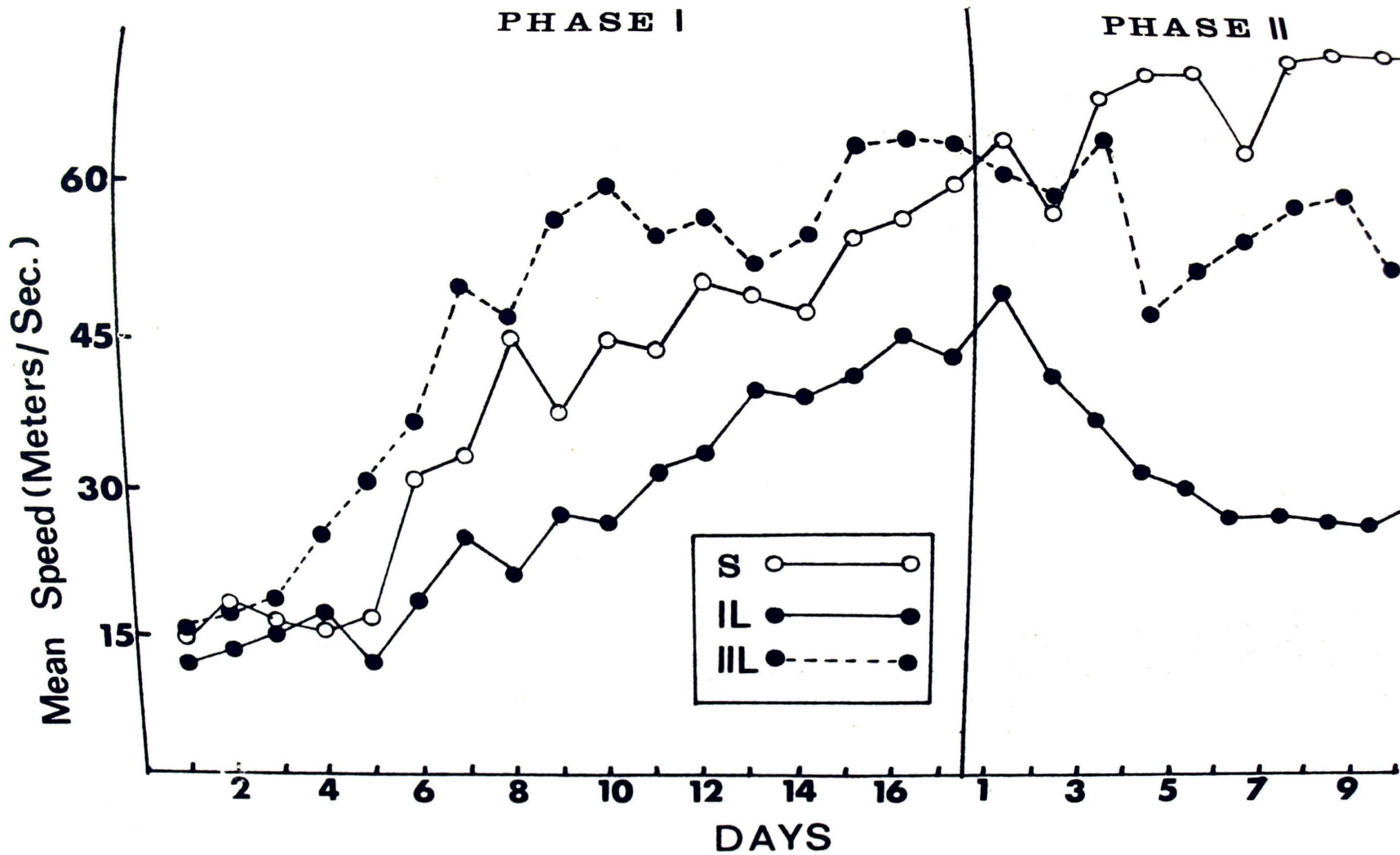


Fig.9 - Mean Goal Speed (meters per second)
for the Anosmic Subjects during
Phase I and II



APPENDIX B: TABLES

Table 1 Experimental Design

	Days 1-5	Days 6-22 (Training)	Days 22-31 (Shift)
ONE WEEK DEPRIVATION FOR ALL SUBJECTS	PRETRAINING FOR ALL SUBJECTS	Normal Group 11L (Multiple pellet large reward) Group 1L (Single pellet large reward) Group S (Small reward)	
		Anosmic Group 11L Group 1L Group S	
		Sham Group 11L Group 1L Group S	

Table 2 Summary of Mean Start Speed Analysis
of Variance - Acquisition Phase

Source	SS	df	MS	F
Between Subjects	250.06	80		
Reward Magnitude (A)	22.14	2	11.07	4.07*
Olfactory State (B)	2.63	2	1.32	.49
A X B	29.25	4	7.31	2.69*
Subject Within Groups (error)	196.04	72	2.72	
Within Subjects	80.18	324		
Trials (C)	5.07	4	1.27	5.08**
A X C	.90	8	.11	.44
B X C	1.25	8	.16	.64
A X B X C	1.16	16	.07	.28
C X Subject Within Groups (error)	71.79	288	.25	

**p < .01
*p < .05

Table 3 Summary of Mean Run Speed Analysis
of Variance - Acquisition Phase

Source	SS	df	MS	F
Between Subjects	27.68	80		
Reward Magnitude (A)	.99	2	.49	1.56
Olfactory State (B)	.23	2	.11	.34
A X B	4.00	4	1.00	3.16*
Subject Within Groups (error)	22.82	72	.32	
Within Subjects	19.09	324		
Trials (C)	.61	4	.15	2.65*
A X C	.69	8	.08	1.50
B X C	.14	8	.02	.31
A X B X C	1.12	16	.07	1.21
C X Subject Within Groups (error)	16.54	288	.06	

*p < .05

Table 4 Summary of Mean Goal Speed Analysis
of Variance - Acquisition Phase

Source	SS	df	MS	F
Between Subjects	208.50	80		
Reward Magnitude (A)	26.61	2	13.30	5.88**
Olfactory State (B)	.23	2	.11	.05
A X B	18.69	4	4.67	2.06***
Subject Within Groups (error)	162.98	72	2.26	
Within Subjects	34.29	324		
Trials (C)	3.40	4	.85	9.43**
A X C	1.67	8	.21	2.32*
B X C	.80	8	.10	1.12
A X B X C	2.47	16	.15	1.71***
C X Subject Within Groups (error)	25.94	288	.09	

***p < .10
 **p < .01
 *p < .05

Table 5 Summary of Mean Start Speed Analysis
of Variance - Shift Phase

Source	SS	df	MS	F
Between Subjects	386.15	80		
Reward Magnitude (A)	.64	2	.32	.07
Olfactory State (B)	19.38	2	9.69	2.01
A X B	18.26	4	4.57	.94
Subject Within Groups (error)	347.86	72	4.83	
Within Subjects	136.15	729		
Trials (C)	60.74	9	6.75	117.49**
A X C	20.70	18	1.15	20.02**
B X C	7.22	18	.40	6.98**
A X B X C	9.14	36	.25	4.41**
C X Subject Within Groups (error)	37.22	648	.06	

**p < .01

Table 6 Summary of Mean Run Speed Analysis
of Variance - Shift Phase

Source	SS	df	MS	F
Between Subjects	116.39	80		
Magnitude Shift (A)	9.80	2	4.90	3.96*
Olfactory State (B)	8.86	2	4.43	3.58*
A X B	8.53	4	2.13	1.72
Subject Within Groups (error)	89.20	72	1.24	
Within Subjects	24.31	729		
Trials (C)	13.80	9	1.53	36.21**
A X C	4.05	18	.22	5.31**
B X C	3.00	18	.17	3.94**
A X B X C	3.46	36	.10	2.27**
C X Subject Within Groups (error)	27.44	648	.04	

**p < .01
*p < .05

Table 7 Summary of Mean Goal Speed Analysis
of Variance - Shift Phase

Source	SS	df	MS	F
Between Subjects	645.75	80		
Magnitude Shift (A)	85.27	2	42.64	6.77**
Olfactory State (B)	62.72	2	31.36	4.98**
A X B	44.30	4	11.07	1.76
Subject Within Groups (error)	453.61	72	6.30	
Within Subjects	92.82	729		
Trials (C)	23.33	9	2.59	87.36**
A X C	14.58	18	.81	27.30**
B X C	17.15	18	.95	32.12**
A X B X C	18.54	36	.51	17.36**
C X Subject Within Groups (error)	19.22	648	.03	

**p < .01