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Stimulus control value of spreading depression demonstrated without shifting depressed structures.

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STIMULUS CONTROL VALUE OF SPREADING DEPRESSION
DEMONSTRATED WITHOUT SHIFTING DEPRESSED STRUCTURES

A Thesis Presented

By

Vaughn Gerald Reed

Submitted to the Graduate School of the
University of Massachusetts in
partial fulfillment of the requirements
for the degree of

Master of Science

April, 1968

Major Subject Psychology

STIMULUS CONTROL VALUE OF SPREADING DEPRESSION
DEMONSTRATED WITHOUT SHIFTING DEPRESSED STRUCTURES


A Thesis Presented

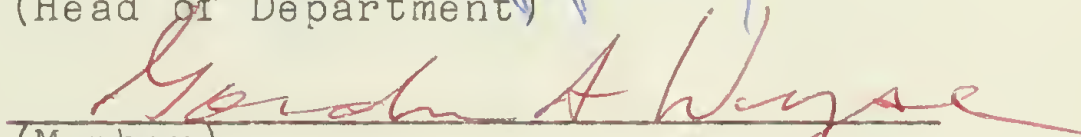
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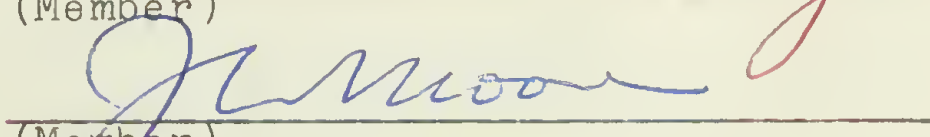
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Abstract

This study employed different concentrations of KCl to induce unilateral cortical spreading depression (SD) during acquisition of an active avoidance on two successive sessions. SD was induced on the same side during both sessions. Relearning savings were calculated in terms of trials to criterion and of total shock sustained during both sessions. Shock duration appeared to be the more sensitive measure of between group differences, although both measures agreed in direction of group differences.

SD impaired acquisition of the task, and during the first session the degree of this impairment was proportional to the concentration of KCl used to induce SD. When KCl concentration was changed between sessions subjects performed more poorly than other subjects that received a constant concentration of KCl for both sessions, whether KCl concentration was increased or decreased between sessions. These results were taken to confirm the hypothesis that SD effects stimulus control over responses learned during its presence.

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STIMULUS CONTROL VALUE OF SPREADING DEPRESSION DEMONSTRATED WITHOUT SHIFTING DEPRESSED STRUCTURES

Introduction

Leão (1944, 1947) demonstrated in his early reports that various forms of chemical, electrical or even mechanical stimulation are capable of inducing spreading depression (SD) in exposed cortex. Electrically, the phenomenon is first characterized by a slow high-amplitude direct current shift, initially negative (5-10mV.), followed after several minutes by a weaker positive potential. These d.c. shifts spread gradually (2-4mm/min) across the cortical surface from the point where the inducing stimulus is applied. They do not spread across the midline sulcus nor inward to subcortical structures, since myelin apparently acts as a barrier (Bures, 1959).

In attempting to explain SD, Burns (1958) and Grafstein (1956) have suggested that the reduction of transmembrane potential resulting from a large increase of extracellular K^+ would be sufficient to depolarize the cortical neural tissue. If such an increase of extracellular K^+ were particularly severe normal neural function may be interrupted for a prolonged period. Another hypothesis (Van Harreveld, 1959; Van Harreveld and Kooiman, 1965) suggests that a direct permeability increase to Na^+ occurs

as a result of neuronal release of glutamic acid in response to severe stimulation. The prolonged intense effect of SD may in fact be due to the complementary interaction of both mechanisms.

Since EEG records and other measures of brain activity and motor reflexes show large, prolonged decreases when SD is induced, Bures (1959) has suggested that a reversible "functional ablation" is a reasonable description of the state of the cortex. If so then SD should be a powerful research tool for the study of cortical aspects of behavior, particularly memory. Bures (1959) has suggested that SD induced in one cortical hemisphere prevents memory trace storage in that hemisphere. It is therefore referred to as the "naive" or "untrained" hemisphere if depressed while a task is learned. Furthermore, a 24 hour interdepression period with both hemispheres nondepressed does not automatically lead to storage of the trace in the naive hemisphere unless the subject is allowed to practice the task for at least a few trials ("transfer trials"). Subsequent to the transfer trials SD can be evoked in the previously normal ("trained") hemisphere and the subject will perform the task at a high level. Without the transfer trials, no such evidence of learning occurs, (Bures, 1959; Russell and Ochs, 1961). On the basis of this it has been suggested (Bures, 1959; Russell and Ochs, 1963) that unilateral depression leads to confinement of the trace in the func-

tional cortex and interdepression trials cause transfer of the trace to the naive hemisphere where it is consolidated.

Although Bures (1959) obtained these results from an active-avoidance shuttlebox situation, Russell and Ochs (1961, 1963) demonstrated a similar effect in an appetitive bar press situation. Ray and Emley (1964) demonstrated support for the hypothesis in the T maze situation, and further investigated the phenomenon by interrupting the consolidation period in the naive hemisphere wether 10 min. after or immediately after the transfer trial. They found evidence of successful transfer in the former case but not in the latter.

Recently Schneider (1967) has presented an alternative explanation of the above data and a hypothesis, which he calls the "confinement-transfer hypothesis." He has emphasized the importance of the stimulus aspects of SD and the effect of SD on other stimuli (see below) which occur in its presence. If these aspects are significant then it can be expected that any change in SD from one session to the next will cause a performance decrement on the basis of a change in stimulation. All of the above experiments use a paradigm which probably involves the maximum possible change between sessions of SD conditions, and therefore change of stimuli, i.e. SD on one hemisphere in one session and on the opposite in the next session. Schneider has attempted to demonstrate an inverse relationship between

savings during relearning and amount of stimulus change, i.e. amount of change of extent of brain area depressed. For example, it has been shown (Schneider, 1966) that animals which learn an active avoidance when non-depressed and are required to relearn with both hemispheres depressed are inferior in relearning to another group which initially learns with one hemisphere depressed.

The stimulus generalization hypothesis gains support from experiments demonstrating that SD alters both internal (e.g. proprioceptive) and external stimuli. Thompson and Enter (1967) showed that shock sensitivity increased in the rat from the bilaterally depressed to unilaterally depressed to non-depressed conditions. Tapp (1962) showed that motor deficit was proportional to KCl concentration used to induce SD. Bures, Buresova and Zahorova (1958) noted the effects of 2% and 25% KCl on escape, avoidance and approach responses and on changes of EEG activity. All 4 measures revealed effects of differing concentrations. For example, 2% KCl never reduced EEG amplitude to less than 20% of normal and a return to 50% of normal occurred within 10 min. 25% KCl reduced EEG amplitude momentarily to zero and recovery to half of normal was not reached until 90 min. later. Apparently, graded sensory and motor deficits and EEG activity decreases occurred whether SD was varied relative to the amount of cortical area affected or the concentration of the inducing agent used. It follows that the

stimulus complex affecting a normal animal is quite different from that of a depressed animal. It should be noted that the stimulus complex associated with SD is graded.

These concentration differences suggest the possibility of demonstrating performance decrements between sessions without changing the cortical region to be depressed, i.e. by varying the concentration from Day 1 to Day 2 without changing the site of administration. Such a manipulation reduces the applicability of the confinement-transfer phenomenon and permits an investigation of the effect of stimulus generalization by varying stimulus intensity in a traditional manner. If successful such a manipulation would contribute further support to the stimulus generalization hypothesis and may suggest methods of isolating this phenomenon from the memory disrupting effect of SD, or may at least have some implications for the latter effect.

EXPERIMENT I

Method

Subjects. Ss were 26 male albino rats (Charles River Breeding Labs, North Wilmington, Mass.), aged 3-6 months at the time of surgery. One died, and another was discarded when screening indicated that it was not depressed on the second session.

Surgery. Surgical preparation of the rats was carried out under sodium pentobarbital (40 mg/kg) anesthesia. Ss were mounted in a stereotaxic apparatus. The skull was exposed by a longitudinal midline incision. A hole 1.5mm in diameter was burred through the skull on each side of the midline, 2mm behind Bregma and 2-3mm lateral to the midline. Care was taken to avoid puncturing the dura. A threaded plastic cannula 1.5mm in diameter (I.D.) and 8mm long (Plastic Products Co., Roanoke, Va.) was mounted over each hole. One jeweller's screw was implanted on each side 6-8mm rostral to the cannulae. An acrylic cement cap was built up over the screws and around the bases of the cannulae. Sterile isotonic saline (0.9% NaCl+ distilled water) was administered to each cannula with the use of a 1 cc syringe (26 gauge needle) without injecting the needle into the brain tissue. The same technique was used later in the experiment to fill the cannula with KCl to initiate SD. Saline was kept in the cannulae at all times, except when KCl solution was applied to induce SD.

Apparatus. The experimental cubicle was a black wooden box ($17\frac{1}{2}$ " high x 15" long x $10\frac{1}{2}$ " wide) with a clear plastic front. It was partitioned in the middle to provide two chambers ($17\frac{1}{2}$ " x 7" x $10\frac{1}{2}$ "). A guillotine-type, manually operated door opened a $3\frac{1}{2}$ " x 5" hole in the partition at floor level to permit movement between the chambers. The floor of the box was constructed of $\frac{1}{8}$ " steel grid bars spaced $\frac{1}{2}$ " apart.

A 6 watt white signal light was mounted in the back of the right chamber 6" above floor level. A photocell and light source were mounted on the back and front, respectively, of the left chamber to provide a photobeam which was broken by the movement of S from the right into the left chamber. A constant current shock supply and scrambler (model LVE 1531) could be activated to provide current to the grid of the right chamber. Other standard relay and timing equipment was employed for the appropriate intervals and latency measures.

Procedure. Animals were trained on a one-way active avoidance task, approximately 24 hours after surgery. Unilateral SD was induced by flushing and filling one of the mounted cannulae with a 10%, 15%, or 20% ($X\% = X \text{ gm KCl} / (100-X)\text{ml distilled H}_2\text{O}$) KCl solution. Since all cannulae were of the same size, the volume administered was 14 μl in all cases. The cannula on the opposite side was flushed and filled with fresh saline, as was the cannula on

the depressed side after the training session. Indications of SD usually occurred 10-20 min. after KCl was applied. When depressed, S would lie down leaning toward the side contralateral to the applied KCl. Other tests used for screening depressed rats were the placing response (Bures, 1959), the crossed foreleg test (Albert, 1966a) and the observation of whether the legs fell through the floor grid of the box (Albert, 1966a). Although not all rats were noticeably deficient on all of these measures, any rat which was not altered on at least one measure was discarded before running (n=1).

Onset of each trial was initiated by placing the subject in the right chamber, facing the back of the box. The CS was a compound stimulus: a manually operated switch made an audible click, the light at the rear of the right chamber was turned on, and the door separating the two chambers was lifted. An interstimulus interval of 8 sec. was followed by an 0.5 mA shock to the floor of the right box until the animal went into the left chamber. S's crossing into the left chamber broke a photobeam which turned off the light CS and the shock UCS, and provided a latency of response record. The intertrial interval was a variable 60 seconds. All subjects were trained to a criterion of 9 avoidances out of 10 trials. Training was discontinued and a score of 40 trials was recorded if a rat failed to reach criterion in 40 trials on any day.

All rats were unilaterally depressed on the same side and underwent the same procedure in each session of the experiment.

Three experimental groups ($n=8$ for each group) were run. All were trained to criterion on Day 1 when unilaterally depressed with a medium (15%) KCl solution. One group (M-M) was retrained on the second day with the same concentration of KCl, another group (M-L) with a lower (10%) KCl solution, and the third group (M-H) with a higher (20%) KCl solution.

Results and Discussion

The data of the experiment were analyzed both with respect to trials to criterion (TTC) and response latency. Kukleta (1967) showed that in a situation similar to this experiment a response latency type of record was more sensitive to between group differences than the trials to criterion measure.

Percent savings $((1 - \text{TTC on Day 2} / \text{TTC on Day 1}) \times 100)$ was computed for each subject. For Ss that performed more poorly on Day 2 than Day 1 ($n=5$) savings was defined as the negative of percent loss $((1 - \text{TTC on Day 1} / \text{TTC on Day 2}) \times 100)$. Homogeneity of variance was a tenable assumption ($F_{5,7} = 2.94$, $p > .05$) when all Ss were considered. However this was clearly not true ($F_{5,3} = 40.6$, $p < .01$) when only those Ss which reached criterion on both sessions ("criterion Ss") were considered. Inspection of the data indicates that this result

was due to a lack of normality as well as differences of amount spread. Therefore non-parametric tests (e.g. Kruskal-Wallis H tests, and Mann-Whitney U tests) were used in this and the following experiment (Siegel, 1956).

Figure 1a shows the mean TTC for the three groups over the two sessions. Figure 1b shows the same data when Ss that failed to reach criterion on either day ("non-criterion Ss") are eliminated from the data of both sessions. More Ss failed to reach criterion on Day 1 ($n=8$) than on Day 2 ($n=3$) ($\chi^2 = 2.53$, $p > .10$). The apparent superiority of group M-M to group M-H was not significant whether all Ss ($U_{8,8} = 31$, $p = .48$) or only criterion Ss ($U_{4,4} = 5$, $p = .24$) were considered. Group M-M was also not significantly better than group M-L for all Ss ($U_{8,8} = 22$, $p = .164$) or for criterion Ss ($U_{4,6} = 6$, $p = .129$). Thus while group differences occurred in the direction predicted by the stimulus generalization hypothesis, these differences did not occur at an acceptable level of significance when savings were analyzed in terms of trials to criterion.

Figures 2a and 2b show the mean total shock durations sustained by each group for both sessions. The between group differences seen on Day 1 in these two figures are chance events (all Ss: $H_2 = 1.8$, $0.3 < p < 0.5$; criterion Ss: $H_2 = 0.4$, $0.8 < p < 0.9$). In fact multiple U tests yielded only a single instance of a significant within day difference, i.e. when only criterion Ss are considered

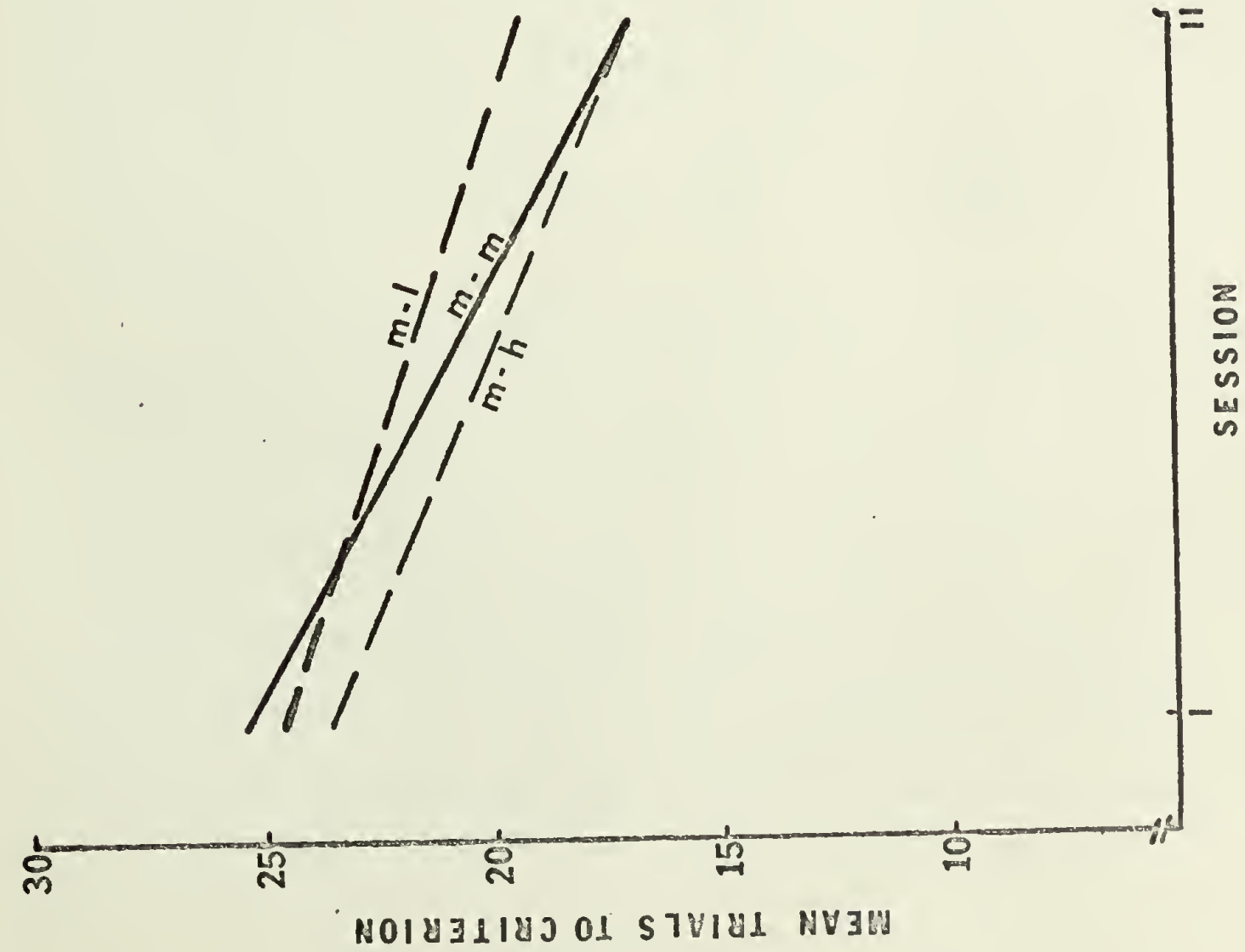


Fig. 1a. Mean trials to criterion for all Ss.

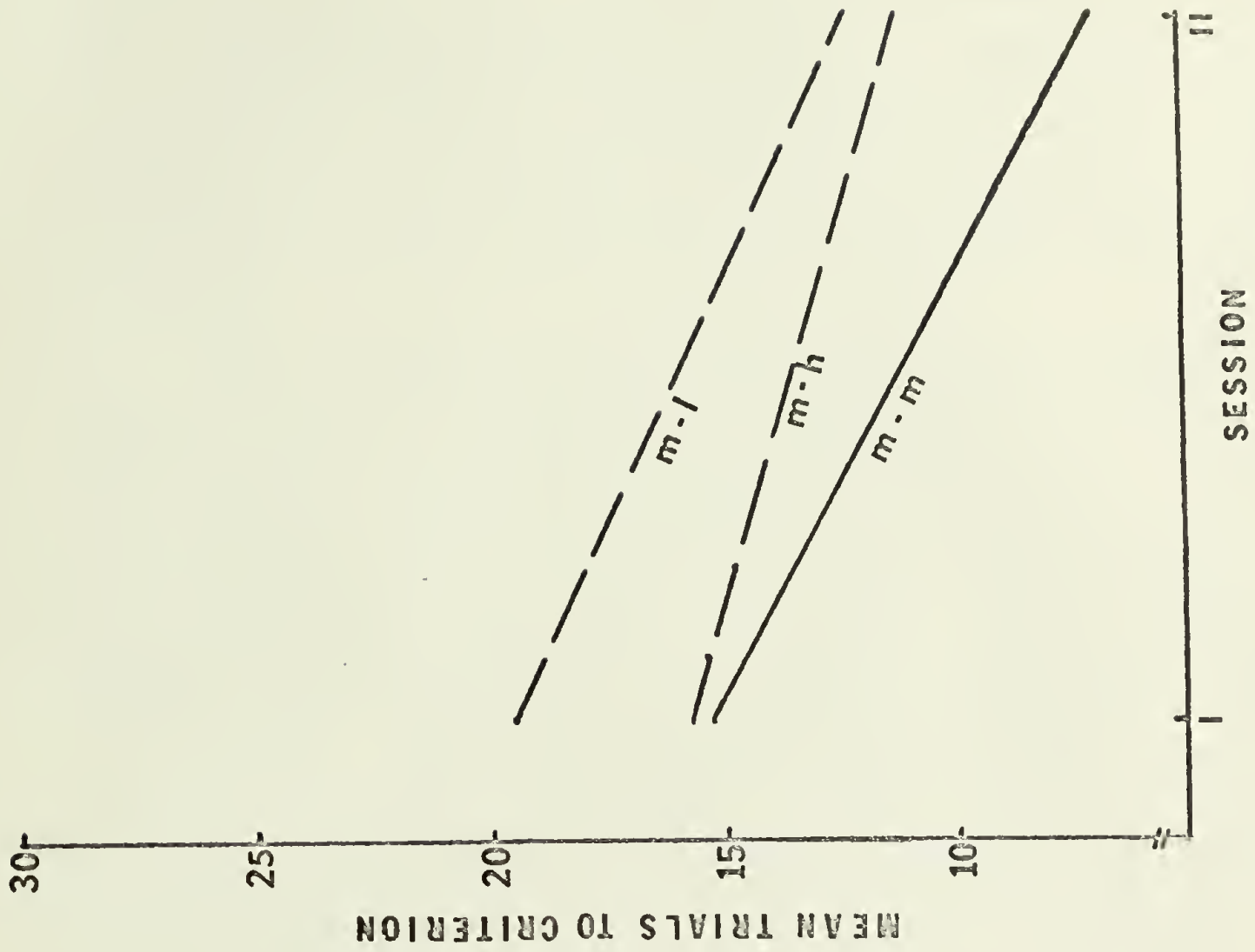


Fig. 1b. Mean trials to criterion for criterion Ss only.

group M-M sustained less shock on Day 2 than group M-L ($U_{4,6} = 1$, $p = .01$). Within day differences are therefore not regarded as important effects by themselves. Rather, significant effects are found primarily to be a function of the amount of improvement over session, i.e. relearning savings.

When all \underline{S} s are considered the shock duration data did not yield a significant savings main effect ($H_2 = 4.35$, $0.1 < p < 0.2$). However group M-M was significantly superior to group M-L ($U_{8,8} = 14$, $p = 0.032$) and the superiority of group M-M to group M-H just missed significance ($U_{8,8} = 16$, $p = 0.052$). When only criterion \underline{S} s are considered a significant savings main effect was obtained ($H_2 = 8.6$, $0.01 < p < 0.02$) and again U tests indicated that group M-M was superior both to group M-L ($U_{4,6} = 0$, $p = 0.005$) and to group M-H ($U_{4,4} = 0$, $p = 0.014$). U tests indicated no differences between groups M-L and M-H whether all \underline{S} s ($U_{8,8} = 30$, $p = .439$) or only criterion \underline{S} s ($U_{4,6} = 7$, $p = .176$) are considered.

If only the motor and sensory impairing effects of SD are considered the superiority of group M-M over M-H would be predicted. However the performance of group M-L should have been facilitated on Day 2 for the same reasons. Since group M-M was also superior to group M-L it seems necessary to conclude that the effective stimulus control of SD was proportional to the similarity of intensities of

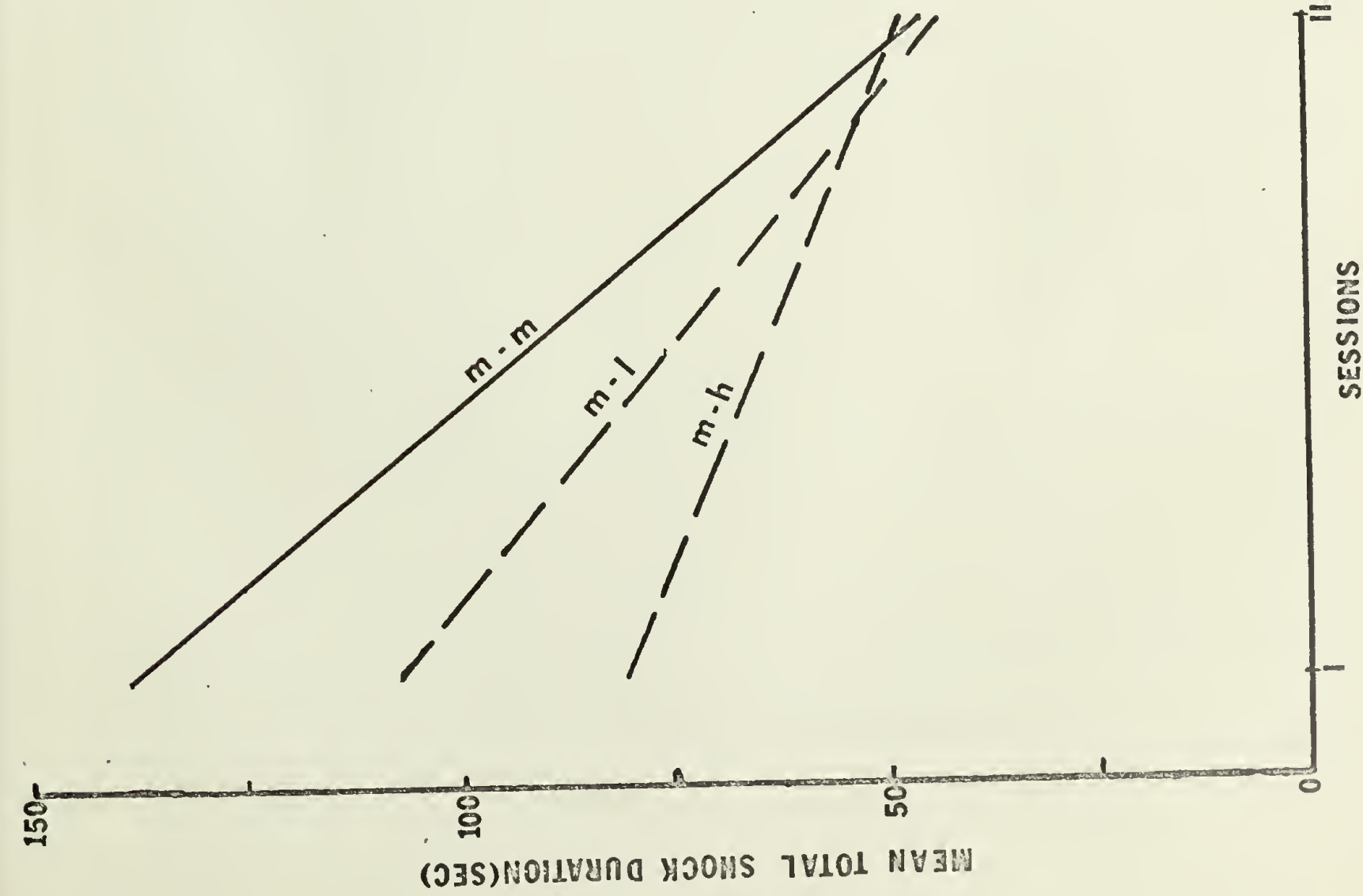


Fig. 2a. Mean total shock duration for all Ss.



Fig. 2b. Mean total shock duration for criterion Ss only.

SD on the two sessions. Thus a performance decrement occurs whether SD intensity is increased or decreased between sessions.

EXPERIMENT II

Introduction

The effect of KCl concentration on performance in Experiment I was not as pronounced as might have been expected. In fact there were no differences on Day 2 between groups M-L and M-H whether all Ss or only criterion Ss were considered. Since even the high KCl concentration used was not extremely detrimental to performance further exploration of large KCl concentration shifts seemed promising. This could be done by employing high and low KCl concentrations on Day 1 as well as Day 2. This would provide information about the effect of the range of KCl concentrations on Day 1, as well as increasing the amount of the concentration shift between sessions.

Method

Subjects. Ss were 22 male albino rats, aged 3-6 months. One died, and another was discarded on the second day when a high KCl solution appeared to induce indications of bilateral SD. Surgery and apparatus were the same as in the previous experiment.

Procedure. One control (N-N) and two experimental (L-H, H-L) groups were run on the same task to the same criterion as in the first experiment. Group N-N (n=8) differed from the other groups only in being sham depressed with a saline solution in each cannula before each session.

Group L-H ($n=6$) was unilaterally depressed with 10% KCl on Day 1 and on the same side with 20% KCl on the following day. Group H-L ($n=6$) was unilaterally depressed with 20% KCl on Day 1 and with 10% KCl on Day 2.

Results and Discussion

Figures 3a and 3b show the trials to criterion (TTC) results obtained from these three groups with all Ss or with only criterion Ss included. The results from the previous experiment have also been included. In this experiment more Ss failed to reach criterion on Day 2 ($n=5$) than on Day 1 ($n=4$) ($X^2 = .142$, $0.7 < p < 0.8$).¹

Analysis of the TTC measure did not indicate a main savings effect whether all Ss ($H_2 = 3.1$, $0.2 < p < 0.3$) or only criterion Ss ($H_2 = 0.9$, $0.3 < p < 0.5$) were considered. U tests between groups indicated no instances of significant differences whether all Ss (see table 1) or only criterion Ss (table 2) were included.² As in the previous experiment virtually all differences were in the direction predicted by a stimulus generalization hypotheses.

The integration of the results of Experiment I with Experiment II permit comparisons between larger samples of Ss. Groups were pooled according to the amount of difference

-
1. Raw data for all Ss of Experiments I and II are presented in Appendix A.
 2. Results of significance tests between groups are presented in Appendix B.

of SD conditions between sessions while also matching groups to balance each other with respect to the direction of shift of KCl concentration. The three resulting pooled groups are (I) no SD change between sessions ((N-N)+(M-M)), (II) slight SD change ((M-L)+(M-H)), and (III) large SD change ((L-H)+(H-L)). When all Ss are considered (Fig. 4a) significant differences were found between groups I and III ($U_{16,12} = 57$, $p < .05$) but not between I and II ($U_{16,16} = 100$, $.05 < p < .5$) or between II and III ($U_{16,12} = 76$, $.05 < p < .5$). No significant differences were found between pooled groups when only criterion Ss were considered, although savings differed between groups in the direction predicted by the stimulus generalization hypothesis.

Figures 5a and 5b show the mean shock durations sustained by each group of both experiments with all Ss or only criterion Ss included, respectively. The effect of KCl concentration on performance on Day 1 is presented below.

Tests for savings by the shock duration measure were calculated and the results are given in table 3 for all Ss and table 4 for criterion Ss. These results indicate relatively good savings for groups M-M, H-L and N-N, approximately in that order, with respect to the other groups. When groups were pooled again as was done for the TTC data above (see Figs. 6a and 6b) savings differences were found as indicated in table 5. These results show

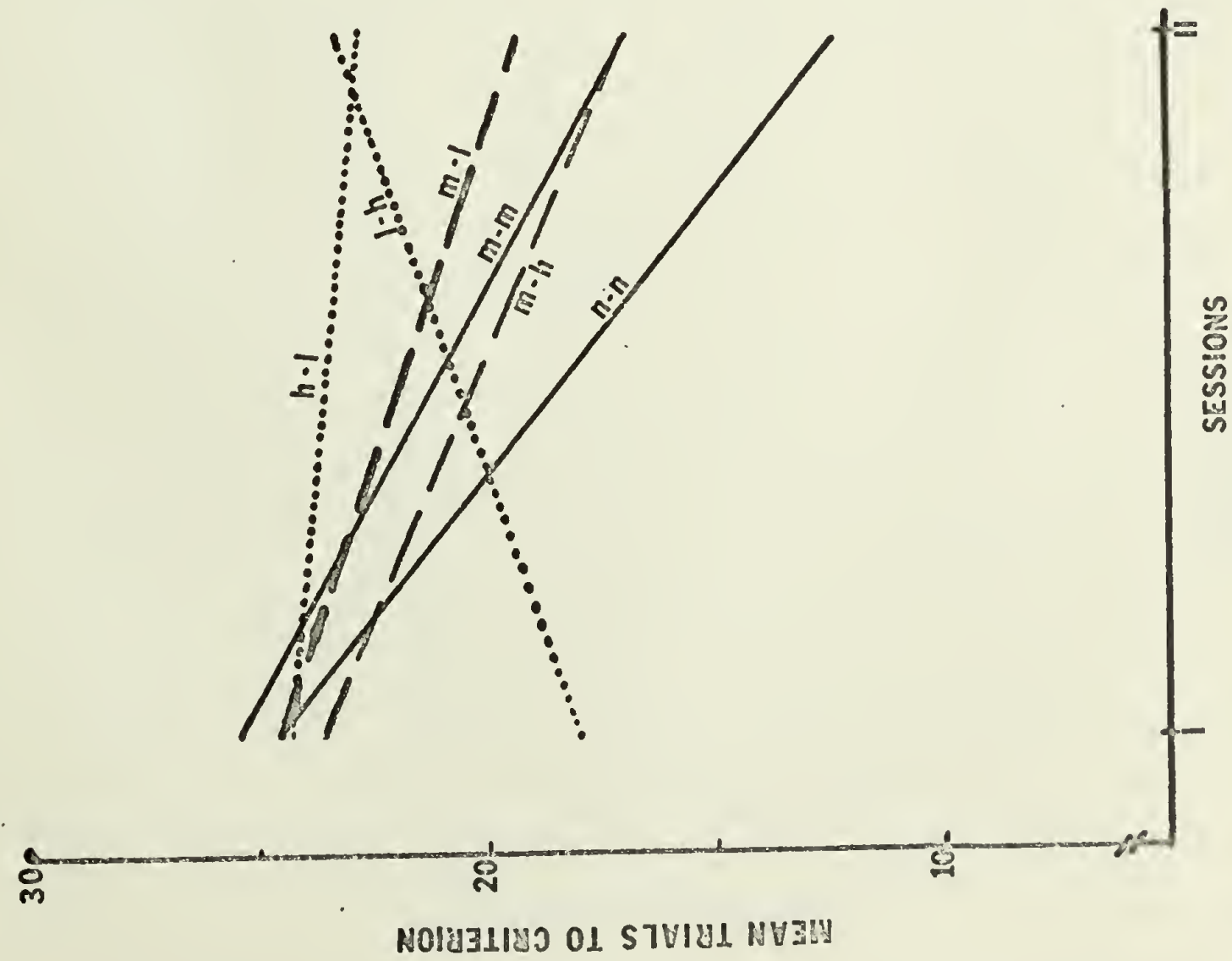


Fig. 3a. Mean trials to criterion for all Ss of each group of experiment I and experiment II.

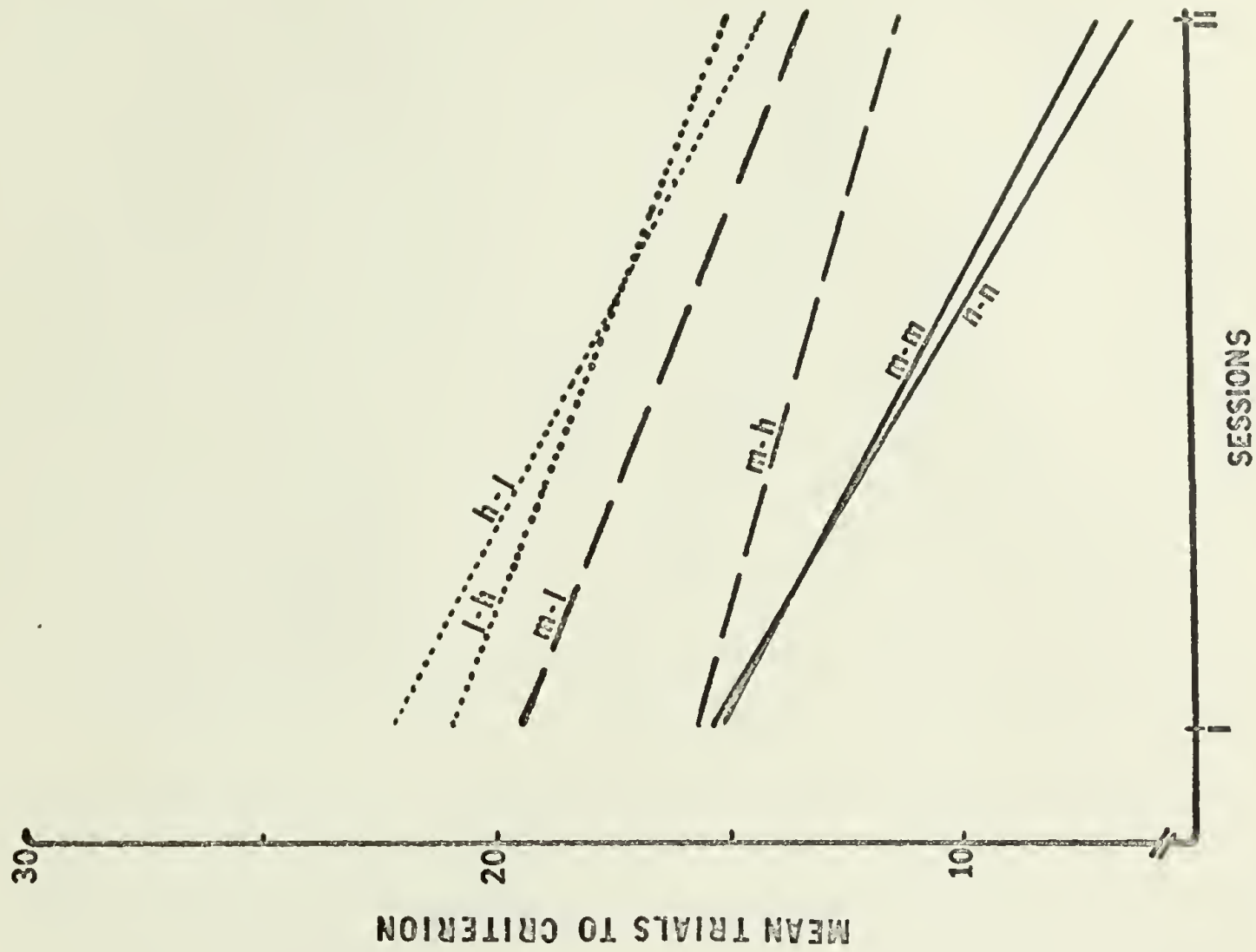


Fig. 3b. Mean trials to criterion for criterion Ss of each group of experiment I and experiment II.

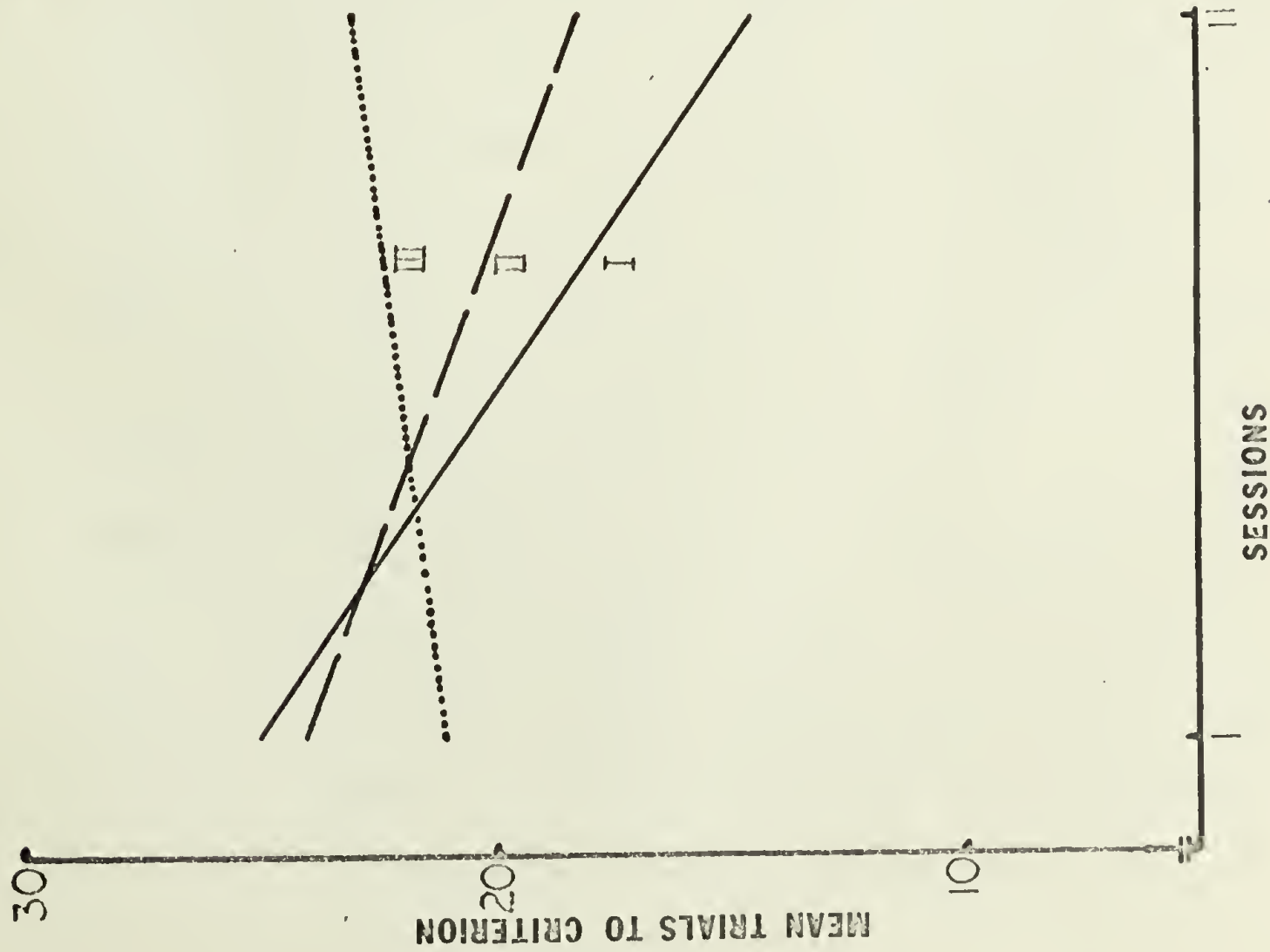


Fig. 4a. Mean trials to criterion for all Ss of each pooled group. $I = (M-M) + (N-N)$, $II = (M-H) + (M-L)$, $III = (H-L) + (L-H)$.

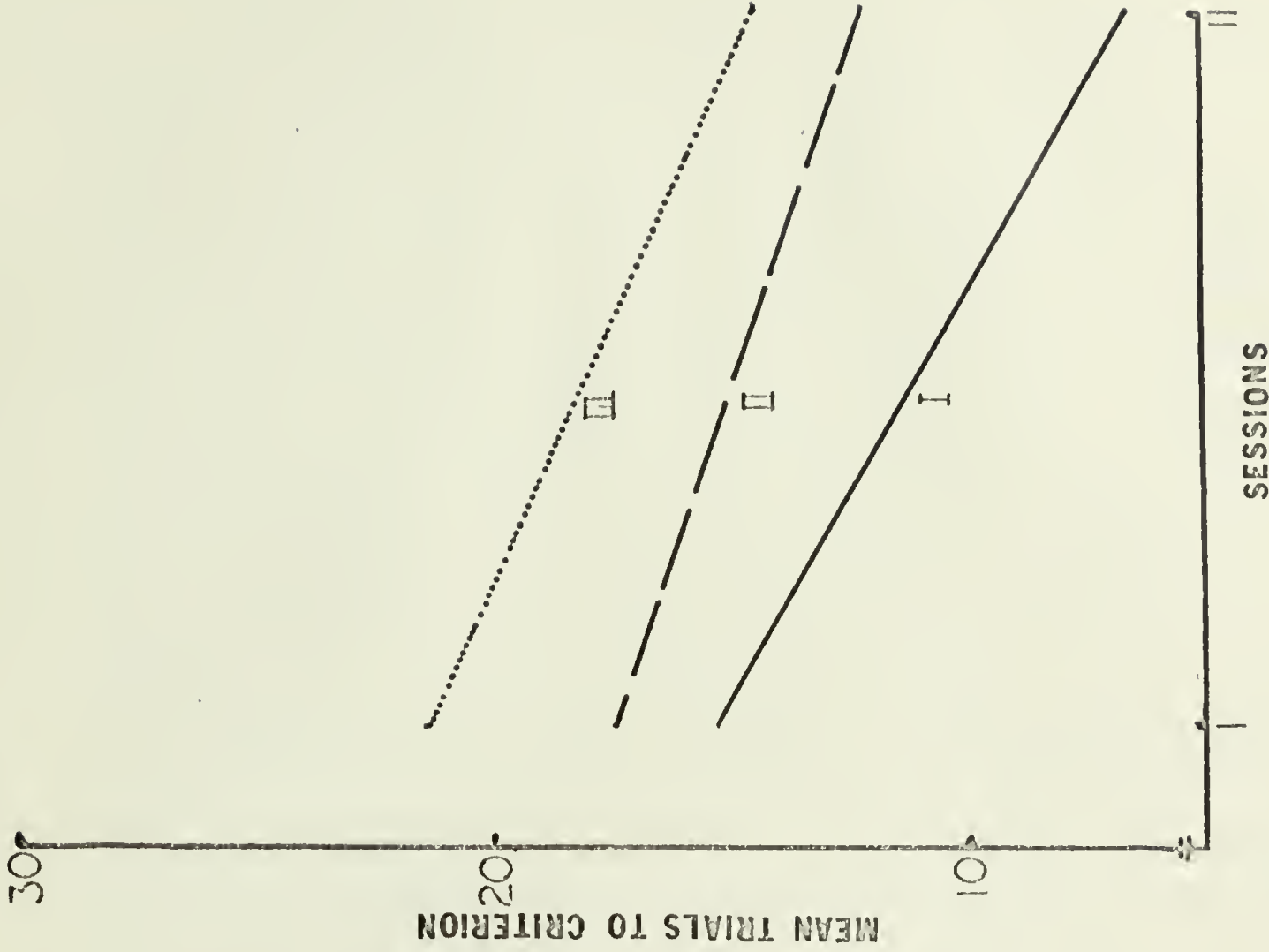


Fig. 4b. Mean trials to criterion for criterion Ss of each pooled group.

the superiority of the no SD change groups (I) to groups which underwent SD change (II and III).

Investigation of figures 5a and 5b also suggests an effect of KCl concentration to performance, at least on Day 1. Results of tests for a KCl concentration effect include the data of all Ss, unless otherwise stated. The KCl concentration main effect did not reach significance ($H_3 = 6.9$, $0.05 < p < 0.10$) for the Day 1 data. However, U tests indicated that on Day 1 group H-L sustained significantly more shock than either the sham depressed Ss ($U_{8,6} = 6$, $p = .010$) or group L-H ($U_{6,6} = 3$, $p = .008$). The difference on Day 1 between the sham depressed group and the pooled data of groups M-M, M-L and M-H approached but did not reach significance ($Z(u) \approx 1.52$, $p = 0.064$). On Day 2 the differences between depressed animals at different KCl concentrations apparently vanished. U tests between these groups were quite non-significant. The sham depressed Ss however still differed significantly on Day 2 from Ss receiving low KCl concentration ($U_{8,14} = 22$, $p = .01$), and high KCl concentration ($U_{8,14} = 24$, $p < .025$).

These results underscore the importance of the effect of KCl concentration on performance and the necessity to offset the direction of change of this effect if a relatively pure influence of stimulus change is to be shown. The high amount of apparent savings of group H-L may be attributed to this effect. In this experiment this balance of direction

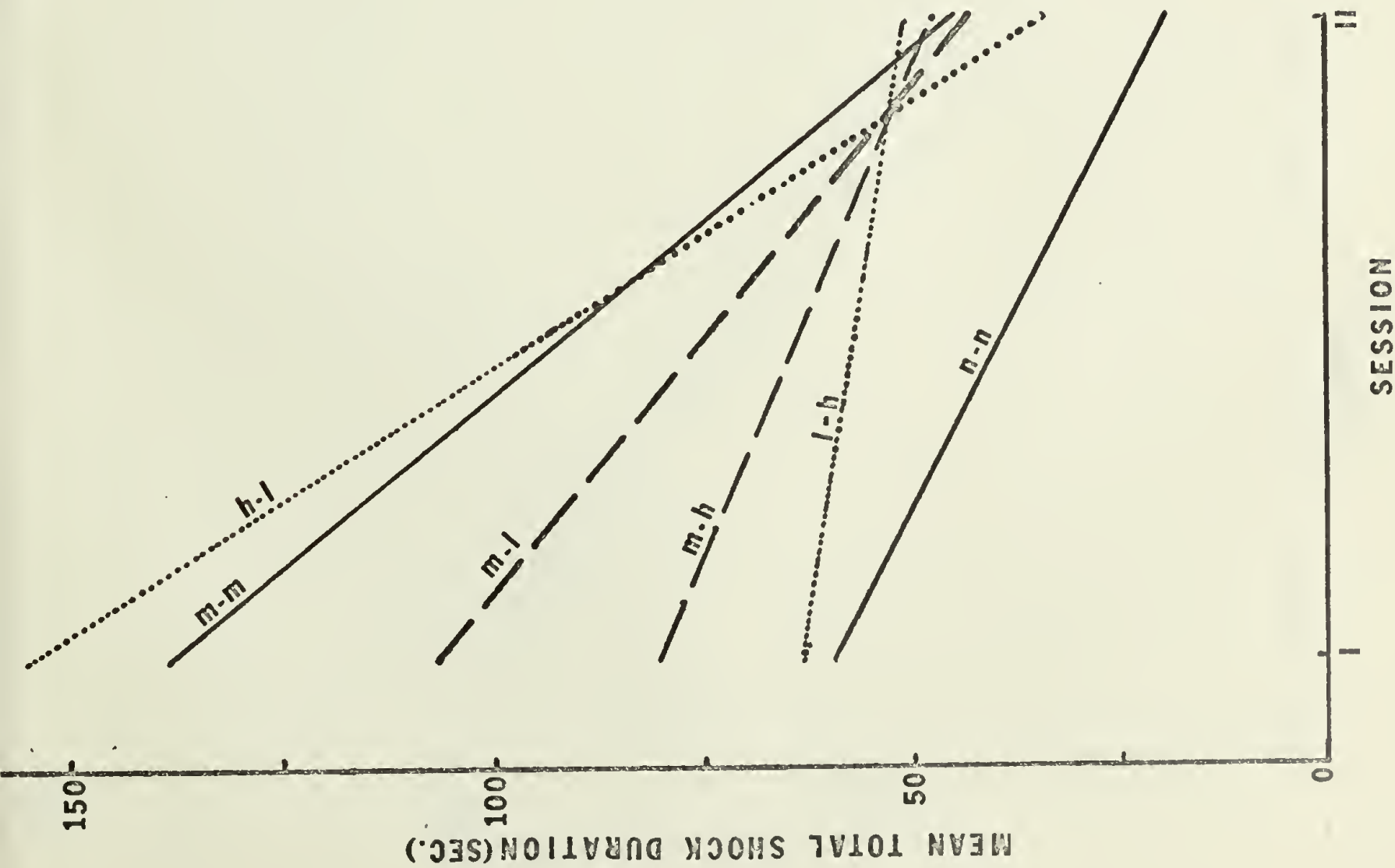


Fig. 5a. Mean total shock duration for all \bar{S}_s of each group of both experiments.

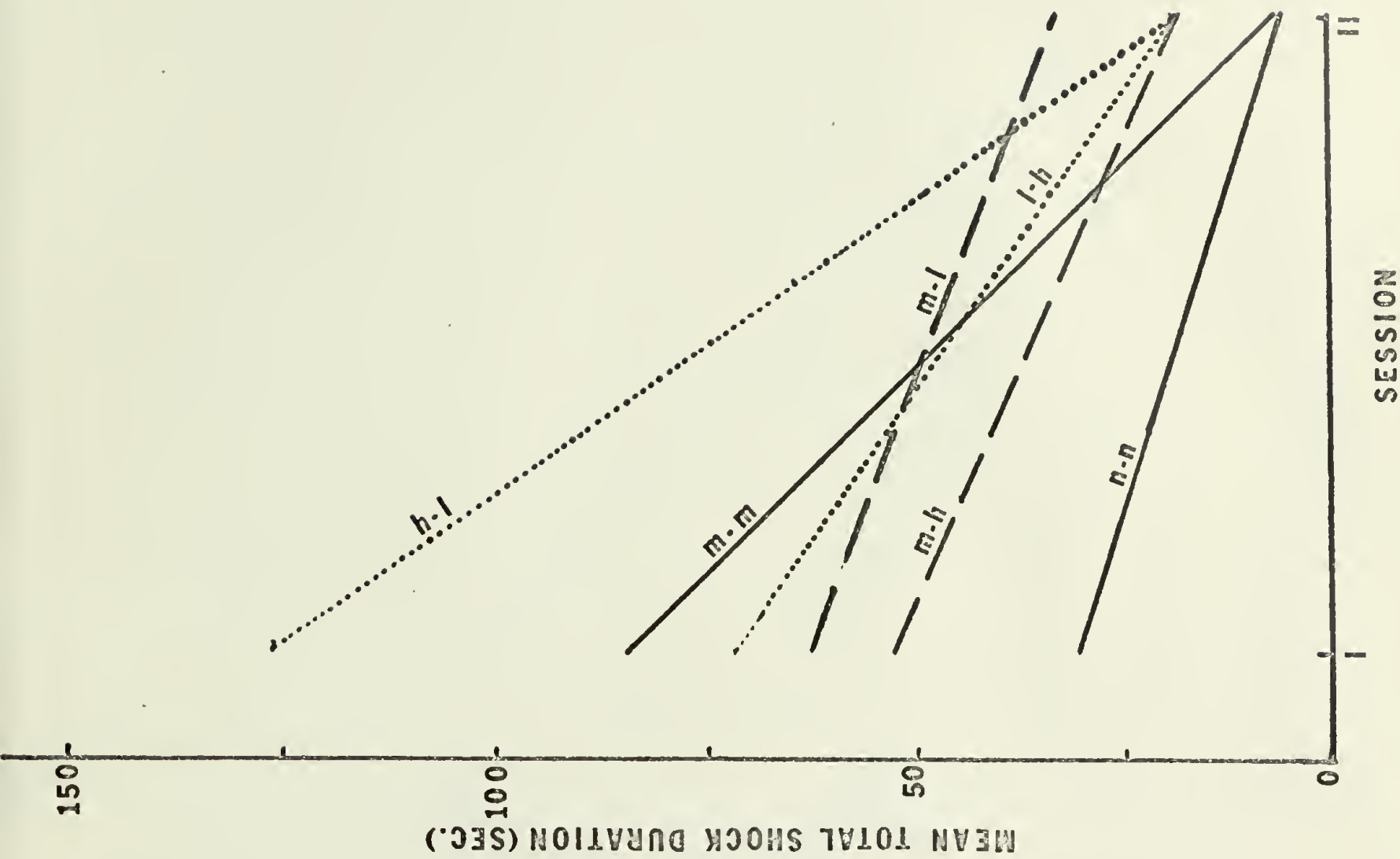


Fig. 5b. Mean total shock duration for criterion \bar{S}_s of each group of both experiments.

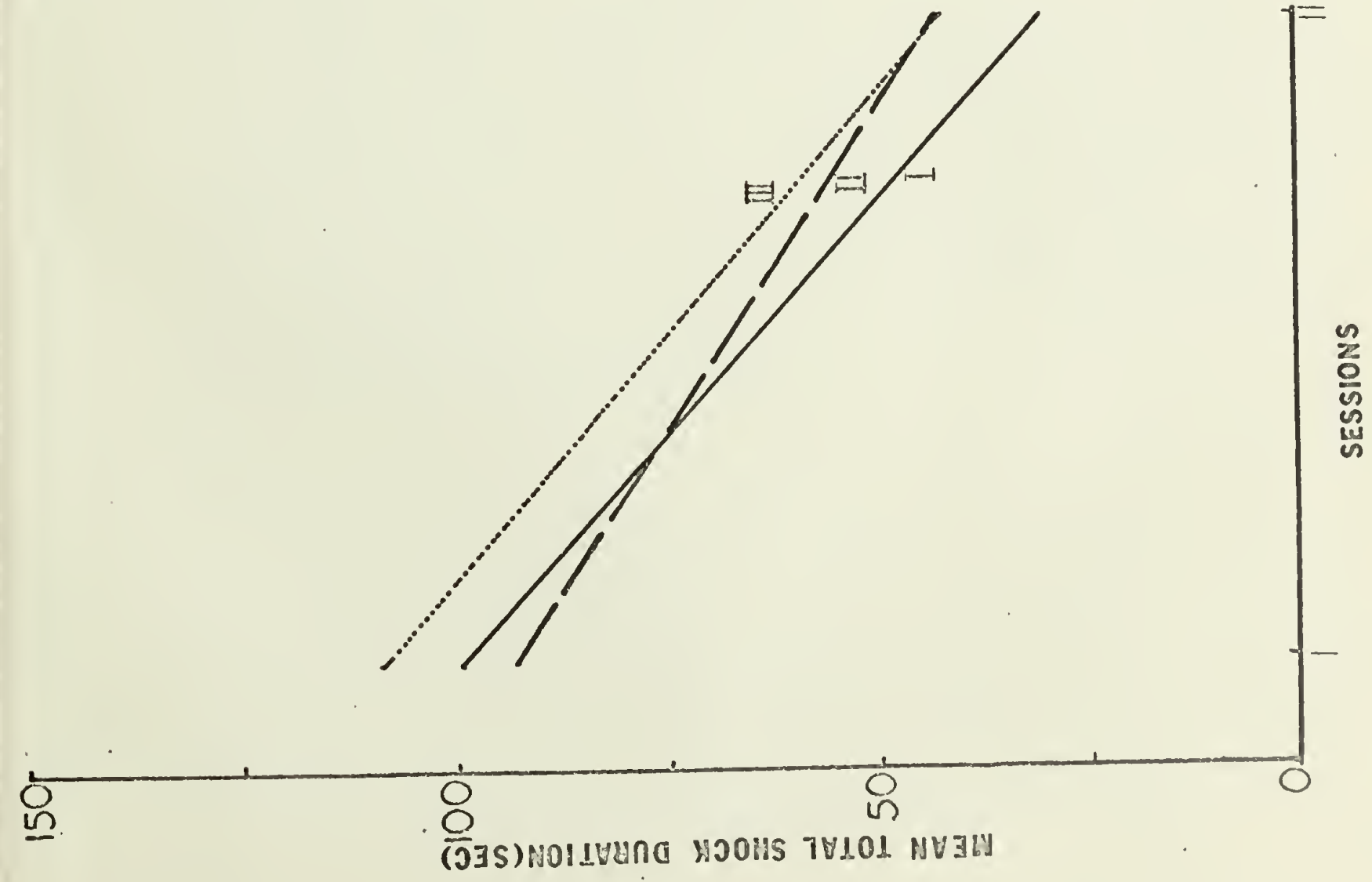


Fig. 6a. Mean total shock duration for all \bar{S}_s of each pooled group.

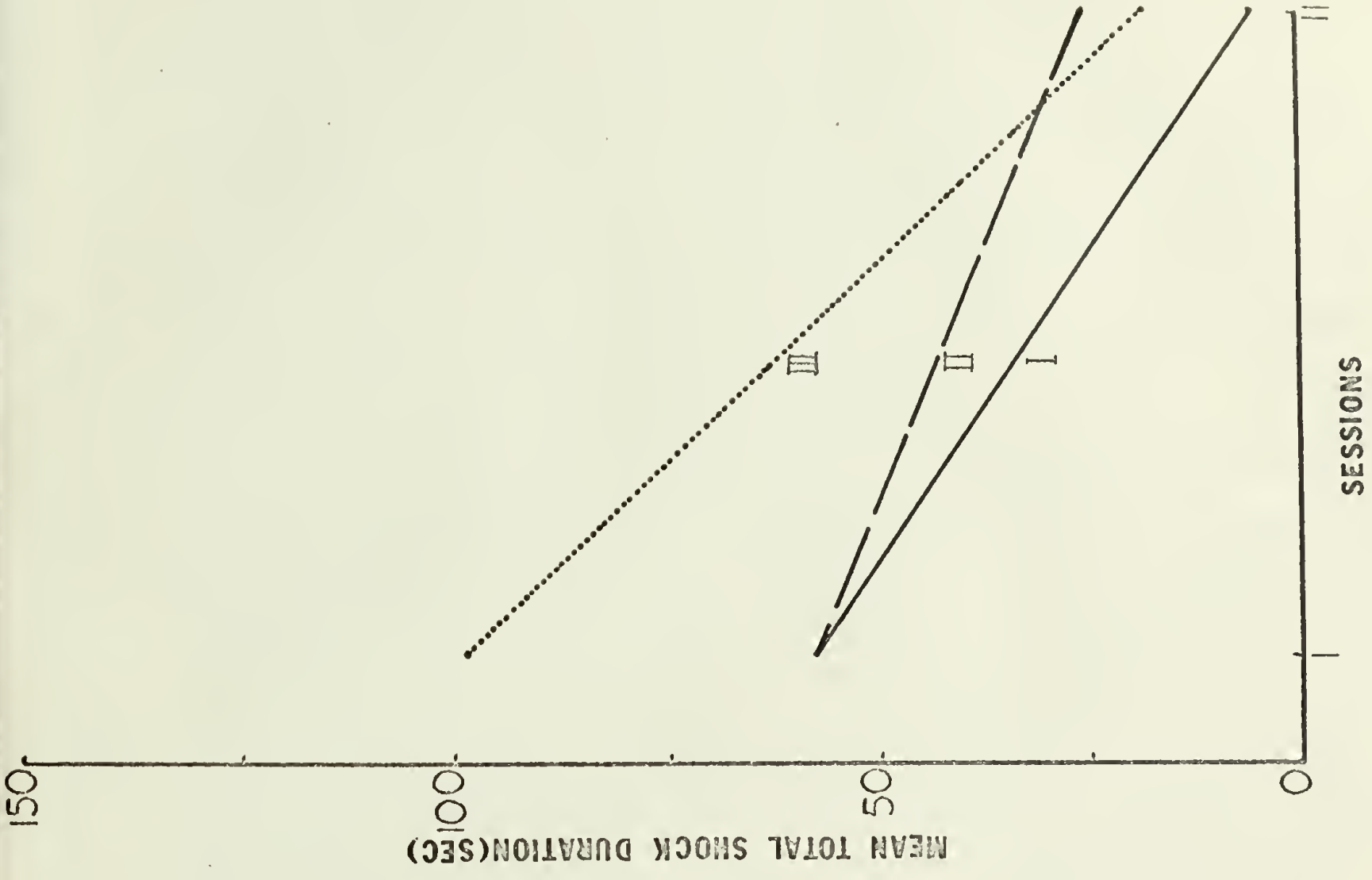


Fig. 6b. Mean total shock duration for criterion \bar{S}_s of each pooled group.

of KCl concentration shift was achieved by pooling groups. Thus a test was provided between pooled groups which differ only with respect to amount of SD change. The larger magnitude shift (group III) led to significantly poorer savings, even in terms of trials to criterion, than no SD change (group I). When shock durations were analyzed group I was also superior to the pooled group (II) undergoing slight concentration change.

One reasonable objection to this analysis is that it may be preferable not to include non-depressed (group N-N) Ss in group I. However, analysis of shock duration data indicates group M-M alone is still significantly superior to pooled group II ($U_{8,16} = 30, .01 < p < .025$) with all Ss included, and is superior both to group II ($U_{4,10} = 0, p < .001$) and to group III ($U_{4,8} = 1, p = .004$) when only criterion Ss are considered.

While the superiority of group III to II with respect to shock duration is not consistent with a stimulus generalization explanation, the KCl concentration effect on the H-L group provides a possible alternative explanation of this apparent contradiction.

GENERAL DISCUSSION

These experiments investigated the capacity of SD to function as a stimulus for avoidance conditioning without changing depressed structures from one session to the next. Since the same hemisphere was intact in both sessions no interruption of memory traces should apply to the results, nor is this experiment perceived as a direct test of the confinement-transfer hypothesis. However, the following conclusions would seem to be reasonably well supported by these experiments:

1. Unilateral application of KCl solutions to exposed cortex impair acquisition of an active avoidance task, and the degree of this impairment is proportional to the concentration of KCl used.
2. In these experiments the effect of KCl concentration apparently was overridden (except when contrasted with the sham depressed group) in the second session by the confounding of at least one other variable, i.e. inter session shift of KCl concentration.
3. By the second session of training a performance deficit occurred if KCl concentration was changed from that used in the first session, whether or not the simple concentration effect of this shift was detrimental to performance.

The most parsimonious assumption consistent with the last of these findings would seem to be that SD can function as a stimulus, per se.

Since the effectiveness of SD is graduated proportional to the concentration of KCl applied, the results also

contribute to the accumulating evidence that SD should be regarded as a graded partial cortical impairment rather than approximating a complete functional decortication. This concentration effect confirms similar results reported by Tapp (1962) and Bures, Buresova and Zahorova (1958).

The differences between the three groups receiving medium strength KCl on Day 1 indicate the variability of the effectiveness of a constant KCl concentration as an SD eliciting stimulus to induce cortical impairment to the same extent between animals. Marshall (1959) also reported considerable variability with respect to whether or not SD is elicited when the stimulus is constant.

The present experiments also confirm an earlier report by Kukleta (1967) that a response latency measure is apparently more sensitive to between group differences in an avoidance situation that is the trials to criterion measure. The requirement of a more sensitive measure in these experiments to detect significant differences is understandable since, as Schneider (1967) has implied, the most potent stimulus aspect of SD is probably its lateralization of motor paralysis and numbed senses. Since lateralization of effects of SD was not changed between sessions, the amount of stimulus change was considerably reduced.

Although the present experiments contribute further

indirect support to the stimulus generalization explanation of previous reports of hypothesized memory blocking manipulations, it cannot be interpreted as direct negation of the latter hypothesis. In fact, experiments performed by Ray and Emley (1964) and by Albert (1966a,b) have avoided the possibility of confounding SD with stimulus generalization by interrupting memory consolidation after learning has occurred rather than during its elaboration. Even Schneider (1967) acknowledges that "no complete answer can be given at the present time for the differential effects of immediate and delayed depression on retention (p. 204)." If interference with memory processes by SD remains as a key method of memory research then the relative contributions of stimulus change and memory disruption to performance decrements will have to be separately estimated and quantified.

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APPENDIX A

- i. Table 1. Trials to criterion for each subject of each group. Ss that failed to reach criterion in at least one session are indicated *.
- ii. Table 2. Shock duration data for each subject of each group. Non-criterion Ss are indicated *.

Group		S ₁	S ₂	S ₃	S ₄	S ₅	S ₆	S ₇	S ₈	$\bar{X}_{all \ Ss}$	$\bar{X}_{cr. \ Ss}$
N-N	Day 1	28	40*	21	40*	40*	9	11	8	24.6	15.4
	Day 2	6	40	8	6	22	6	1	10	12.4	6.2
	% Sav.	79	0	62	85	45	33	91	-20	46.9	49.0
M-M	Day 1	22*	40*	13	10	31	40*	7	40*	25.4	15.25
	Day 2	40	17	7	1	19	23	1	28	17.0	7.0
	% Sav.	-45	57.5	46	90	39	42.5	86	30	43.25	65.25
M-L	Day 1	2	18	27	35	4	40*	31	40*	24.6	19.5
	Day 2	26	7	15	6	9	35	17	40	19.4	13.3
	% Sav.	-92.3	61	44.4	82.9	-55.6	12.5	45.2	0	12.3	14.3
M-H	Day 1	10	9	40*	31	6	14	40*	40*	23.75	15.8
	Day 2	17	1	17	24	40	3	13	21	17.0	11.8
	% Sav.	-41.2	88.9	57.5	22.6	-85	78.6	67.5	47.5	29.6	37.2
H-L	Day 1	40*	21	25	21	17*	22			24.3	22.3
	Day 2	40	11	13	22	40	11			22.8	14.3
	% Sav.	0	47.6	48.0	-4.5	-57.5	50			13.9	35.3
L-H	Day 1	34	15*	16	9*	25	9			18.0	21
	Day 2	20	40	28	40	7	5			23.33	15
	% Sav.	41.2	-62.5	-42.9	-77.5	72	45.6			-4.0	29.0

TABLE 1

Group		S ₁	S ₂	S ₃	S ₄	S ₅	S ₆	S ₇	S ₈	\bar{X} all Ss	\bar{X} cr. Ss
N-N	Day 1	49.5	180.5*	42	82.5*	56.5*	20.5	26	17	59.3	31.0
	Day 2	30	98	9.0	4.0	23.0	11.0	2.0	5.0	19.4	6.0
	% Sav.	94.0	45.7	78.6	95.1	59.3	41.5	92.3	70.6	72.1	75.4
M-M	Day 1	91*	273*	127	30	154	164*	25	210*	138.3	84.0
	Day 2	55	47	7.0	2.0	15	179	1.0	57	45.4	6.3
	% Sav.	42.9	82.8	94.5	93.3	90.3	-8.4	96.0	72.9	70.5	93.5
M-L	Day 1	10	68	78	46	34	391*	141	90.5*	107.3	62.8
	Day 2	56	14	22	16	35	84	54	66	43.4	32.8
	% Sav.	-82.0	79.6	71.8	65.2	-2.3	78.5	61.7	27.1	37.45	32.3
M-H	Day 1	40	24	87*	109	44*	35	209.5*	95.5*	80.5	52.0
	Day 2	34	5	48	31	164	4	39	56	47.6	18.5
	% Sav.	15.0	79.2	44.8	71.6	-73.1	88.6	81.4	41.4	43.6	63.6
H-L	Day 1	298*	132	227	68	126*	77.5			154.8	126.1
	Day 2	66	19	31	18	71	6			35.2	18.5
	% Sav.	77.9	85.6	87.3	73.5	43.7	92.3			76.7	84.7
L-H	Day 1	121	53.5*	62	40.5*	71	32.5			63.4	71.6
	Day 2	22	38	17	198	8	25			50.5	18.0
	% Sav.	83.4	29.0	72.6	-79.6	88.7	33.1			37.9	69.5

TABLE 2

TABLE 1

Probabilities associated with differences of trials to criterion between groups by Mann-Whitney U test for superiority of savings of a row group over a column group for all Ss.

	N-N	M-M	M-H	M-L	H-L	L-H
N-N		.439	.323	.117	.114	.071
M-M			.480	.164	.207	.114
M-H				.191	.207	.141
M-L					.475	.377
H-L						.242
L-H						

TABLE 2

Probabilities associated with differences of trials to criterion between groups by Mann-Whitney U tests for superiority of savings of a row group over a column group for criterion Ss.

	N-N	M-M	M-H	M-L	H-L	L-H
N-N			.365	.214	.278	.278
M-M	.365		.243	.129	.343	.171
M-H				.305	.443	.343
M-L						
H-L				.381		.343
L-H				.457		

TABLE 3

Probabilities associated with a Mann-Whitney U test for superiority of savings of a row group over a column group for all Ss, using shock duration data. * indicates ($.25 < p < .5$)

	N-N	M-M	M-L	M-H	H-L	L-H
N-N			.097	.117	*	.114
M-M	*		.032	.052		.071
M-L						
M-H			*			*
H-L		*	.03	.041		.09
L-H			*			

TABLE 4

Probabilities associated with a Mann-Whitney U test for superiority of savings of a row group over a column group for criterion Ss only, using shock duration data. * indicates $.25 < p < .5$.

	N-N	M-M	M-L	M-H	H-L	L-H
N-N			.089	.123	*	*
M-M	.056		.01	.01	.029	.014
M-L						
M-H			.176			
H-L			.019	.171		.171
L-H			.129	*		

TABLE 5

Probabilities associated with a Mann-Whitney U test for superiority of savings of a row group over a column group when groups have been pooled according to amount of SD change. Shock duration data used. $I=(N-N)+(M-M)$, $II=(M-H)+(M-L)$, $III=(L-H)+(H-L)$.

	All <u>Ss</u>			Criterion <u>Ss</u>		
	I	II	III	I	II	III
I		.05	N.S.		.01	.05
II			N.S.			
III					.05	

