THE EFFECT OF BAR HOLDING TRAINING ON SUBSEQUENT SHOCK ESCAPE BEHAVIOR UNDER DIFFERENT SHOCK INTENSITIES IN RATS WITH SEPTAL LESIONS

by

John W. Moore

A.A., Christopher Newport College, 1968

B.S., Old Dominion University, 1969

ABSTRACT OF THESIS

Submitted in partial fulfillment
of the requirements for the degree
of Master of Arts in Psychology in
the Graduate School of Morehead
State University

July, 1974

The purpose of this study was to evaluate the effect of bar holding training on shock escape performance in rats with septal lesions. During the bar holding training period, the subjects learned to keep the bar depressed to avoid shock. The training period was used in an attempt to control for septal inability to remain near the bar in shock escape. Although septals were able to learn the task to a criterion, their retention of bar holding ability was significantly below control retention. During the shock escape portion of the experiment, the septal animals held the bar as much or more than controls, but septal speed in escaping shock was significantly inferior to control speed. During the last three days of shock escape an additional variable of different shock levels was introduced to determine if altered sensitivity to shock was a factor in septal performance. There were no effects attributable to varied shock intensity. It was concluded that inability to remain near the bar is a factor in septal performance on shock escape, but other factors affecting performance have not been isolated.

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Accepted by the faculty of the School of Education, Morehead State University, in partial fulfillment of the requirements for the Master of Arts degree.

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Director of Thesis

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July 23, 1974
(date)

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

APPENDIX

Table | Page

INTRODUCTION

The limbic system is a portion of the brain which includes the amygdala, hippocampus, hypothalamus, cingulate gyrus, and septum. The limbic system as a whole is important in emotional behavior, but isolating the influence of any single structure is difficult because the parts are all interconnected. Research into the specific functions of the septal area began with the work of Brady and Nauta (1953). They destroyed the septum in rats and found hyperemotionality and a change in the conditioned emotional response. McCleary (1961) found differences in passive and active avoidance behavior which seemed to indicate a loss of inhibition after septal destruction. Using evidence gathered from a number of studies, McCleary (1966) formulated the disinhibition hypothesis. He maintained that the septal area normally functions to inhibit behavior. The effect of septal lesions is explained by hypothesizing a removal of the normal inhibitory mechanism which results in disinhibition of responding.

Experiments involving appetitive reinforcement appear to substantiate the disinhibition hypothesis. Septal animals generally respond at higher rates for appetitive reinforcement. Harvey and Hunt (1965) found that septal animals exhibit higher rates of bar pressing on a fixed interval reinforcement schedule. On a fixed ratio schedule, septals will maintain higher ratios than controls to receive reinforcement

(Buckland & Schwartzbaum, 1970). Hothershall, Johnson, and Collen (1970) found that septal animals could maintain a mean fixed ratio schedule of 627 while controls were able to achieve a mean of 123. Appetitive reinforcement is given to an animal on a differential reinforcement of low response rates (DRL) schedule only after he has withheld his response for a specific time interval since his last response. Septals demonstrate higher response rates on the DRL schedule and do not receive as many reinforcements as controls (Ellen & Aitken, 1971). Since it is necessary to inhibit responding for a specific time period, septals are inferior on the DRL task. Septal animals also exhibit higher response rates in extinction (Schwartzbaum, Kellicut, Spieth, & Thompson, 1964). If one assumes that a normal animal develops inhibition during extinction which slows his responding, higher septal response rates could be the result of a loss of inhibition.

Further evidence supporting McCleary's hypothesis comes from passive avoidance and certain active avoidance experiments. In passive avoidance experiments the animal must learn to inhibit a response that was previously rewarding in order to avoid punishment. A typical experiment would involve training the animal to eat or drink from a metal cup. During the passive phase of the experiment the cup is electrified. A normal animal will learn to passively avoid by withholding his response after only one shock trial, but septals show a severe decrement in passive avoidance (Kaada, Rasmussen, & Kviem, 1962) and keep returning to receive the shock. Slotnick and Jarvik (1966) devised an experiment in which mice were required to suppress activity to avoid shock. Septal mice were unable to learn to suppress their activity and continued receiving shocks. Septal behavior in passive avoidance indicates an inability to inhibit a response and substantiates the disinhibition hypothesis. Two-way active, or shuttle, avoidance uses two shock chambers. A discriminative stimulus is used as a signal that shock is about to begin. In order to avoid shock, the animal must run to the opposite box. Since shock alternates between the two boxes, the animal "shuttles" between the chambers to avoid being shocked. In two-way active avoidance experiments septal animals are superior to controls in avoiding shock (Schwartzbaum, Green, Beatty, & Thompson, 1967; Kenyon & Krieckhaus, 1965b). Unlike passive avoidance, effective responding in the two-way active avoidance situation does not require inhibition of a previously rewarded response, but disinhibition of the freezing response. Unlike some normal animals who may crouch or freeze to avoid returning to the compartment where they have just been shocked, septal animals run to the safe side almost immediately (Kenyon & Krieckhaus, 1965b). The disinhibition of responding predicted by McCleary's hypothesis seems to be substantiated by septal performance on two-way active avoidance.

While the findings from passive and two-way active avoidance seem to substantiate McCleary's hypothesis, there are other experiments which seem to refute, or at least cast doubt upon, disinhibition in septal responding. In one-way active avoidance, as in two-way active avoidance, two boxes are used. One box is always used to shock the animal and the other box is always shock free. To effectively avoid shock the animal should run to the safe box as soon as possible. Septals do not avoid the shock as well as controls in one-way active avoidance (Kenyon & Krieckhaus, 1965a). Zucker (1965) believed that the factor of handling the animals between trials may have been responsible for the poor performance of septals. The usual method for beginning a new trial in one-way active avoidance is lifting the animal from the "safe" box and placing him back into the start box. Zucker varied the procedure by devising an experiment in which the animals were never handled when being placed back into the start box and found that septals actually learned the correct response more quickly than controls. Zucker's arrangement suggests that septal performance in previous one-way active avoidance studies may have been influenced by differential responses to handling. Another experimental procedure which seems to provide evidence contradictory to the disinhibition hypothesis is Sidman avoidance (Sidman, 1953). In Sidman avoidance failure to make the correct response puts the animal on a preset shock-shock interval. If the animal does make the correct response, shock is delayed by a preset response-shock interval. The most efficient behavior is making the correct response just before the shock is to begin. Experiments have shown that septals minimize shock with fewer presses than controls (Morgan & Mitchell, 1969; Sodetz, 1970). Septal performance in Sidman avoidance provides the disinhibition hypothesis with a problem since one would expect more presses from septals if responding were disinhibited.

Disinhibition of responding in septal lesions would indicate that septals might perform well in a shock escape experiment. In a shock escape task the animal must perform a response, such as pressing a bar, to terminate shock. Escape differs from avoidance in that the animal cannot stay away from the shock entirely in the escape situation. Gotsick, Osborne, Allen, and Hines (1971) found that septals were inferior to controls in a shock escape task. However, the poor septal performance was not viewed as disproving the disinhibition hypothesis. It was noted that septal rats did not remain near the bar during the intertrial interval. This observation is consistent with findings of higher intertrial activity by septals in other shock situations (Dalby, 1970; Lubar, Brener, Deagle, Numan, & Clemens, 1970). Inferior performance by septals in shock escape might involve two factors. Heightened intertrial interval activity may be preventing the septal animals from staying near the bar. Even when septals are near the bar there is still a possibility that they are at a disadvantage because they may be more sensitive to shock. Lints and Harvey (1969) found that septal animals are more sensitive to shock than controls. However, the Lubar, et al. study found no differences between septals and controls in detection threshold for shock.

The first phase of the present experiment attempted to control for septal failure to remain near the bar. The subjects were trained to avoid shock by keeping the bar depressed. Migler (1963) has shown that rats will stay on the bar for longer periods of time if the shock escape situation is changed from the usual bar press method. He trained one group of rats to press the bar to escape shock and another group to escape by releasing the bar. The group which had been trained to escape by releasing the bar displayed more bar holding behavior. Dinsmoor and Hughes (1956) trained their rats to escape shock and observed that some of the _Ss_ kept the bar depressed throughout the intertrial interval. They did not require the animals to release the bar to escape shock, so the animals could press the bar and remain on it without being shocked.

After the bar holding training portion of the experiment was completed, the effects of the training were observed on shock escape behavior. It was expected that bar holding training would facilitate shock escape performance by keeping the *Ss* nearer the bar during the intertrial interval. The purpose of the experiment was to investigate the effect of bar holding training on subsequent shock escape behavior. A second factor was whether or not altered sensitivity to shock was having an effect on septal performance. If these two factors were influencing septal performance, shock escape behavior could be interpreted as being supportive of the disinhibition hypothesis.

METHOD

Subjects - The subjects were 33 male albino rats of the Wistar strain weighing 250-300 g. at the beginning of the experiment. The animals were randomly divided into a control group containing 16 Ss and an experimental group with 17 Ss. They were housed in individual cages and given ad lib food and water throughout the experiment.

Apparatus - All phases of the experiment were conducted in two Grason-Stadler operant conditioning chambers (GSC 1101) housed in sound attenuating chambers. Conditions were controlled by electromechanical programming equipment. Grason-Stadler shock generators (700) were used to deliver a constant current shock to the grid floor of the operant conditioning chambers. The latencies were timed by two General Radio Counters (1191-B) and the data were printed by General Radio data printers (1137-A).

Procedure - The experimental animals received lesions of the septal area while under ether anesthesia and the unoperated control group was placed in the stereotaxic instrument (Krieg Model #51200) and their scalps were incised while under ether anesthesia. The septal lesions were produced by passing a 3.0 mA d.c. current of 20 sec duration between a nichrome electrode, insulated except for 0.5 mm at the tip, and a rectal electrode. The lesions were placed bilaterally and at a depth of 5.0 and 5.5 mm below the surface of the brain. At the conclusion of the experiment, lesioned Ss were sacrificed, perfused intracardially with physiological saline and a 10% formalin solution and the brains were examined for damage to the septal area.

Training began two weeks after surgery. In the bar holding part of the experiment, the S was placed in the chamber in a shock free situation for one minute. After this initial minute, the animal received a 1 mA footshock which could be terminated by a bar press. Once the bar was pressed, shock was immediately terminated. As long as the bar remained depressed, the box remained shock free, but when the animal released the bar, shock began 3 sec later. The Ss were run for one session daily with a session consisting of the one minute shock free period plus 15 min of bar holding training. Measures taken during the bar holding phase of the experiment were total bar time (number of sec S kept the bar depressed during a session) and number of bar presses.

When an S held the bar 80% (720 sec) of the time during a session, he was considered to have reached criterion. Once an animal reached criterion, he was returned to his cage after completing the session and was not run again until the two day retention sessions. After 11 days of training, 16 controls and 13 septals had reached criterion. The 4 septals who were unable to reach criterion were excluded from the remainder of the experiment.

The 29 remaining Ss were again run on bar holding for two days to check for retention of the behavior. Conditions during this segment were identical to the original bar holding sessions.

On the day following the last bar holding session, the shock escape portion of the experiment began. To begin a trial in shock escape, the animal was placed in the chamber in a shock free situation for one minute. After the initial minute, the animal received a 1 mA footshock which continued until he pressed the bar. The chamber was then shock free for a 60 sec intertrial interval. Holding the bar during the intertrial interval had no effect on the shock-shock interval. There was one session daily for three days, with each session consisting of 10 trials. If the animal failed to press the bar within 5 minutes, the trial was terminated and the shock free intertrial interval began. Measures taken during the shock escape portion were: 1) latency to the bar to the nearest 0.001 sec, 2) number of bar presses, and 3) bar time to the nearest 0.1 sec.

Based on a comparison of their performance on shock escape, the two groups of animals were separated into two groups of septals and two control groups. Subjects were matched on the basis of their speed scores. The speed scores were calculated by taking the reciprocal of (latency + 1) for each animal on the third day of shock escape. The reciprocal of (latency + 1) is called a speed score because the higher the score, the faster the animal pressed the bar once shock began. The mean reciprocal of (latency + 1) for the four groups was the following: .5815 for the 8 Ss in the 1.0 mA control group, .5825 for the 8 Ss in the 0.6 mA control group, .4961 for the 6 Ss in the 1.0 mA septal group, and .4937 for the 7 Ss in the 0.6 mA septal group. This portion of the experiment involved a shock escape task identical to the one previously described with the exception that one septal group received a 1.0 mA footshock while the other received 0.6 mA and one control group received 1.0 mA while the other received 0.6 mA. The choice of assigning the 0.6 mA or 1.0 mA condition was decided by a coin toss.

RESULTS[1]

In all of the subjects there was bilateral destruction of the medial and lateral septal nuclei. The lesions were bounded laterally by the lateral ventricles and dorsally by the corpus callosum. On one subject there was slight damage to the corpus callosum. Although some of the lesions extended ventrally to the anterior commissure, they were generally slightly high and left some of the area above the anterior commissure intact. None of the lesions extended anteriorally beyond the genu of the corpus callosum or posteriorally beyond the columns of the fornix.

Figure 1 illustrates the mean percentage of bar holding time for the criterion day and the two days of retention training. An indépendent $\underline{t}$ test was performed on bar holding time in seconds for the last day of the retention session. The controls held the bar for a significantly longer time than the septals ($\underline{t} = 2.461$, $\underline{df} = 26$, $p < .05$).

Figure 2 shows the mean bar holding time in seconds during the six days of shock escape. The first three days compare septal and control performance, while the last three days compare performance for the four conditions of 0.6 mA septal, 1.0 mA septal, 0.6 mA control, and 1.0 mA control

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[1] Individual scores can be found in Appendix A. Summaries of the analyses of variance used to evaluate the data can be found in Appendix B.

Figure 1. Mean percent of bar holding time for the criterion day and the two retention days.

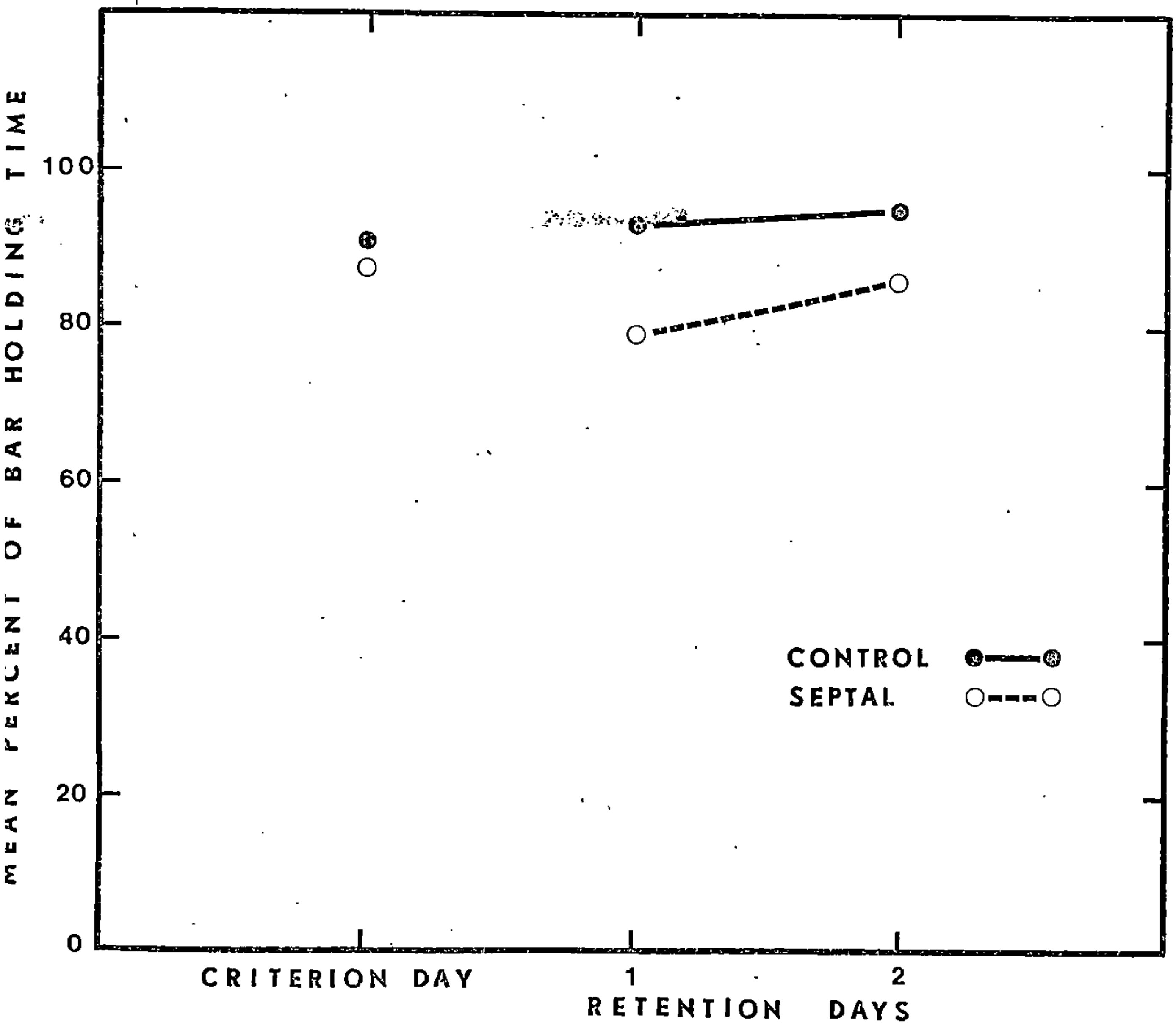
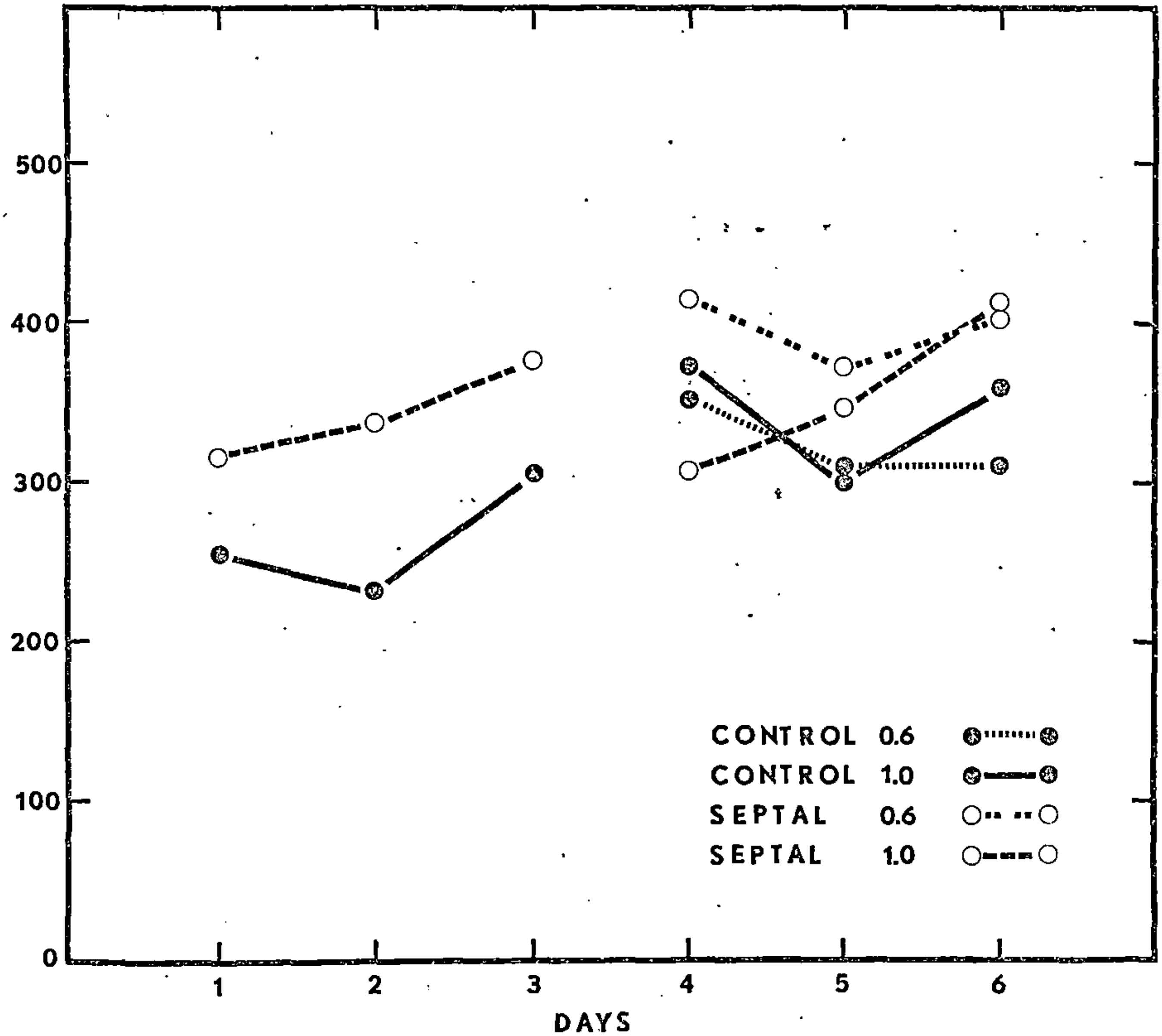

MEAN PERCENT OF BAR HOLDING TIME
100
80
60
40
20
0
CONTROL
SEPTAL
CRITERION DAY
1
2
RETENTION DAYS

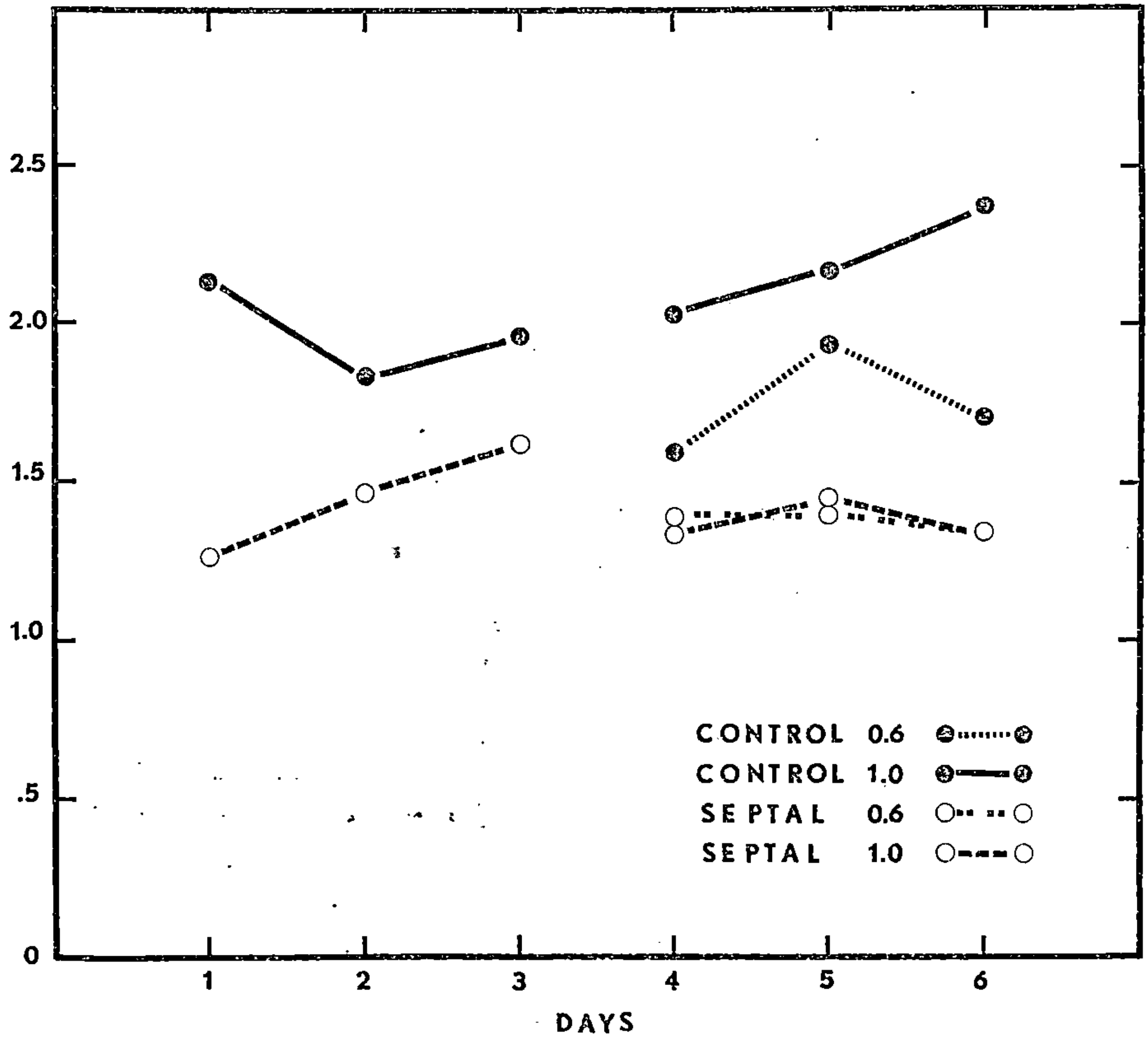
Figure 2. Mean bar holding time in seconds for all groups during the 6 days of shock escape.


500
400
300
200
100
0
1
2
3
4
5
6
DAYS
CONTROL 0.6
CONTROL 1.0
SEPTAL 0.6
SEPTAL 1.0

groups. A one between and one within analysis of variance for the first three days of shock escape yielded the following for bar holding: the septals held the bar for a significantly longer time period than the controls (F = 10.37, df = 1/27. $p<.01$), both groups increased their bar holding over days (F = 3.40, df = 2/54, $p<.05$), and there was no groups by days interaction ($F<1.00$). A two between and one within analysis of variance was used to evaluate the last three days of bar holding. The between groups factors evaluated the differences between septal and control and the 1.0 mA and 0.6 mA shock conditions. There were no significant differences between the main effects or for interactions (all $p>.10$).

Figure 3 illustrates the mean reciprocal of latency (1/latency) scores for the 6 days of shock escape. This score can be viewed as a "speed" score because the greater the speed with which the subject pressed the bar once the shock began, the higher the score. The reciprocal of latency scores diminish the effects of subjects with long latencies. A one between and one within analysis of variance was performed on the first three days of shock escape. The control group was significantly faster than the septal group (F = 6.44, df = 1/27, $p<.05$), there was no days effect ($F<1.00$), nor was there a significant groups by days interaction (F = 2.72, df = 2/54, $.05<p<.10$). A two between and one within analysis of variance was performed on the last three days of shock

Figure 3. Mean reciprocal of latency for all groups during the 6 days of shock escape.


2.5
2.0
1.5
1.0
.5
0
1
2
3
4
5
6
DAYS
CONTROL 0.6
CONTROL 1.0
SEPTAL 0.6
SEPTAL 1.0

escape and gave the following results: the controls had significantly faster scores than the septals ($F = 5.80$, $df = 1/25$, $p < .05$), there were no significant differences for the two shock conditions, the days factor, or for any interactions (all $p > .10$). Another method for evaluating speed of responding is reciprocal of (latency + 1) scores. Adding 1.0 to the latency before taking the reciprocal has the effect of lessening the influence of subjects with extremely short latencies. Figure 4 shows the mean 1/(latency + 1) scores for the six days of shock escape. A one between and one within analysis of variance was used to evaluate the first three days of shock escape and it was found that controls were significantly faster than septals ($F = 9.17$, $df = 1/27$, $p < .01$), there was no days effect ($F = 1.51$, $df = 2/54$, $p > .10$), or groups by days interaction ($F = 2.89$, $df = 2/54$, $.05 < p < .10$). A two between and one within analysis of variance was used to evaluate the last three days of shock escape. The controls were superior to the septals ($F = 6.72$, $df = 1/25$, $p < .05$). There were no significant differences for the shock conditions, the days factor, or any interactions (all $p > .10$).

The eight septals who reached criterion on the second day of bar holding training were designated good bar holders while the five who reached criterion on subsequent days were designated poor bar holders (Table 6). Figure 5 shows the mean bar holding time for good and poor bar holders during

Figure 4. Mean reciprocal of (latency + 1) for all groups during the 6 days of shock escape.

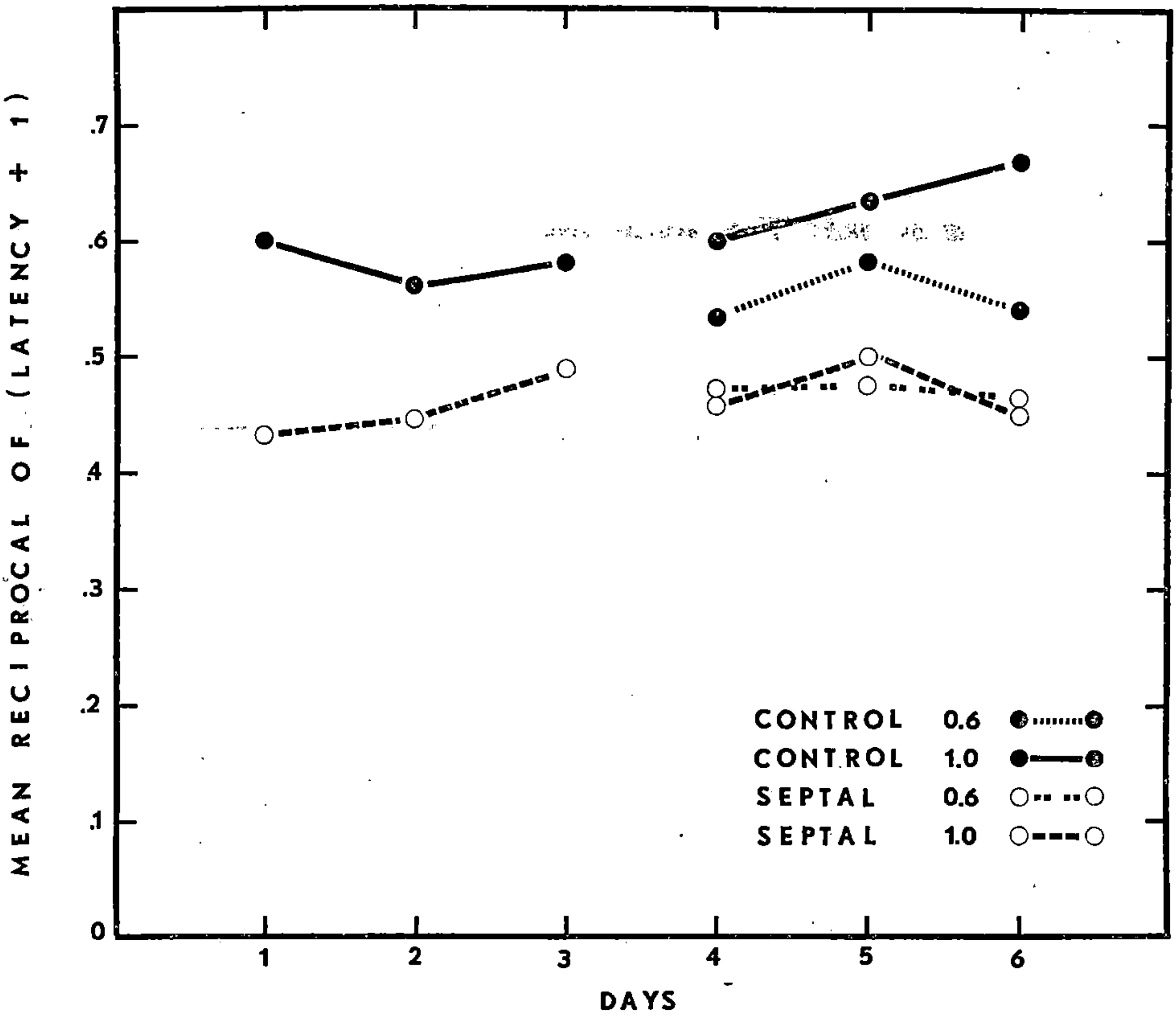
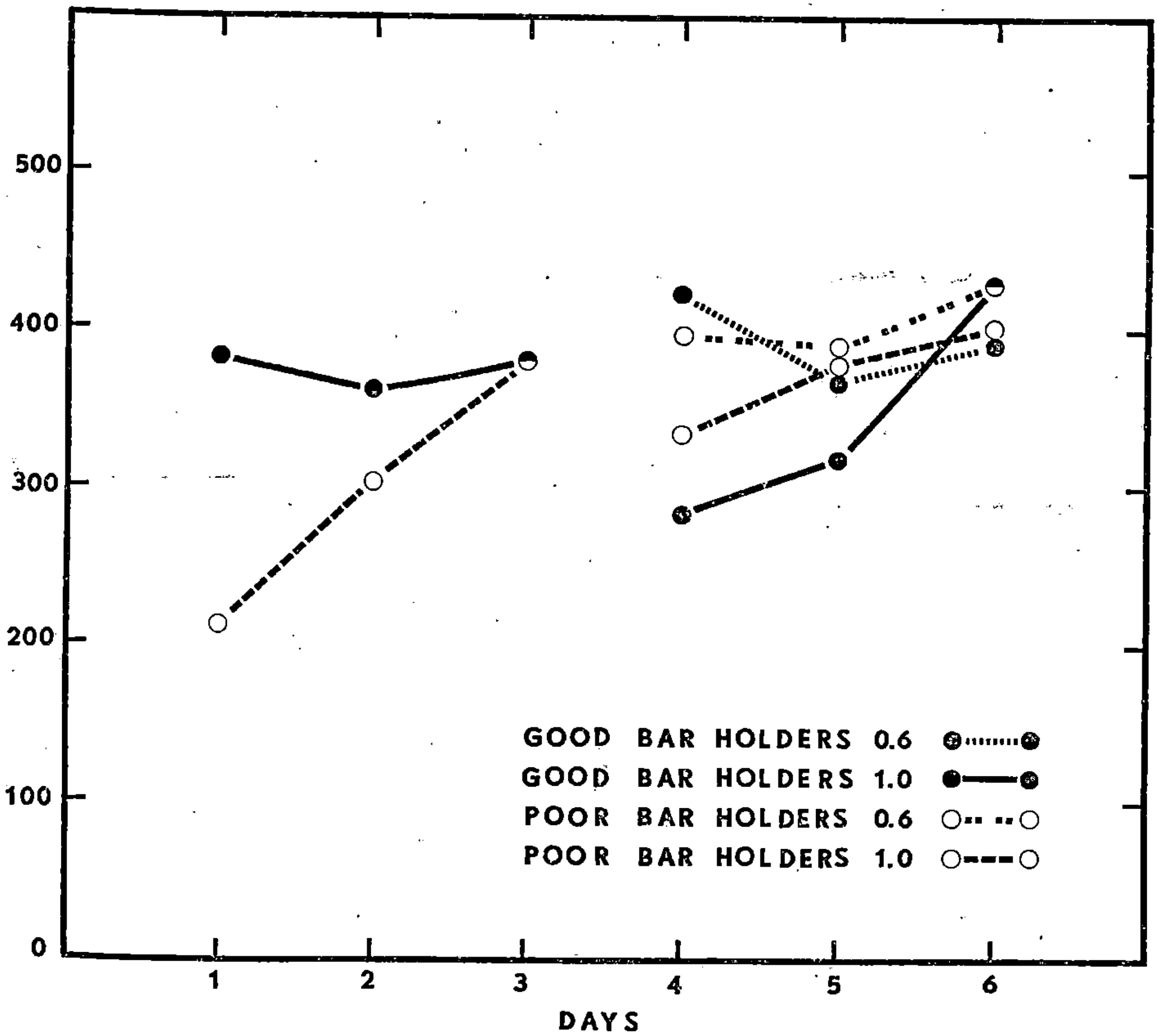

MEAN RECIPROCAL OF (LATENCY + 1)
0
.1
.2
.3
.4
.5
.6
.7
1
2
3
4
5
6
DAYS
CONTROL 0.6
CONTROL 1.0
SEPTAL 0.6
SEPTAL 1.0

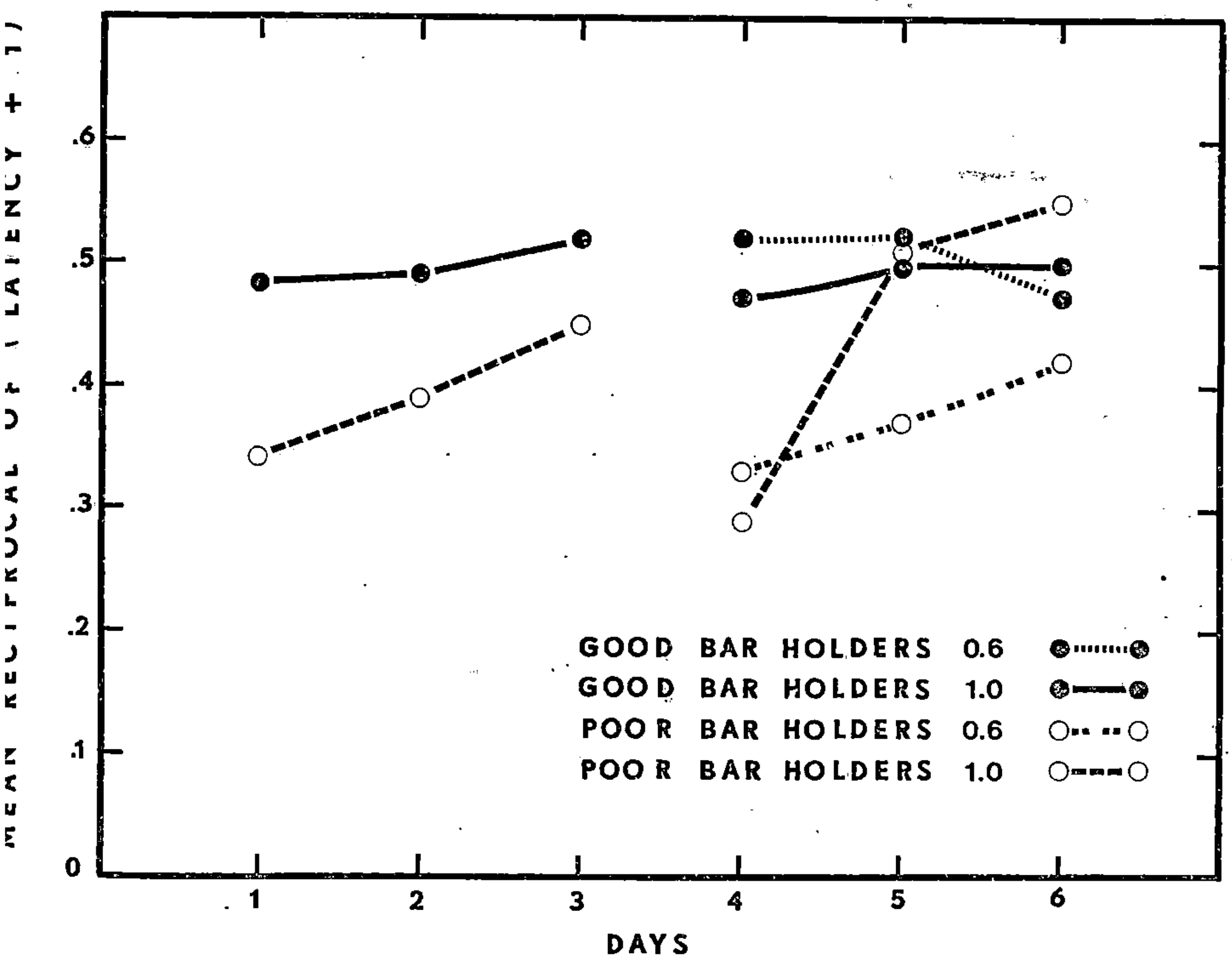
Figure 5. Mean bar holding time during shock escape for septals who were good and poor bar holders during bar holding training.


500
400
300
200
100
0
1
2
3
4
5
6
DAYS
GOOD BAR HOLDERS 0.6
GOOD BAR HOLDERS 1.0
POOR BAR HOLDERS 0.6
POOR BAR HOLDERS 1.0

the six days of shock escape. A one between and one within analysis of variance was performed on the bar holding times for both groups for the first three days. The good bar holders held the bar for a significantly longer period of time than the poor holders ($F = 5.20$, $df = 1/11$, $p < .05$), there were no significant differences for days, and there was no interaction (all $p > .10$). A two between and one within analysis of variance was used to evaluate the last three days of shock escape. The between factors were good and poor bar holders and 0.6 and 1.0 mA shock factors. There were no significant main effects or interactions (all $p > .10$).

Figure 6 represents the mean reciprocal of (latency + 1) scores for good and poor bar holders during the six days of shock escape. A one between and one within analysis of variance yielded the following for the first three days: there were no significant differences for groups, the days factor, or interaction (all $p > .10$). A two between and one within analysis of variance was performed on the last three days. There were no significant differences for group effects or days (all $F < 1.00$), days by bar holding ability interaction ($F = 3.19$, $df = 2/18$, $.05 < p < .10$), or days by shock condition interaction ($F = 1.31$, $df = 2/18$, $p > .10$). There was a significant difference for days by bar holding ability by shock condition interaction ($F = 4.00$, $df = 2/18$, $p < .05$). This indicates that the effect of bar holding ability on performance over days is dependent on the shock level.

Figure 6. Mean reciprocal of (latency + 1) during shock escape for septals who were good and poor bar holders during bar holding training.



MEAN RECIPROCAL OF (LATENCY + 1)
.6
.5
.4
.3
.2
.1
0
1
2
3
4
5
6
DAYS
GOOD BAR HOLDERS 0.6
GOOD BAR HOLDERS 1.0
POOR BAR HOLDERS 0.6
POOR BAR HOLDERS 1.0

DISCUSSION

One of the problems affecting septal behavior in previous shock escape studies was the inability to remain near the bar during the intertrial interval. The Gotsick, et al. study (1971) suggested that septals were not as likely to remain as near the bar during the intertrial interval as the controls. In the present experiment septals were able to learn bar holding to a criterion, but showed significantly less retention of this behavior than controls on the last day of the retention training. This would seem to indicate that septals could not retain the ability to stay near the bar. However, during shock escape there was a reversal of bar holding behavior on the first three days with septals holding significantly longer than controls. The last three days of shock escape show no significant differences, but the septals were still holding longer. Bar training does help alleviate the problem of septal inability to remain near the bar during the intertrial interval. If failure to remain near the bar was the only reason for poor septal performance, the bar holding task should result in septal performance which is comparable to that achieved by the controls.

The speed scores for septals and controls show that the bar holding task did increase septal performance in comparison to the Gotsick, et al. study, but septal scores were still significantly below controls. The control animals in the Gotsick, et al. study started with low speed scores and increased their performance until the fifth day. In the present study the controls maintained about the same level of responding throughout the six days of shock escape. This indicates that bar holding training is isolating some factor that is related to efficient shock escape behavior. The septals in the present study had a mean reciprocal of latency on their first day of shock escape that was 200% higher than the Gotsick, et al. septals had on their last day. The bar holding training resulted in improvement of both control and septal performance on their first exposure to shock escape.

There may be two factors involved in the superior responding on shock escape by animals who have received bar holding training. Bar holding may simply teach the animals that a bar press will eliminate shock. On the other hand, bar holding may not only teach the <u>Ss</u> a method for the elimination of shock, but it may also serve to keep the animals nearer the bar during the intertrial interval. The second explanation seems more plausible when one considers that most of the controls (12 out of 16) had only two days of bar holding training, yet their first day's shock escape performance was comparable to their responding during the rest of the experiment. The bar holding training probably had a twofold effect on subsequent shock escape. The animals learned that the bar turned off shock, and they learned to stay near the bar during the intertrial interval. It should be noted that although the Gotsick, et al. experiment was also a shock escape task, the intertrial interval was 90 sec as compared to 60 sec in the present study. The difference in intertrial interval may have been a factor in the performance differences. With the 60 sec intertrial interval in the present study, the subjects did not have as much time to stray from the bar. The additional 30 sec in the intertrial interval may have been responsible for septal inability to remain near the bar in the Gotsick, et al. study.

Even though septals in the present experiment performed better than septals in earlier studies, the fact remains that septal responding is still inferior to control. To investigate whether or not there was a relationship between performance in the training period and in shock escape, the septals were divided into a poor bar holding and a good bar holding group. The good bar holders had reached criterion on the second day of bar holding training, while the poor bar holders reached criterion on days 3 through 8. On the first day of shock escape (Fig. 5), the poor holders were well below the good bar holders in time on the bar. By the third day there was no difference between the two groups and there were no significant differences for the four groups during the last three days. This indicates that even septals who are unable to learn the bar task quickly will develop bar holding behavior during shock escape. The speed scores (Fig. 6) are similar to the bar holding scores for the first three days with the poor holders being below the good holders. The difference between the groups, however, was not significant. The only significant difference for the last three days was an interaction of bar holding ability and shock level over days. It appears that the speed with which a septal learns to bar hold bears no consistent relationship to his performance in subsequent shock escape.

The 0.6 mA and 1.0 mA conditions were used during the last three days of shock escape to see if altered sensitivity to footshock might be having an adverse influence on septal behavior. The differences in shock intensity had no significant effect on septal or control behavior. There may be several reasons why no differences existed. The difference between the two shock intensities may not have been of a great enough magnitude to isolate the effect of altered sensitivity. Since both sets of animals were responding to shock quickly (average mean time was less than one second on all days for all groups), they may not have discriminated the change.

There is also a possibility that a factor is influencing behavior in shock escape that has not been isolated. Although the septals held the bar as much as the controls, they may have strayed further from the bar during the time they were off the bar. This possibility would bring the results of the present experiment in line with the disinhibition hypothesis. The normal inhibitory forces which would serve to keep the animal in the vicinity of the bar may be absent after septal lesions.

The behavior which was useful during the bar holding portion may have been maladaptive during shock escape. Based on the mean percent bar holding time on the first day of shock escape as compared with the last day of bar holding training, the septals held the bar for 33% less time and the controls for 52% less time. This indicates that the controls were able to efficiently escape shock without relying on bar holding as much. It is easier to stay over the bar and press immediately upon shock onset than to remain on the bar, raise up, and then press when shock begins. The superior control performance may have been due to septal inability to discover a better method for escaping shock once they had been trained to hold the bar.

It is not possible from the results of the present experiment to determine how much of an improvement bar holding made in speed scores over what would normally be expected. The only available comparison was with the Gotsick, et al. experiment. To directly measure the effect of bar holding training it would be necessary to have a septal and control group who received no training, but were exposed to the same shocks as the groups who were trained. It would be possible to see the relative influences of bar holding on the different groups and determine if there may be different effects on septal and control behavior.

Septal performance in shock escape seems to be affected by several variables. Without prior training septals will not remain near the bar during the intertrial interval. With bar holding training they can be taught to stay on the bar for longer periods of time, but there is still a possibility that they do not stay near the bar when they are not holding. Although the effect was not seen in the present experiment, septals may be more sensitive to footshock than controls. The hypothesized influences can all be viewed as examples of disinhibition of responding. The results of the present experiment indicate that septal inability to remain near the bar is a factor in shock escape performance. Although all of the factors and relative contribution of each factor for septal performance are still not known, the results of the present experiment provide support for McCleary's disinhibition hypothesis.

REFERENCES

Brady, J.V., & Nauta, W.J.H. Subcortical mechanisms in emotional behavior: Affective changes following septal forebrain lesions in the albino rat. Journal of Comparative and Physiological Psychology, 1953, 46, 339-346.

Buckland, G.H., & Schwartzbaum, J.S. Fixed ratio performance for sucrose under nondeprived conditions following septal lesions in rats. Psychonomic Science, 1970, 18, 271-283.

Dalby, D.A. Effect of septal lesions in the acquisition of two types of active avoidance behavior in rats. Journal of Comparative and Physiological Psychology, 1970, 73 278-283.

Dinsmoor, J.A., & Hughes, L.H. Training rats to press a bar to turn off shock. Journal of Comparative and Physiological Psychology, 1956, 49, 235-238.

Ellen, P.,& Aitken, W.C. Absence of temporal discrimination following septal lesions. Psychonomic Science, 1971, 22, 129-132.

Gotsick, J.E., Osborne, F.H., Allen, C.J., & Hines, K.M. Factors affecting performance on a shock escape task in rats with septal lesions. Physiology and Behavior, 1971, 6, 199-201.

Harvey, J.A., & Hunt, H.F. Effect of septal lesions on thirst in the rat as indicated by water consumption and operant responding for water reward. Journal of Comparative and Physiological Psychology, 1965, 59, 49-56.

Hothershall, D., Johnson, D.A.,& Collen, A. Fixed-ratio responding following septal lesions in the rat. Journal of Comparative and Physiological Psychology, 1970, 73, 470-476.

Kaada, B., Rasmussen, E. & Kviem, O. Impaired acquisition of passive avoidance behavior by subcallosal, septal, hypothalamic, and insular lesions in rats. Journal of Comparative and Physiological Psychology, 1962, 55, 661-670.

Kenyon, J., & Krieckhaus, E.E. Decrements in one-way avoidance learning following septal lesions. Psychonomic Science, 1965, 3, 113-114. (a)

Kenyon, J., & Krieckhaus, E.E. Enhanced avoidance behavior following septal lesions in the rat as a function of lesion size and spontaneous activity. Journal of Comparative and Physiological Psychology, 1965, 59, 466-469. (b)

Lints, C.E., & Harvey, J.A. Altered sensitivity to footshock and decreased brain content of serotonin following brain lesions in the rat. Journal of Comparative and Physiological Psychology, 1969, 67, 23-31.

Lubar, J.F., Brener, J.M., Deagle, J.H., Numan, R., & Clemens, W.J. Effect of septal lesions on detection threshold and unconditioned response to shock. Physiology and Behavior, 1970, 5, 459-463.

McCleary, R.A. Response specificity in the behavioral effects of limbic system lesions in the cat. Journal of Comparative and Physiological Psychology, 1961, 54, 605-613.

McCleary, R.A. Response-modulating functions of the limbic system: Initiation and suppression. In E. Stellar & J.M. Sprague (Eds.), Progress in physiological psychology. Vol. 1. New York: Academic Press, 1966.

Migler, B. Bar holding during escape conditioning. Journal of the Experimental Analysis of Behavior, 1963, 6, 65-72.

Morgan, J.M., & Mitchell, J.C. Septal lesions enhance delay of responding on a free operant avoidance schedule. Psychonomic Science, 1969, 16, 10-11.

Schwartzbaum, J.S., Green, R.H., Beatty, W.W., & Thompson, J.B. Acquisition of avoidance behavior following septal lesions in the rat. Journal of Comparative and Physiological Psychology, 1967, 63, 95-104.

Schwartzbaum, J.S., Kellicut, M.H., Spieth, T.M., & Thompson, J.B. Effects of septal lesions in rats on response inhibition associated with food reinforced behavior. Journal of Comparative and Physiological Psychology, 1964, 58, 217-224.

Sidman, M. Two temporal parameters of the maintenance of avoidance behavior by the white rat. Journal of Comparative and Physiological Psychology, 1953, 46, 253-261.

Slotnick, B.M., & Jarvik, M.E. Deficits in passive avoidance and fear conditioning in mice with septal lesions. Science, 1966, 154, 1207-1208.

Sodetz, F.J. Septal ablation and free-operant avoidance behavior in the rat. Physiology and Behavior, 1970, 5, 773-777.

Zucker, I. Effect of lesions of the septal-limbic area on the behavior of cats. Journal of Comparative and Physiological Psychology, 1965, 60, 344-352.

APPENDIX A

INDIVIDUAL DATA

TABLE 1

Bar Holding Time in Seconds for Septal and Control Groups on the Final Bar Holding Retention Day

Septal Group		Control Group	
Subject	Bar Time	Subject	Bar Time
7	833.0	2	887.9
9	735.3	4	876.5
11	671.5	6	853.5
13	819.5	8	905.8
15	780.6	10	870.1
19	850.4	12	811.7
21	836.3	14	821.2
23	378.6	16	818.3
25	883.3	18	847.7
27	858.3	20	851.7
29	847.7	22	861.4
31	863.8	24	882.0
33	773.3	26	868.8
		28	863.6
Mean	779.7	30	816.0
		32	848.4
		Mean	855.3

TABLE 2

Bar Holding Time in Seconds for Septal and Control Groups during the First Three Days of Shock Escape

Subject	Day: 1	2	3
	Septal Group		
7	371.9	390.8	199.7
9	172.8	246.6	241.0
11	265.3	330.0	309.9
13	490.7	342.5	398.4
15	416.9	283.8	468.3
19	488.8	245.1	346.4
21	313.6	447.5	433.5
23	83.0	335.4	465.8
25	391.0	314.4	337.6
27	246.4	438.1	452.0
29	398.1	341.1	370.8
31	402.3	434.4	503.5
33	64.2	253.2	372.4
Mean	315.8	338.7	376.2
	Control Group		
2	259.0	160.9	334.5
4	280.6	95.6	333.2
6	142.1	186.3	167.9
8	193.7	191.7	255.0
10	227.9	332.8	452.8
12	360.9	207.9	202.0
14	293.8	456.5	395.5
16	189.1	191.1	234.4
18	382.7	320.3	390.7
20	382.3	111.3	234.1
22	216.0	110.2	348.3
24	278.4	235.0	233.4
26	329.5	374.6	314.1
28	453.0	239.1	275.9
30	58.0	210.3	286.3
32	33.2	252.7	431.0
Mean	255.0	229.8	305.6

TABLE 3

Bar Holding Time in Seconds for all Groups during the Last Three Days of Shock Escape

Subject	Day: 4	Day: 5	Day: 6
	Septal 0.6 mA Group		
13	371.6	417.6	371.6
19	315.3	331.7	364.2
21	395.5	414.3	430.9
23	478.1	447.5	488.7
25	427.0	308.6	475.1
29	407.7	368.9	472.2
31	514.3	323.4	219.5
Mean	415.6	373.1	403.2
	Control 0.6 mA Group		
2	437.7	369.9	307.6
6	355.6	84.4	68.3
14	561.7	487.2	538.1
24	263.1	292.1	223.1
26	301.2	334.9	182.3
28	210.3	318.6	542.3
30	330.1	226.3	308.4
32	343.4	360.4	302.0
Mean	350.4	309.2	309.0
	Septal 1.0 mA Group		
7	255.6	178.7	370.4
9	388.4	314.9	457.9
11	330.4	289.8	429.3
15	264.3	480.8	486.1
27	510.7	450.0	464.3
33	97.2	364.0	280.2
Mean	307.8	346.4	414.7
	Control 1.0 mA Group		
4	451.9	468.2	416.3
8	357.6	267.2	442.2
10	444.5	389.6	364.7
12	294.2	197.6	253.9
16	138.1	33.0	366.8
18	547.2	547.5	459.3
20	542.2	337.7	363.4
22	201.5	170.6	208.8
Mean	372.2	301.4	359.4

TABLE 4

Reciprocal of Latency and (Latency + 1) for Septal and Control during the First Three Days of Shock Escape

		Septal Group					
		Reciprocal of Latency			Reciprocal of (Latency + 1)		
Subject	Day:	1	2	3	1	2	3
7		1.751	2.605	1.957	.550	.636	.608
9		.615	1.185	.840	.376	.427	.434
11		1.488	.613	.542	.358	.201	.197
13		1.698	1.212	2.404	.539	.491	.648
15		2.063	2.417	1.983	.584	.623	.566
19		.315	.637	.250	.233	.246	.183
21		1.129	.882	1.896	.432	.454	.585
23		.640	.906	1.738	.212	.243	.470
25		1.138	1.075	1.310	.454	.456	.447
27		.673	.720	1.628	.334	.378	.540
29		.568	1.744	.930	.324	.510	.404
31		2.616	1.840	2.998	.627	.572	.719
33		1.641	3.121	2.441	.569	.656	.632
Mean		1.256	1.458	1.609	.430	.453	.493
		Control Group					
2		2.425	1.422	2.486	.674	.510	.680
4		2.896	3.035	2.039	.651	.730	.633
6		1.376	1.546	1.088	.490	.515	.462
8		1.859	2.454	1.088	.576	.655	.412
10		2.418	2.120	2.457	.651	.650	.670
12		2.756	1.824	1.961	.702	.575	.614
14		3.105	2.232	2.097	.613	.600	.639
16		1.368	.926	2.411	.487	.377	.565
18		2.808	2.164	2.872	.718	.649	.692
20		1.753	1.365	1.934	.528	.482	.515
22		2.403	1.624	1.360	.642	.543	.551
24		.958	1.620	2.420	.454	.519	.549
26		2.700	2.514	2.127	.708	.650	.628
28		2.233	1.969	1.591	.647	.584	.592
30		.921	.887	1.468	.439	.437	.554
32		2.067	1.496	1.990	.590	.506	.556
Mean		2.128	1.825	1.962	.598	.561	.582

TABLE 5

Reciprocal of Latency and (Latency + 1) for all Groups during the Last Three Days of Shock Escape

Subject	Day:	Reciprocal of Latency 4	5	6	Reciprocal of (Latency + 1) 4	5	6
Septal 0.6 mA Group							
13		1.610	1.785	1.620	.570	.620	.513
19		.345	.421	.488	.241	.277	.313
21		1.658	1.167	1.398	.542	.425	.494
23		1.218	1.317	1.382	.420	.469	.526
25		1.036	1.087	1.652	.394	.423	.551
29		1.056	1.531	.518	.390	.462	.237
31		2.719	2.469	2.303	.711	.661	.555
Mean		1.377	1.397	1.337	.467	.477	.456
Septal 1.0 mA Group							
7		1.693	2.051	1.739	.481	.570	.562
9		.887	.678	1.333	.460	.380	.535
11		.719	.566	.865	.288	.356	.358
15		2.557	1.785	1.882	.646	.561	.575
27		1.362	2.023	1.750	.519	.611	.569
33		.763	1.572	1.830	.398	.537	.552
Mean		1.330	1.446	1.342	.465	.502	.450
Control 0.6 mA Group							
2		1.992	2.442	1.761	.612	.679	.567
6		.770	.995	.962	.405	.477	.447
14		2.404	2.357	2.143	.700	.692	.665
24		2.783	2.950	3.376	.676	.651	.734
26		1.596	2.373	1.624	.567	.645	.579
28		.580	.401	.250	.313	.222	.164
30		1.120	1.548	1.582	.430	.575	.564
32		1.407	2.413	1.914	.536	.681	.581
Mean		1.582	1.935	1.702	.530	.578	.538
Control 1.0 mA Group							
4		.864	2.172	2.738	.392	.673	.702
8		1.899	2.167	1.745	.613	.627	.598
10		2.334	2.571	2.439	.661	.691	.683
12		1.885	1.783	2.940	.590	.614	.704
16		3.012	1.644	1.924	.709	.540	.593
18		2.958	3.172	2.884	.742	.753	.717
20		1.651	1.760	2.119	.523	.532	.616
22		1.553	2.051	2.154	.585	.610	.649
Mean		2.020	2.165	2.368	.602	.630	.658

TABLE 6

Bar Holding Time in Seconds during Bar Holding Training for Septals Who were Designated Good Bar Holders (Reached Criterion of 720 Seconds on Second Day) and Poor Bar Holders (Reached Criterion on Subsequent Days)

Subject	Day: 1	2	3	4	5	6	7	8
7*	401.9	851.0						
9	56.2	156.5	641.7	710.4	763.5			
11*	168.0	762.4						
13*	188.6	801.4						
15*	557.5	788.7						
19	0.5	521.1	806.5					
21*	404.5	751.6						
23	573.2	350.9	796.7					
25*	715.3	824.4						
27	110.7	40.2	134.9	709.1	804.4			
29*	701.0	792.2						
31*	593.3	749.4						
33	2.8	16.2	33.8	7.7	45.0	369.4	504.4	748.4

*Good Bar Holders

APPENDIX B

SUMMARIES OF ANALYSES OF VARIANCE

TABLE 7

Anova Summary Table: Bar Holding for Septal and Control Groups during the First Three Days of Shock Escape

Source	df	MS	F
Total	86		
Total Between	28		
Septal vs Control	1	138078.04	10.37**
Error 1	27	13321.17	
Total Within	58		
Days	2	31297.54	3.40*
Septal vs Control X Days	2	4626.36	.50
Error 2	54	9200.78	

*$p < .05$

**$p < .01$

TABLE 8

Anova Summary Table: Bar Holding for All Groups during the Last Three Days of Shock Escape

Source	df	MS	F
Total	86		
Total Between	28		
Septal vs Control	1	43133.45	1.53
0.6 mA vs 1.0 mA	1	1447.63	.05
Operation X Shock	1	20403.48	.72
Error 1	25	28159.59	
Total Within	58		
Days	2	12126.94	1.67
Days X Operation	2	9240.85	1.27
Days X Shock	2	8557.70	1.18
Days X Operation X Shock	2	6921.59	.95
Error 2	50	7269.23	

TABLE 9

Anova Summary Table: Reciprocal of Latency for Septal and Control Groups during the First Three Days of Shock Escape

Source	df	MS	F
Total	86		
Total Between	28		
Septal vs Control	1	6.05	6.44*
Error 1	27	.94	
Total Within	58		
Days	2	.15	.65
Septal vs Control X Days	2	.63	2.72
Error 2	54	.23	

*$p < .05$

TABLE 10

Anova Summary Table: Reciprocal of Latency for all Groups during the Last Three Days of Shock Escape

Source	df	MS	F
Total	86		
Total Between	28		
Septal vs Control	1	6.64	5.80*
0.6 mA vs 1.0 mA	1	1.97	1.72
Operation X Shock	1	.46	.40
Error 1	25	1.14	
Total Within	58		
Days	2	.27	1.90
Days X Operation	2	.07	.48
Days X Shock	2	.21	1.45
Days X Operation X Shock	2	.05	.33
Error 2	50	.14	

*$p < .05$

TABLE 11

Anova Summary Table: Reciprocal of (Latency + 1) for Septal and Control Groups during the First Three Days of Shock Escape

Source	df	MS	F
Total	86		
Total Between	28		
Septal vs Control	1	.3185	9.17**
Error 1	27	.0347	
Total Within	58		
Days	2	.0063	1.51
Septal vs Control X Days	2	.0121	2.89*
Error 2	54	.0042	

*$p < .05$
**$p < .01$

TABLE 12

Anova Summary Table: Reciprocal of (Latency + 1) for all Groups during the Last Three Days of Shock Escape

Source	df	MS	F
Total	86		
Total Between	28		
Septal vs Control	1	.2525	6.72*
0.6 mA vs 1.0 mA	1	.0864	2.30
Operation X Shock	1	.0026	.07
Error 1	25	.0376	
Total Within	58		
Days	2	.0083	1.86
Days X Operation	2	.0004	.10
Days X Shock	2	.0080	1.80
Days X Operation X Shock	2	.0010	.23
Error 2	50	.0045	

*$p < .05$

TABLE 13

Anova Summary Table: Bar Holding for Good and Poor Septal Bar Holders during the First Three Days of Shock Escape

Source	*df*	*MS*	*F*
Total	38		
Total Between	12		
Good vs Poor	1	53438.59	5.20*
Error 1	11	10278.89	
Total Within	26		
Days	2	12122.39	1.42
Good vs Poor X Days	2	22819.13	2.66
Error 2	22	8565.40	

*$p < .05$

TABLE 14

Anova Summary Table: Bar Holding for Good and Poor Septal Bar Holders under Both Shock Intensities during the Last Three Days of Shock Escape

Source	df	MS	F
Total	38		
Total Between	12		
Poor vs Good	1	649.77	.04
0.6 mA vs 1.0 mA	1	16325.58	1.01
Good/Poor X Shock	1	3012.69	.19
Error 1	9	16122.69	
Total Within	26		
Days	2	8926.49	1.26
Days X Good/Poor	2	1719.57	.24
Days X Shock	2	12008.41	1.70
Days X Good/Poor X Shock	2	3133.36	.44
Error 2	18	7104.26	

TABLE 15

Anova Summary Table: Reciprocal of (Latency + 1) for Good and Poor Septal Bar Holders during the First Three Days of Shock Escape

Source	*df*	*MS*	*F*
Total	38		
Total Between	12		
Good vs Poor	1	.0995	1.81
Error 1	11	.0548	
Total Within	26		
Days	2	.0139	2.70
Good vs Poor X Days	2	.0036	.70
Error 2	22	.0051	

TABLE 16

Anova Summary Table: Reciprocal of (Latency + 1) for Good and Poor Septal Bar Holders under Both Shock Intensities during the Last Three Days of Shock Escape

Source	df	MS	F
Total	38		
Total Between	12		
Poor vs Good	1	.0177	.45
0.6 mA vs 1.0 mA	1	.0094	.24
Good/Poor X Shock	1	.0270	.69
Error 1	9	.0391	
Total Within	26		
Days	2	.0021	.66
Days X Good/Poor	2	.0102	3.19
Days X Shock	2	.0042	1.31
Days X Good/Poor X Shock	2	.0128	4.00*
Error 2	18	.0032	

*$p < .05$