

RESPONSE VARIABILITY AND DISCRIMINATION REVERSAL
LEARNING FOLLOWING SEPTAL LESIONS IN RATS

by

CHRISTOPHER THOMAS CHERRY

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Approved by:

James C. Mitchell
Major Professor

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TABLE OF CONTENTS

ACKNOWLEDGMENTS.....	iii
INTRODUCTION.....	1
METHOD.....	10
Subjects.....	10
Surgery and Histology.....	10
Apparatus.....	11
Procedure.....	11
Shaping.....	11
Testing.....	14
EXPERIMENT I.....	15
EXPERIMENT II.....	15
RESULTS.....	16
Histological.....	16
Behavioral.....	19
DISCUSSION.....	26
REFERENCES.....	29

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A common characteristic that animals with lesions in the septal area exhibit is a marked perseveration of learned responses. This effect is particularly evident in situations that require the animal to withhold or change a previously rewarded response. One of the first and best known interpretations of this effect of septal lesions was that proposed by McCleary (1961). Based primarily on his own findings, McCleary suggested that animals sustaining damage in the septal area suffer a general loss of response inhibition. In a study of passive avoidance behavior in cats, McCleary reported that cats given bilateral lesions in the subcallosal cortex, including the anterior septal area, were unable to withhold their approach to food. He found that most animals required only two shocked approaches to learn to avoid the food. The cats with septal lesions, however, were unable to withhold their approach response following the two shocked responses. McCleary's findings were replicated by Kaada, Rasmussen, & Kveim (1962) who tested rats in the passive avoidance task. They found that control animals quickly learned to avoid an electrified water dish, but a group with septal damage perseverated in returning to the electrified dish.

In McCleary's (1961) study, cats having septal lesions were also found to be at least as good as normal cats in acquisition of an active avoidance response. Since then, a number of experiments have demonstrated that septal lesions facilitate acquisition of an active avoidance response (Fox, Kimble, & Lickey, 1964; Krieckhaus, Simmons, Thomas, & Kenyon,

1964; Van Hoesen, MacDougall, & Mitchell, 1969)

The notion of an inhibitory loss in animals with septal lesions has been extended to investigations of other behavioral tasks. Douglas & Raphelson (1966b) used rats with septal lesions to test the hypothesis that spontaneous alternation involves an underlying inhibitory process. They reported that the mean alternation rate for the group with septal damage was not reliably different from chance (chance being 50% alternation). The control group alternated at a level significantly higher than chance. This indicated that the group with septal lesions tended to perseverate, turning into the same alley while the controls turned into the alley opposite to the one taken on the previous trial. Clody & Carlton (1969) compared the rate of spontaneous alternation in a group of rats with septal lesions to the rate of a control group under two different lighting conditions. There was an initial dark phase in which the alternation rate for the group with septal damage was not reliably different from the control group rate. In the succeeding light phase, however, the group with septal lesions alternated at a significantly lower rate while the control group rate increased over the previous rate. In the last phase, again under dark conditions, the group with septal lesions increased to approximately the same level reached in the previous dark phase.

Clody and Carlton also tested rats with septal lesions in the cross-shaped maze under light conditions and found that the group with septal lesions alternated at below chance level while

the controls alternated at a rate greater than chance. Their findings suggest that light is aversive to animals with septal lesions which in some way results in a marked increase in stereotyped behavior.

The failure to inhibit responding has also been held to account for impaired discrimination reversal learning in animals with septal lesions. Zucker & McCleary (1964) trained control cats and cats with septal lesions on a position habit in a Wisconsin General Testing Apparatus. The animals were then trained to the same criterion for two reversals of the position habit. The results revealed that the cats with septal lesions made reliably more perseverative errors following each reversal. In another study, Zucker (1965) attempted to define more precisely the deficit in discrimination reversal performance of cats with septal damage. He used two groups of animals which were tested in three tasks. One group was tested on a successive discrimination, followed by extinction of the response, and, lastly, on a simultaneous discrimination. The other group was tested on the same set of tasks, but in the reverse order, i.e., simultaneous discrimination, extinction, and then successive discrimination. He found that the animals with septal lesions learned the successive discrimination in as many trials as the control group when that task was learned last in the series. When the rats with septal damage were trained on the successive task first, however, they needed a reliably greater number of trials during acquisition than the control group. Zucker's findings suggest that when the rats

with septal damage were learning the successive task, they were unable to refrain from responding on the trials in which the incorrect or negative stimulus was presented first. When the successive task followed extinction of the simultaneous discrimination, however, the group with septal lesions learned as quickly as the control group. Zucker (1965) believed that was due to the attenuating effect of the prior series of nonreinforced trials. Zucker examined the possibility that the deficit of cats having septal lesions in the successive discrimination was due to lesion induced hyperactivity. The results, however, revealed no significant differences in activity level between groups over three days of recorded activity.

Hyperactivity resulting from septal lesions has also been suggested as an explanation for impaired performance of animals with septal lesions in maze learning. Thomas, Moore, Harvey, & Hunt (1959) tested rats with septal lesions in a Lashley type III maze and found that these subjects required more trials than controls to reach a criterion of six consecutive errorless runs. On the first trial, the group with septal lesions made reliably more errors and took a considerably longer time to learn the maze than the control group. In discussing their results, Thomas et al. (1959) maintained that hyperactivity in the rats with septal damage would account for the excessive time on the first trial. When placed in the maze for the first time, the animals with septal lesions would make periodic bursts of running up and down the same alley. This disinhibition of activity, they suggest, would also account for the greater error

score for the animals with septal lesions since such outbursts of running up and down the alley would cause them to pass by the open door into the alley.

Douglas and Raphelson (1966a) have suggested that if animals having septal lesions are hyperactive, then they should run more in an activity or exercise wheel than control animals. If, on the other hand, rats with septal lesions exhibit an increased reactivity to novel stimuli, then they should engage in more exploration in a strange cage than controls. Empirically, Douglas and Raphelson found that the rats with septal lesions averaged significantly fewer wheel turns than controls. On the measure of exploratory behavior, the rats with septal damage were reliably more active than the controls during the first session. By the end of the second session both groups were less active, but the group with septal damage decreased their activity to a greater extent than the controls. They concluded that hyperactivity cannot account for the behavior of animals with septal lesions in all situations. They argued that in a novel situation, an animal with septal damage would show increased activity initially but will habituate very quickly.

Schwartzbaum & Gay (1966) have provided additional evidence to show that animals with septal lesions do not exhibit a general hyperactivity. They reported that when rats sustaining septal damage were placed in an open field situation, they typically froze and remained immobile for the entire five minute recording session. In the study cited previously by Thomas et al., it was reported that the animals given septal lesions

showed the hyperactive exploratory behavior only at the beginning of training which accounted for the greater error score for these animals on the first trial. As training continued, this behavior decreased, indicating that the rats with septal damage were becoming habituated to the novelty of the maze. It seems then, that the deficient behavior of rats with septal lesions in spontaneous alternation or discrimination reversal learning is not simply the result of an inhibitory loss which leads to hyperactivity. Hyperactivity could impair performance in the beginning of training, but that would not account for enhanced perseveration during subsequent testing since these animals would by then be accustomed to the apparatus.

The present investigation will examine the hypothesis that impaired discrimination reversal performance of animals with septal lesions is the result of a lesion induced enhancement of a rats natural tendency to cling to walls (thigmotaxis) as well as a heightened aversion to light. The possibility of enhanced thigmotaxis affecting the behavior of animals with hippocampal lesions was investigated by Hostetter and Thomas (1967). Previous studies of animals with lesions in the hippocampal area have established the similarity between the inhibitory deficit in these animals and that of animals having septal lesions. Hippocampal lesions have impaired passive avoidance learning (Kimble, 1963), successive discrimination learning (Kimble, 1963), reversal of a position habit (Niki, 1966), as well as to facilitate active avoidance (Isaacson, Douglas, & Moore, 1961). In their experiment, Hostetter and Thomas sug-

gested that the impaired maze performance in animals with hippocampal lesions reported by Kimble (1963) might have resulted from a lesion induced tendency of the rats to repeatedly follow the walls into the side alleys. They tested this by comparing the performance of rats with hippocampal lesions and controls in an alley and an elevated T-maze. They found that the animals with hippocampal damage were impaired on both the alley and the elevated maze. It was concluded that the behavior of rats with hippocampal lesions was not disrupted by thigmotaxis since there were no walls to cling to in the elevated maze. It is possible, however, that although thigmotaxis could be ruled out, that the greater error score of animals with hippocampal lesions might be due to an enhanced attention to some other cue in the elevated maze, namely the edge of the maze.

In a study of exploratory behavior, Kimble (1963) has provided evidence of enhanced clinging in animals with hippocampal lesions. He reported observations of rats with hippocampal lesions in an open field which revealed that initially the animals ran rapidly along the perimeter of the field, stopping only rarely. They crossed the interior of the field only after about five minutes. Enhanced thigmotaxis in animals with septal lesions has been found to alter the social attractiveness of rats in the open field (Jonason & Enloe, 1971). The number and duration of physical contacts between pairs of rats were recorded and the results indicated that septal lesions increased bodily contact or clinging between pairs of rats with lesions.

An investigation of shuttle-box avoidance behavior by

Schwartzbaum, Green, Beatty, & Thompson (1967) revealed an aversion to light in animals with septal lesions. In their series of experiments, animals with septal lesions were unable to meet the criterion for adaptation to a light-on conditioned stimulus. When the light came on, they exhibited a consistent avoidance reaction by jumping into the dark side of the shuttle-box. Aversion to light in animals with septal damage has also been revealed in an investigation of maze performance. In the first of two closely related investigations, Ellen & Bate (1969) recognized the similar inhibitory deficit found in rats with septal and hippocampal lesions as well as a tendency of rats with hippocampal damage to perseverate in following the peripheral alleys in Hebb-Williams mazes (Kimble, 1963). They hypothesized that animals with septal lesions would also show less variability in the number of paths taken in a Dashiell maze. Their findings indicated that the rats with septal lesions chose peripheral paths more frequently than controls which, they suggested, indicated a failure in these animals to use response-produced proprioceptive stimuli as cues to alternate turns in crossing the maze. This possibility was examined in their second experiment (Ellen & Bate, 1970) where rats with septal lesions and control animals were trained to run a Dashiell maze under two conditions of differentially cued paths, white central and black outer paths, and black central and white outer paths. The white paths appeared to be aversive to the animals with septal lesions. Even when these animals followed their preferred peripheral pathway, they made reliably fewer error-

less runs (an error being a turn away from the goal). It was observed that as the animals with septal damage approached the goal from a black peripheral pathway and had to cross a white path directly before the goal, they made a number of turns away from the goal. In addition, they exhibited sufficient crouching and stretching behavior at this point to suggest that the white pathway was aversive.

From what has been presented, it appears that thigmotaxis and light aversion influence the behavior of animals with septal damage in such tasks as reversal learning and variability in choice of maze paths taken. The experiments of the present investigation were carried out in an open field apparatus in order to minimize the possibility of thigmotaxis and light aversion producing position preferences in rats with septal damage. In the first experiment, rats with septal damage and controls were trained to respond at a ten-position horizontal response panel. In this situation, it was expected that animals having septal damage would accumulate responses in a distribution which would be similar in degree of variability to the response distributions of control animals. In the first part of the second experiment rats with septal lesions and control animals were trained to a position habit in the open field followed by two reversals. In the second part, rats with septal damage and control animals were again trained on a position habit and two successive reversals. Now, however, walls were added between the starting-feeding chamber and the response panel, and the level of illumination was increased. This was done in

an attempt to maximize the disruptive effect thigmotaxis and light aversion would have on reversal of the position habit.

METHOD

Subjects

Subjects were 59 male Long-Evans (Carworth) hooded rats, 200 to 300 grams at the start of shaping. All animals were individually caged and given ad lib laboratory rat chow and water prior to experimental testing. All animals were experimentally naive prior to surgery.

Surgery and Histology

Surgery proceeded under Equi-Thesin anesthesia. Bilateral electrolytic lesions of the septal area were produced by a stereotaxically guided stainless steel electrode insulated except for .5 mm of the tip. Stereotaxic coordinates used were 1.5 mm anterior to bregma, .5 mm lateral to the midline sinus, and 5.6 mm ventral to the surface of the skull with the incisor bar located 5 mm above the horizontal interaural plane. A direct current of 1.5 ma was passed for 20 seconds through the stainless steel electrode with a rectal cathode completing the circuit. For control animals, the electrode was lowered to 3 mm ventral to the skull surface and no current was passed. At least five days were allowed for recovery following surgery.

At the end of testing, the animals were anesthetized with Equi-Thesin and perfused with .9% saline and 10% formalin. The brains were removed and placed in acid formalin. The brains of experimental animals were imbedded in celloidin, mounted, and sectioned at 25 micra. Every fifth section was taken, stained

with cresyl violet and mounted on slides. Operated control brains were cut into sections with a scapel for gross examination for septal damage and possible infection.

Apparatus

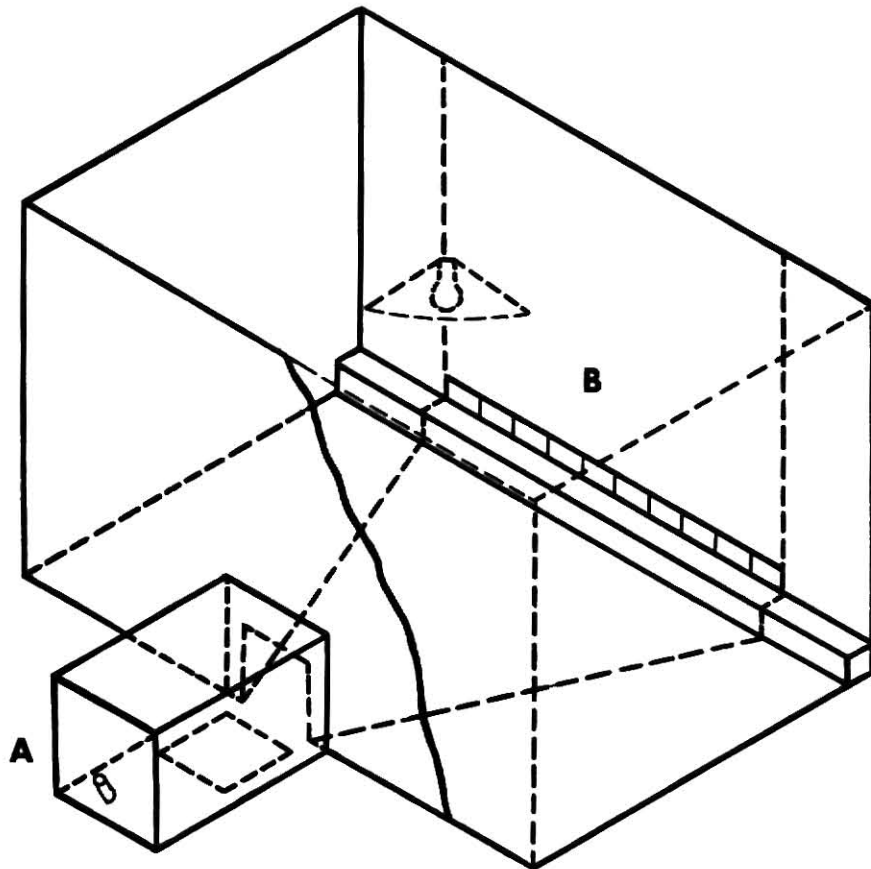
The experimental chamber was an adaptation of apparatus used by Antonitis (1951). As illustrated in Fig. 1, it consisted of an enclosed open field, 30 in. X 21 in. with a 19 in. high ceiling. A 7 1/2 watt red or 25 watt white bulb, centered over the field provided the only illumination. A 6 X 6 X 10 in. starting-feeding chamber contained a food cup in the back wall. A 4 in. square treadle just inside the starting chamber reset the feeder when the animal returned for reinforcement. The response panel, across from the starting-feeding chamber, was a 20 X 1 in. slot centered and positioned 1 1/2 in. above the floor. Ten pedals, 2 in. long were mounted in the slot and separated by 1/8 in. strips of sheet metal mounted on the surface of the wall. All pedals were individually connected to switches and counters. A 30 in. long piece of 1 1/2 in. angle iron was mounted below the response panel as a way of making the animal respond in a straight-on position. All surfaces were painted a semigloss white except for the response pedals which were a flat black. The walls added in Experiment II were also flat black.

Procedure

Shaping: Before shaping began, all animals were allowed three days to adjust to a 23 hour deprivation schedule. With the 7 1/2 watt red bulb as the light source, the animal was

Figure Caption

Fig. 1. The open field apparatus used in both experiments. Broken lines running across the field from the starting-feeding chamber to the response panel indicate the location of the walls in the second part of Experiment II. The exploded view of the response panel indicates the pedals masked in part one (cross-hatching) and part two (stippling) of Experiment II. A: starting-feeding chamber, B: response panel. The broken line square on the floor of the starting-feeding chamber represents the food magazine reset treadle.



placed in the center of the open field and allowed to explore the field and the starting-feeding chamber. At this time also a single 45 mg Noyes pellet was delivered at ten minute intervals, as long as the animal periodically returned to retrieve the pellet in the feeding chamber, thereby crossing the treadle which reset the feeder for the next reinforcement. Additional responses at the panel were also reinforced with one Noyes pellet. In order to hasten the shaping procedure, cups of wet lab chow were placed in back of the pedals. When the animal tried to get at the wet chow, it would inadvertently press one of the pedals, resulting in reinforcement. Once the animal learned the response, it was allowed to respond until satiated, returned to its home cage, and put back on ad lib food and water until two days before testing. This was a necessary procedure since a combined group of five animals with septal lesions and five controls had to be shaped several weeks prior to being tested, i.e., while another group was being tested. All animals were shaped by this procedure, except in part two of Experiment II where walls were added, beginning with shaping.

Testing: Two days before testing began, the group to be tested was returned to the 23 hour deprivation schedule. During each session, the animal being tested was chosen at random from the group and placed in the center of the open field facing the feeding chamber. All animals were tested once a day and each was allowed to accumulate 50 responses per session.

Experiment I: Free Open Field Horizontal

Position Response Task

Subjects for the experiment were 12 animals with septal lesions and 8 operated control animals. Each animal was tested for 50 reinforced responses each day for 20 consecutive days. The total number of responses made at each pedal were recorded. Each animal's distribution was determined by averaging the last five days of reinforced responding. On day 21 all animals were tested as usual, except that reinforcement was discontinued. An animal was continued on extinction as long as it made 50 responses in less than 30 minutes each day.

Experiment II: Position Habit Acquisition and Reversal

in the Open Field and in the Presence of Walls

and Increased Illumination

For Experiment II, 22 animals with septal lesions and 17 operated controls served as subjects. After shaping, the first part of Experiment II was begun with 11 animals having septal damage and nine operated control animals. All animals were tested for five days of free responding, where responses at all pedals were reinforced. On the sixth day the pedals were masked, as indicated in Fig. 1, with pieces of white plexiglass. At the start of acquisition, the reinforced positive and nonreinforced negative side for an animal was determined by its response distribution on the last free responding day. The side on which the animal made the least number of responses became the positive side. Each animal was tested for 50 responses per day which included reinforced and nonreinforced responses. The

responses an animal made at the negative side and corrected by responding immediately after at the positive side, were counted as negative responses. Each animal was tested on acquisition until it reached a criterion of 45 or more responses out of 50, to the positive side, for three consecutive days. Subjects that performed at criterion were then tested to the same criterion on two successive reversals of the position discrimination. Subjects that failed to perform at criterion within 20 days were terminated.

In the second part of Experiment Two, 11 animals with septal lesions and 8 controls served as subjects. Testing followed the same procedure used in the first part of the experiment. Beginning with shaping, however, walls were added to the apparatus, (as indicated in Fig. 1) and used throughout this half of the experiment. In addition, a 25 watt white bulb was substituted for the red bulb beginning with the second day of free responding. The pedals masked for this half of the experiment are shown in Fig. 1.

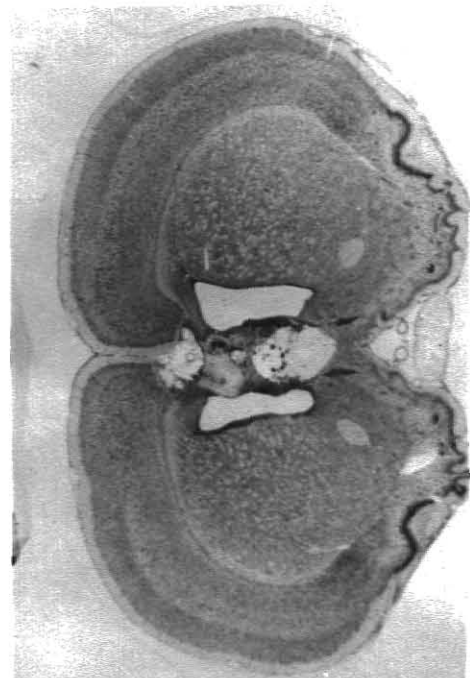
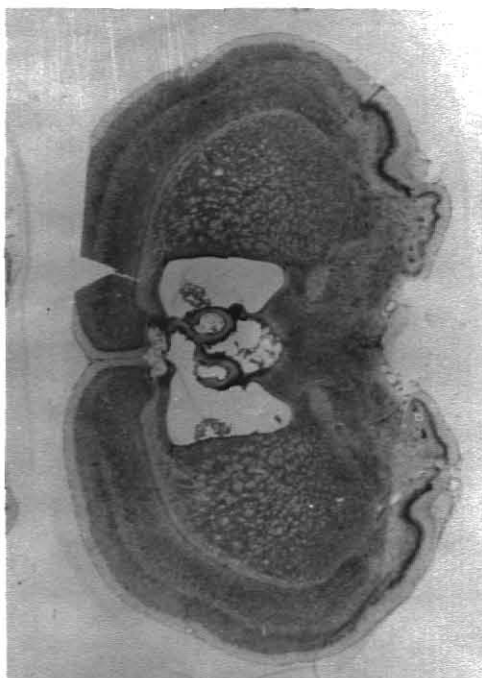
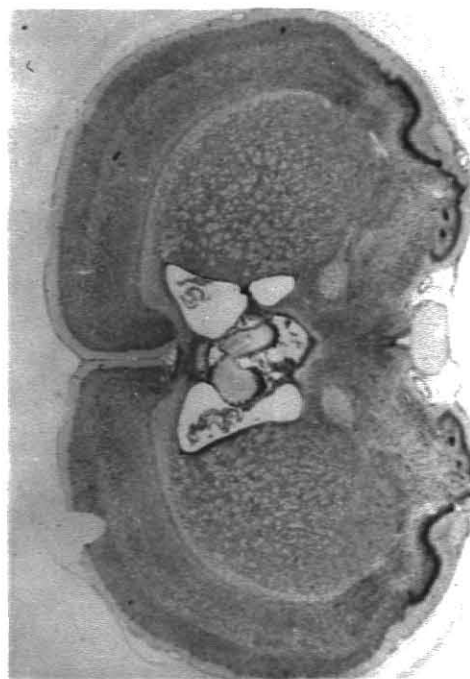
RESULTS

Histological

Representative coronal sections of two septal lesions are shown in Fig. 2. All lesions were examined to determine the extent of destruction to septal nuclei and surrounding structures. The typical rostral extent of the lesions was a point slightly posterior to the genu of the corpus callosum while the caudal extent was in the vicinity of the superior fornix. Damage extended dorsally to the corpus callosum with damage

Figure Caption

Fig. 2. Photomicrograph of coronal sections showing the major extent of two representative septal lesions.



to that structure in some instances. The ventral extent included most of the medial and lateral septal nuclei down to the anterior commissure. In a few lesions there was incidental damage to the cingulate cortex, columns of the fornix, anterior commissure, and caudate nucleus. The majority of the animals had some enlargement of the lateral ventricles. Gross examination of the operated control brains showed no signs of septal damage or of infection.

Behavioral

The response frequency distributions for animals with septal lesions and control animals in Experiment I are presented in Fig. 3. The distributions represent an average of the last five days of reinforced responding. For purposes of statistical analysis, each subject's most preferred position (the position with the most responses), and the number of positions with responses were regarded as measures of variability. These values are presented in Table 1. A t test for uncorrelated scores revealed a reliable difference between the number of responses in the most preferred position for the group with septal lesions ($\bar{M} = 32.33$) and the control ($\bar{M} = 19.25$) group ($t = 2.83$, $df = 18$, $p < .05$). A comparison of the number of positions with responses for the group with septal damage ($\bar{M} = 5.33$) and the control group ($\bar{M} = 8.5$) revealed a reliable difference on this measure ($t = 2.58$, $df = 18$, $p < .05$). By both measures of variability the group with septal damage responded in a more stereotyped manner than the control group. They showed a greater tendency to perseverate in responding at one preferred position in

Figure Caption

Fig. 3. Response frequency distributions for animals with septal lesions and control animals in Experiment I. The distributions represent an average of the last five days of testing at 50 responses per day.

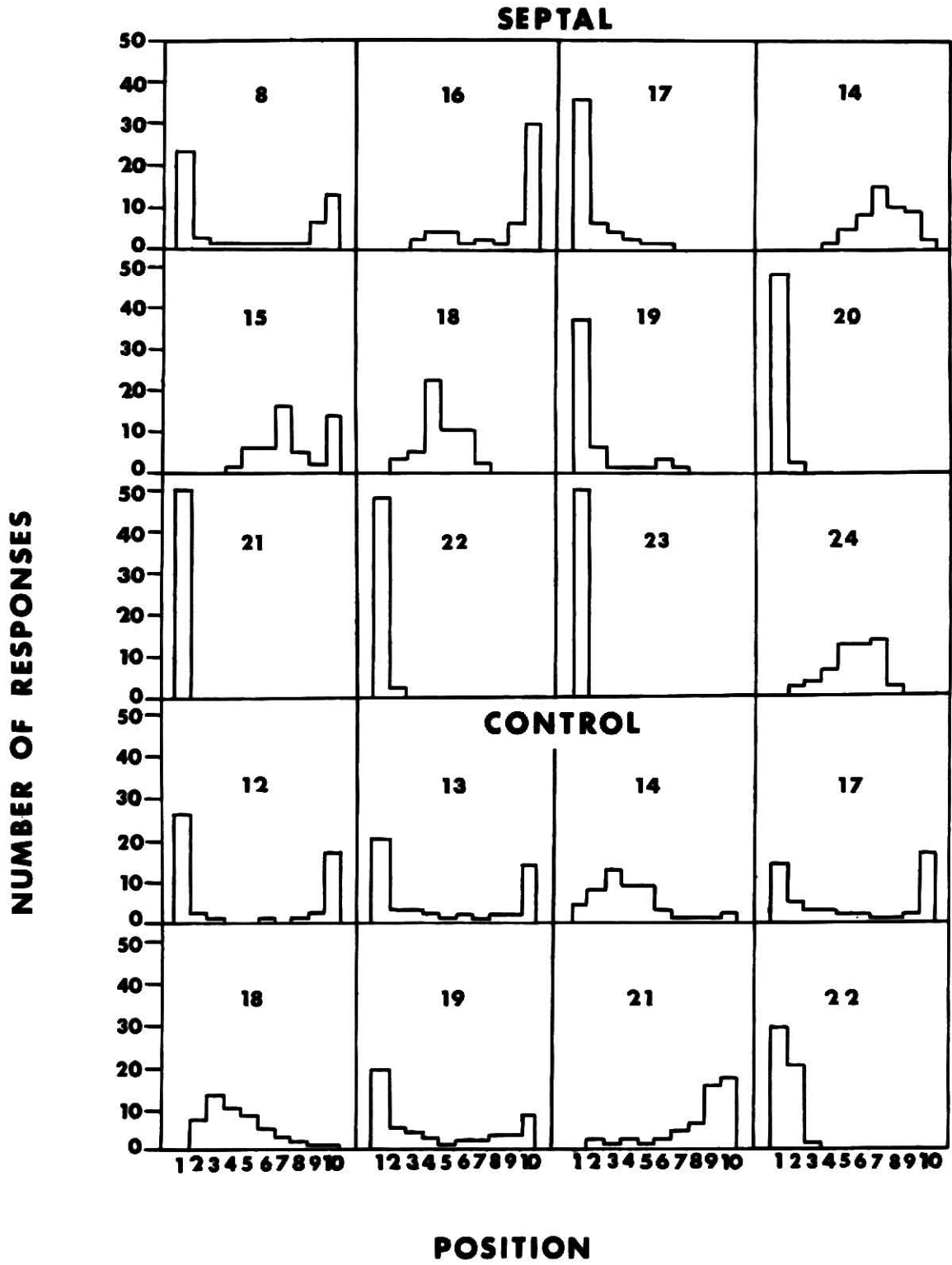


TABLE 1

The Average Number of Responses in the Preferred Position (RPP), and
 Number of Positions Used (NPU) for the last Five Testing Days,
 and the Number of Days to Extinction (DTE) in Experiment I.

Septal Animal	RPP	NPU	DTE	Control Animal	RPP	NPU	DTE
8	23	10	5	12	26	7	1
14	15	7	11	13	20	10	5
15	16	7	7	14	13	10	3
16	30	8	6	17	17	10	2
17	36	6	5	18	13	9	2
18	22	6	4	19	19	10	8
19	37	7	12	21	17	9	3
20	48	2	7	22	29	3	4
21	50	1	18	Mean	19.25	8.5	3.5
22	48	2	3				
23	50	1	18				
24	13	7	6				
Mean	32.33	5.33	8.5				

addition to using fewer positions

Comparison of the number of days to extinction for the group with septal lesions ($\bar{M} = 8.5$) and the control group ($\bar{M} = 3.5$) revealed a reliable difference ($t = 2.98$, $df = 18$, $p < .01$) which indicated a greater tendency for animals with septal damage to persevere at responding after reinforcement was withdrawn.

The range and average number of days to criterion for the successive discriminations of Experiment II are presented in Table 2. Table 3 is a summary of the Analysis of Variance (ANOVA) for unequal groups with repeated measures performed on the data of Experiment II. The ANOVA revealed a reliable treatment effect for lesion ($F = 56.58$, $df = 1/31$, $p < .001$, and for walls and increased illumination ($F = 7.43$, $df = 1/31$, $p < .05$). Overall, animals with septal lesions took fewer days to reach criterion than control animals, and both groups tested in the presence of walls and greater illumination reached criterion in fewer days than animals tested in the open field. Comparison of groups across different phases revealed reliable differences on acquisition ($t = 3.91$, $df = 18$, $p < .01$), first reversal ($t = 3.14$, $df = 18$, $p < .01$), and second reversal ($t = 2.87$, $df = 16$, $p < .05$) in part one. Similar comparison of groups across each phase of part two also revealed reliable differences in acquisition ($t = 4.3$, $df = 17$, $p < .001$), first reversal ($t = 2.41$, $df = 16$, $p < .05$), and second reversal ($t = 4.31$, $df = 15$, $p < .001$). In both parts of the experiment and in each phase, the animals with septal damage took fewer days to reach

TABLE 2

The Range and Average Number of Days to Criterion
for Animals with Septal Lesions and Control
Animals in the Successive Discriminations
of Experiment II

Group	Acquisition		1st Reversal		2nd Reversal	
	Mean	Range	Mean	Range	Mean	Range
Part One						
Septal	7.10	3-13	8.27	5-20	8.20	4-15
Control	13.44	7-19	14.66	7-20	13.63	9-20
Part Two						
Septal	5.0	3-7	6.54	5-9	6.10	4-9
Control	13.13	7-22	11.40	7-20	13.50	6-17

TABLE 3

Analysis of Variance of Acquisition, First and Second
Reversal for Animals in both Open Field and Walls
and Increased Illumination Conditions

Source	<u>df</u>	<u>MS</u>	<u>F</u>
Lesion vs. Control (A)	1	804.14	56.58 **
Open Field vs. Walls and Increased Illumination (B)	1	105.72	7.43 *
A x B	1	2.92	<1
Error	31		
Acquisition vs. First vs. Second Reversal (C)	2	15.5	2.4
A x C	2	4.1	<1
B x C	2	5.8	<1
A x B x C	2	17.34	2.7
Error	62		

* $p < .05$

** $p < .001$

criterion than control animals

DISCUSSION

The open field nature of the apparatus was expected to eliminate possible position biases resulting from suspected tendencies in animals with septal lesions to follow or cling to the walls of the apparatus. Additional position biases resulting from a possible tendency in animals with septal lesions to avoid light was reduced by the use of a low level illumination. The results of the first experiment, however, indicated that subjects with septal lesions nonetheless acquired a response pattern that was reliably less variable than that for control animals. In addition, subjects that responded at the ends of the panel tended to be more stereotyped. Observation of subjects' performance indicated that animals with septal damage ran faster and consequently made more responses within a given period than control animals. The results of the first experiment also revealed prolonged extinction of the response in subjects with septal damage. These findings are consistent with previous investigations which suggested that septal lesions produce a general disinhibition leading to perseverative behavior that persists after a change in experimental conditions (Ellen, Wilson, & Powell, 1964; LaVaque, 1966; Van Hoesen, MacDougall, & Mitchell, 1969).

As the comparisons revealed, subjects in the second experiment that sustained lesions in the septal area were superior to control animals in acquisition and both reversals of the position discrimination. In the first part of the second experiment, where walls were absent and a low level of illumination

was used, the animals were expected to be unimpaired in position reversal. In the second part, however, the addition of walls between the starting chamber and response wall and the increased illumination were expected to produce deficient reversal performance. Instead, the walls and greater illumination facilitated performance in all subjects in the acquisition and reversal of the position habit. Although thigmotaxis and aversion to light may yet be shown to result from lesions in the septal area, the effect was clearly not revealed in the present experiment. The present findings are of interest, however, because they are not at all consistent with past investigations (Schwartzbaum & Donovanick, 1968; Zucker & McCleary, 1964). These investigators reported that on original learning of the discrimination, there were no differences between groups, but that animals with septal damage were impaired on reversal of the discrimination. The results of the present experiments revealed a consistently superior performance, in animals with septal damage, in all phases of the experiments. Observation of subjects' rates of responding suggested that animals with septal damage completed their 50 daily responses in much less time than control animals. In addition, the group with septal damage made fewer superfluous pedal presses following the reinforced response than control animals.

These observations suggest the possibility that one or both of two mechanisms could account for the superior performance in the subjects with septal lesions. One possible mechanism would be the shorter delay in reinforcement for the generally faster

animals with septal lesions. The other would be an enhanced sensitivity or attention to the secondary reinforcing value of the food magazine click. Fallon and Donovanick (1970) suggested that the effect of septal lesions appears to be an enhancement of the animals motivational reactivity. In an experiment then, as in the present one, where an animal is responding for positive reinforcement, animals with septal lesions might be expected to respond at a faster rate than controls. It might also be argued that if septal lesions do increase motivational reactivity, that an animal with such lesions would also make greater use of whatever secondary reinforcing cues were available.

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RESPONSE VARIABILITY AND DISCRIMINATION REVERSAL
LEARNING FOLLOWING SEPTAL LESIONS IN RATS

by

CHRISTOPHER THOMAS CHERRY

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In an open field apparatus, animals with septal lesions and operated control subjects were trained to respond along a horizontal panel stretching across one wall, and were then subjected to extinction. On two measures of variability, there was reliably greater stereotyped performance and increased resistance to extinction in the group with septal damage. Similar groups were trained on a discrimination reversal in the open field, and also under conditions of increased illumination and with the addition of walls between the start box and response panel. The results revealed superior reversal performance in the group with septal lesions, under both the open field and walled conditions. A faster rate of responding observed in the group with septal lesions could account for their increased stereotypy. Their superior reversal performance could be due to an ability to tolerate delays in reinforcement, possibly by virtue of an enhanced sensitivity to secondary reinforcing cues.