1956

Changes in noise-maintained behavior following septal forebrain lesions in the albino rat.

BOSTON UNIVERSITY
GRADUATE SCHOOL

Dissertation

CHANGES IN NOISE-MAINTAINED BEHAVIOR FOLLOWING LESIONS IN THE SEPTAL FOREBRAIN REGION OF THE ALBINO RAT

by

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Submitted in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
1956

PhD
1956
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ACKNOWLEDGEMENT

Appreciation is expressed to Professor J.M. Harrison who made this dissertation possible. Professors Margolis and Berkeley were very helpful with appropriate suggestions. Words of encouragement from Professors Reyna and Pinard have been gratefully received. To my wife a special note is in order for her patience and help in many ways.

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CHAPTER I

INTRODUCTION AND REVIEW OF THE LITERATURE

Introduction to the Problem

The experiments reported here began with a preliminary study of the effects of lesions of the hippocampus on observed cage behavior of albino rats. This preliminary work was undertaken after Brady and Nauta's report of correlative behavior changes in albino rats following the placement of septal forebrain lesions (4). The hippocampus, through the fornix discharge system, is intimately related to the septal region of the forebrain (19).

Following ablation of large amounts of tissue at the rostral end of the hippocampus, and including other parts of the forebrain, it was found that albino rats exhibited similar behavior to that described by Brady and Nauta (4). This behavior consisted of a group of responses which might loosely be described as hypersensitivity to auditory and tactile stimulation. It was found that ablation of dorsal and caudal aspects of the hippocampus without involvement of the forebrain region did not result in the typical hypersensitivity.

The major problem of this dissertation was the determination of the extent to which the casually observed hypersensitivity was reflected in more carefully defined classes of behavior.

General Anatomical Orientation

The following description of the septal region in the albino rat is based on the works of Craigie (7), Johnston (15), Gurdjian (11), Brodal (6), and Nauta (19). A diagram of a parasaggital section of the rat's brain is shown in Figure 1.

Efferent fibers from the hippocampus collect into bundles of fibers which are referred to as fimbria. From the fimbria the massive descending columns of the fornix and the precomis_sural fornix fibers arise. Fibers of the precommissural fornix either synapse in the septum or pass directly to the lateral and periventricular areas of the hypothalamus and the preoptic region. Fibers of the fornix columns run behind the anterior commissure to the anterior nucleus of the thalamus, the lateral and periventricular areas of the hypothalamus, and to the mammillary bodies. Fibers from the septal nuclei join the fornix columns and distribute to the anterior nuclei of the thalamus and to the habenula via the stria medullaris. Other septal efferents join the precommissural fornix and end for the most part in the preoptic area and the hypothalamus. Fibers from the hypothalamus synapse in the septum and pass through to reach the hippocampus. Fibers also enter the septal region from the olfactory tubercle and the olfactory bulbs.

Review of the Literature

Spiegal, Miller, and Oppenheimer (23) have found the following symptoms in cats following the placement of large bilateral lesions in the columns

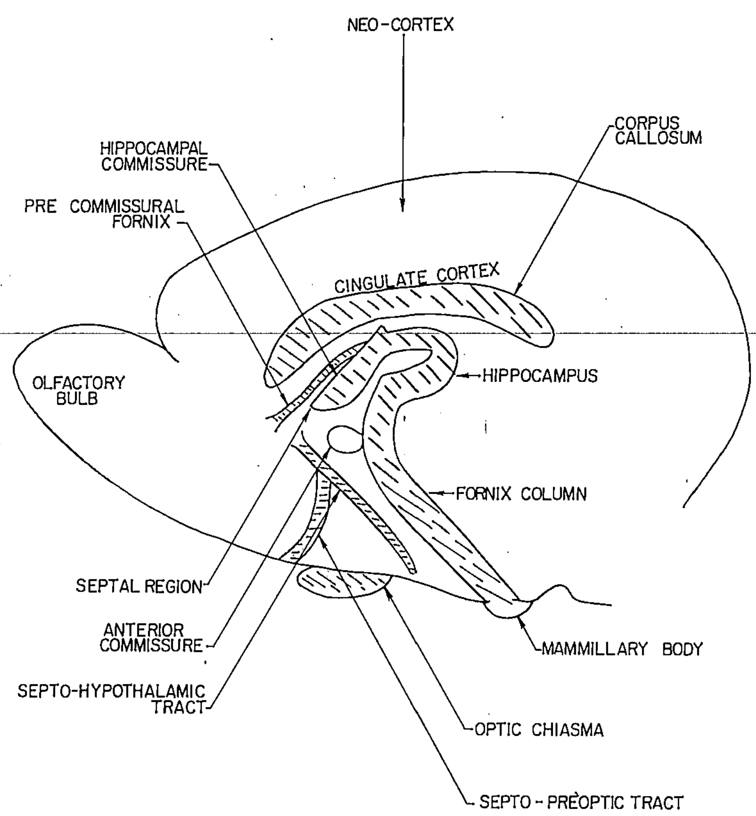

FIGURE 1
DIAGRAM OF A PARASAGITTAL VIEW OF THE RAT BRAIN

of the fornix and the septum: abnormal increase in motor activity and restlessness, hissing and clawing, attacks of violent motor activity every five to fifteen minutes during which the animal banged against the side and top of the small restraining cages. It was possible to precipitate these attacks by lifting the animal by the back of its neck. Unilateral destruction of the column of the fornix, puncture of the fornix, or puncture of the hippocampal commissure failed to produce any change in the animal's cage behavior. Green and Arduini (10) have reported that following the placement of electrolytic lesions in the septal region rabbits have appeared "hyperesthetic and unusually alert and fearful."

In Brady and Nauta's (4) study of the effects of lesions in the septal region on the behavior of the albino rat, the outstanding symptoms were as follows: Almost any auditory stimulus would produce an explosive startle reaction. The typical exploratory behavior of the normal rat was replaced by freezing behavior to the presentation of an innocuous object such as a pencil. Objects were attacked with vigorous biting. A magnet-like reaction was manifested to an object moved slowly about the snout. Handling the animal was difficult. It would flee from the experimenter and when captured would bite fiercely. When provoked it would leap about in rabbit-like fashion. If placed in a cage with other animals continuous fighting with loud and frequent vocalization was observed. Using an objective rating scale these investigators have noted a gradual decline in symptoms over a twelve day period. In a subsequent experiment, Brady and Nauta (5) found a sudden decline in the magnitude of the symptoms between the 30th and 45th postoperative days. By 60 days virtually all signs of what they designated as increased "emotional reactivity" had disappeared. They concluded that the differences in the duration of symptoms between the animals of the two experiments might be due to differences in the frequency of handling. The animals of the first group had been handled daily for 12 days for rating purposes. Animals in the second experiment were handled only on five occasions postoperatively (at 1, 15, 30, 45, and 60 days).

Brady and Nauta (4, 5) were concerned with the effect of lesions in the septal region on what they termed a "conditioned emotional response." The "conditioned emotional response" (CER) was defined in the following way: Animals were subjected to an unconditioned stimulus, i. e., an electric shock to their feet delivered through the floor of a grill box. The unconditioned stimulus was then paired with a conditioned stimulus, viz., a clicking sound. The animals within a few training sessions responded to the conditioned stimulus by crouching, becoming immobile, and defecating. Postoperatively it was found that although the septal animals showed a greater startle reaction and a higher score on an emotional rating scale, they appeared to have lost the CER. They no longer crouched and "froze" upon presentation of the conditioned stimulus but instead moved about the box. The writers recognized the possibility that the animals with septal lesions may have moved rather than frozen upon presentation of the conditioned stimulus because of a hypersensitive physiological state due to the lesion. In a follow-up experiment, with the same CS and UCS, but using cessation of a lever pressing response for food as the CER, Brady and Nauta found that postoperatively, again, there was some attenuation of the CER. The CER returned for all animals by sixty days.

Brady and Nauta (4) used a "stabilimeter-like apparatus" (a small box mounted upon the platform of a 5-pound postage scale) to record the magnitude of a rat's jump to a loud sound. A 22-caliber blank pistol fired at about two feet provided the startle stimulus. Vertical movements were recorded on a moving tape.

The Problem to be Investigated

The present investigation was planned primarily to study under experimental conditions changes in sensitivity to auditory stimulation in rats with septal lesions. It was decided to investigate behavior changes produced by septal lesions by measuring changes in behavior which occurred under fixed contingencies between that behavior and certain sounds. Essentially, this was achieved in the major study by allowing the animal to escape from a loud noise by pressing a lever.

In a supplementary study a second way of studying the effect of the septal lesion on the animal's behavior was by the measurement of the interfering effects of a noise with an ongoing activity. It would seem that noise intensities could be found which, although not suppressing preoperative behavior, might well suppress ongoing activity for the animal with a septal lesion.

Relevant Behavioral Methods

After searching for a response measure that would give constant, quantifiable results, it was decided that the so-called Skinner box technique (22) offered several advantages. Within a relatively isolated environment, a given response measure, e.g., a lever pressing response, can be maintained through the use of stimulus and motivational factors. When food is used as a reinforcement, stimulus control of the rate of lever pressing may be attained by the appropriate use of discriminative stimuli and reinforcement schedules.

Hefferline (13) and Keller (16) have conditioned rats to make lever-pressing avoidance responses to avoid a bright light. In these experiments some stimulus control was maintained over the response, but the control was not sufficient to maintain constant rates of response from the animals. Sidman (21) has recently demonstrated stimulus control using electric shock as an unconditioned stimulus. He has obtained constant lever pressing shock avoidance rates from rats. The rates can be controlled by varying the parameters of shock delay both as contingencies of the response and of the apparatus schedule. Ferster (9) has corroborated Sidman's demonstration of stimulus-maintained behavior. He has also shown that shock-maintained avoidance behavior may be alternated during the same session with food maintained behavior through the use of discriminative stimuli. Estes and Skinner (8), as well as Jetter, Lindsley, and Wohlwill (14) have demonstrated that suppression of food maintained behavior may be attained by the pairing of a conditioned stimulus (CS) with an unconditioned stimulus (UCS). Estes and Skinner, in their experiment with rats, used electric shock as the UCS and a buzzer as the CS. Jetter et al used the same type of CS. For the UCS a loud noise was employed. This latter study was done with only one dog as a subject.

In a preliminary study in the Boston University laboratory control animals have repeatedly demonstrated that lever pressing behavior is maintained indefinitely by noise intensities above a critical level. The day by day variation for noise-maintained behavior, as judged by inspection, is apparently of the same order as that for food schedules. In spite of this variability the intensity-latency functions remain discriminable once the animal has learned the response and the suitable intensities have been ascertained (12). These controls have been run according to the usual procedure for months with no significant change in their day by day results.

CHAPTER II

METHODOLOGY AND DESIGN OF THE EXPERIMENT

The Subjects

The subjects used in the experiments were 15 male albino rats.

The Apparatus

The Apparatus used in the experiments was a modified Skinner box. The inner dimensions of the box were 18 1/2" x 13 1/2" x 26 1/2". Adjacent to the food cup was a response lever. Above the food cup two lights were mounted. These came on for a one second interval at each positive reinforcement (food). A University Tweeter loud speaker (model 4401) was mounted at the top of the box for the reproduction of an auditory stimulus. Figure 2 is a picture of the box. On the outside of the box, but in the same room, was an automatic feeder (Gerbrands, Anger type). An Ampex tape recorder #600 was used as a source of limited white noise of adjustable intensity for the auditory stimulus. The Ampex #600 has a frequency response up to 15,000 cy/sec. The Tweeter was connected to the output of the amplifier by a 1-f condenser. Consequently, the noise reaching the animal consisted principally of high audio frequencies, i.e., 1000 to 15,000 cy/sec. In an adjacent room there was a relay control unit, a cumulative response recorder (Gerbrands model B), and a Program timer (Gerbrands). An electronic timer recorded the total time the noise was on. Separate counters

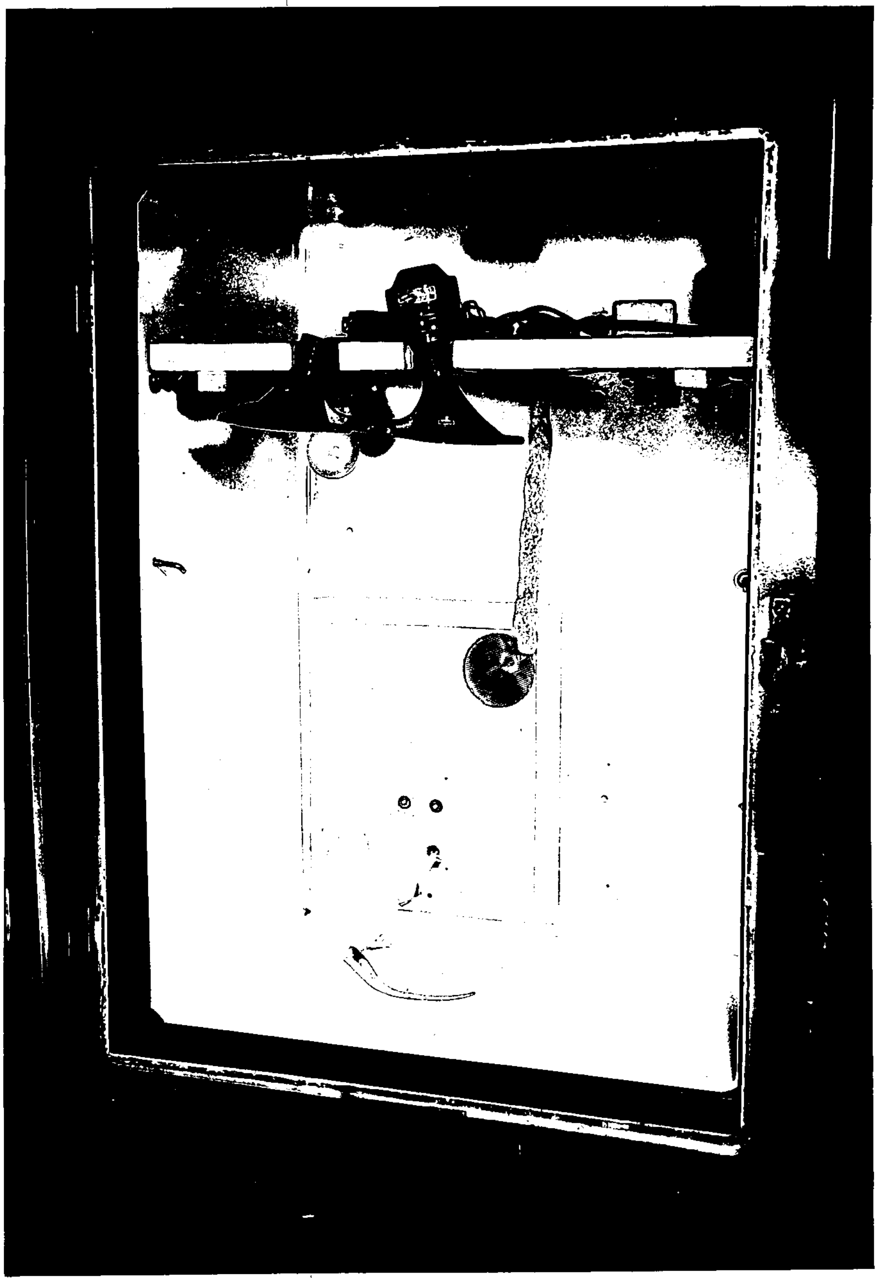

FIGURE 2
RAT AT WORK IN SKINNER BOX

recorded the number of lever pressing responses, the number of times the noise was terminated (negative reinforcement), and the number of times a pellet of food was delivered to the animal following a lever press (positive reinforcement). There was provision for magazine training as a first step in conditioning.

The Scope of the Study

Cage behavior observations

Each rat was observed daily for varying amounts of time pre- and postoperatively. These observations were made for a sufficiently long time so that some definite statements could be made as to the presence or absence of symptoms characteristic of the septal syndrome. The following is the list of symptoms employed in a check list for rating the animal pre- and postoperatively: An exaggerated startle to a puff of air on the dorsal surface (the startle would carry the animal to the proximity of the top of his home cage); an exaggerated startle to noises such as hand clapping; an exaggerated startle to touching the fur of the animal's back; a freezing response for up to sixty or more seconds following the startle response to auditory or tactile stimuli; freezing to the presence of an object slowly introduced into the cage; biting if handled; squealing if handled; a magnet-like reaction to a probe rotated in front of his nose; a magnet-like reaction when the probe touched the vibrissae; a rabbit-like hopping reaction if released from the cage and stimulated; whirling and gyrations when stimulated.

The presence or absence of a symptom was indicated by a plus or minus sign respectively. Doubtful instances were indicated by a question mark, Plus signs were assigned a value of two, question marks a value of one, and minus signs were considered to be zero. Each day the symptom scores were summed, and this total represented the syndrome rating for the day.

Experiment I: The noise-maintained behavior experiment

This was the basic experiment of this investigation. Its purpose was to ascertain if a septal animal is more or less sensitive to noise. According to cage behavior observations, it would appear likely that the septal animal would be hypersensitive to noise. This should be reflected in noise-maintained behavior. Two ways of quantifying the effectiveness of noise as a response maintainer were decided upon. The first was simply the lowest noise intensity level which would maintain a constant rate of lever pressing to turn off (or to keep off) this noise. The noise level to which the animal would respond constantly may be considered as a critical intensity.

The second measure of the effectiveness of noise was the latency time elapsing between the onset of noise and the lever press which turned the noise off. The longer the latency to turn the noise off the less effective is the noise as a maintainer of the response. Preliminary observations suggested that the septal animal's hypersensitive cage behavior would result in a lower critical noise intensity and a shorter cumulative latency time (total time the noise was on for a session) for noise-maintained behavior.

Experiment II: The noise interference experiment

This experiment was a supplement to experiment I. It was conducted for the purpose of further testing some of the conclusions arising from the noise-maintenance experiment. The technique was essentially that of studying the suppressing effect of three noise intensities (roughly commensurate with the intensities employed in the former experiment) on a food maintained response rate. It was felt that a noise level that failed to interfere preoperatively might become an effective interfering stimulus postoperatively. Or, an effective preoperative stimulus might become more effective as a suppressive agent postoperatively.

The Design of the Experiment

Preoperative conditioning procedure

All of the animals, whether experimental or control, were trained preoperatively to a positive reinforcement schedule with Purina lab chow pellets (45 mg). Following magazine training to the point where they invariably turned to the food tray at the sound of the magazine and the appearance of the light over the tray, the animals were trained to a constant rate of response to a one minute variable interval food schedule.

The experiment I rats were then subjected to a training schedule which depended upon a noise as a direct maintainer of the lever pressing response. The apparatus was set so that a noise was constantly present in the box unless the animal pressed the lever. On a regular reinforcement schedule a lever press was followed by a silent period of 17 seconds. If the animal responded during the silent period, a further 17 seconds was added to the period commencing from the time of the second press (12). Four animals were run on the noise-maintained schedule until they reached a steady rate of response. During the initial training a middle range intensity of noise was used to avoid traumatizing the animal. Once an animal had reached a steady response rate the functional relation between the intensity of sound and the cumulative latency time for a session was plotted daily. Intensity was varied until at least three intensity-latency functions were constantly discriminable, by inspection, for each animal. The maximum intensity produced a high constant rate of responding. The middle intensity resulted in an obviously lower rate. For the lowest intensity the animal responded at approximately the no-noise operant level for each animal. Each animal was usually run an hour a day. A no-noise operant rate was established during the first 15 minutes in the box. The remaining 45 minutes was divided into three sessions of 15 minutes each at a different descending intensity value. Between intensities the door of the box was opened, and a screen was placed across the opening for a period of one minute. This prompted the animal to leave the lever and move about the box. Possible interaction between intensities was eliminated by this procedure.

The experiment II rats were run on a one minute variable interval food schedule. The first twenty minutes was considered as representative of their rate of responding without the presence of an interfering noise. Interfering noise stimuli of three different ascending values were introduced once the food rate was constant. Between each five minute presentation of noise the animal was allowed to regain his approximate no-noise rate of responding. For three animals response rates were taken for one session under the three noise intensities. (Only one session was employed because it had already been empirically established that after a few sessions the animal adapted to the various noise values, i.e., the noise no longer suppressed their lever-pressing behavior on the food reinforcement schedule.) Four other animals were run until they had adapted to the several noise values. This latter group of rats was run in order to ascertain if the noise to which the normal animal had adapted would be suppressive to the animal with the septal lesion. For every session response rates under each intensity were plotted for each of these animals. A daily session lasted from sixty to ninety minutes.

<u>Surgical procedure</u>

The aim of surgery was to make a lesion in the septal region which would be sufficient to sever bilaterally a large portion of the fibers of the fornix system, as well as other septal fibers. An attempt was made to introduce this lesion to all but the surgical control rat. Anesthesia was produced with nembusen injected peritoneally 55 mg. /kg. The scalp was opened and the calvarium bared by gently scraping the periosteum laterally from the bone. A 1/16" burr hole was made in the skull approximately 1-2 mm rostral and 1.5 mm lateral to the coronal suture at the midline. The cutting instrument, essentially a needle with the point bent at a right angle and sharpened on the sides, was sunk to a measured depth and then rotated 180° medially. This insured a paramedian lesion. The length of the bent end of the needle was 2.5 mm. The incision was sprinkled with Sulfanilimide, closed with Michel clips, and the animal was given a massive dose of Duracillin.

<u>Postoperative study</u>

Immediately following recovery from anesthesia the animal was rated for the presence or absence of symptoms characteristic of the septal animal. The experiment I rats were studied in respect to the number of days required for the return of the lever-pressing response, the critical noise intensity, and the cumulative latency times. The number of days required for the return of the lever-pressing response was also recorded for each rat of experiment II. Once the no-noise food schedule was up to its preoperative level, each rat was tested under the preoperative conditions.

Controls

Two animals served as pre- and postoperative subjects on a food-maintained schedule. The purpose of the food-maintained response before and after surgery was to provide a rough check on the animal's capacity to press the lever following surgery at a rate commensurate with his preoperative rate. For the noise animals any possibility of interaction of the food schedule was controlled out by fattening the noise animals on ad libitum feeding, and also by providing extra wet Purina mash for the animal at least one hour before each experimental session.

One animal was run as a control of the effects of a superficial operation on noise-maintained behavior. The animal was anesthetized, and a small lesion was introduced by inserting a hypodermic needle which passed through the corpus callosum and penetrated the caudate.

Two animals were run to ascertain if they could make a noise discrimination both pre- and postoperatively. This procedure consisted of training the animal to make a discrimination between a variable interval food reinforcement schedule (S^D) and a no-food reinforcement situation (S^Δ). Under the S^D conditions noise of varying values was present. Under S^Δ conditions there was no noise in the box. Another variable interval schedule automatically switched the discrimination conditions aperiodically. A Skinner box essentially the same as the one used for all the other experiments reported here was employed for this discrimination test.[1] The same noise source was used. Under the discrimination situation described here the hungry animal should become conditioned to respond at a much higher rate under the S^D situation than under the S^Δ if he were able to discriminate the noise from no noise.

All animals on a food-maintained schedule were run at from 70-80% body-weight and were fed on a 23 hour feeding schedule.

Histological study

After varying periods of time the rats were sacrificed and their brains were studied histologically. The brain tissue was stained with a Cajal Method II silver technique (1). They were then infiltrated and embedded in paraffin and sectioned at 15 microns. Every fifth section was mounted for examination.

1 Acknowledgment is made to George Samuel Grosser for his assistance and the use of his apparatus in this part of the experiment.

CHAPTER III

RESULTS OF THE EXPERIMENTS

Cage Behavior

The syndrome ratings of each of the critical experimental animals for various numbers of postoperative days are given in figures 3, 4, and 5. This rating is composed of the total symptom score. Five of the preoperative rats are not represented here for reasons to be noted under the appropriate sections.

Experiment I: The Noise Maintained Behavior Experiment

Experimental animals

Four rats were trained preoperatively under the noise-maintained behavior conditions. One of these animals, H 28,[2] died a few days postoperatively before any significant data was obtained from him.

Figure 6 shows the pre- and postoperative cumulative latencies of the several intensity parameters for H 25. This animal was run on 65 days of the 99 day period. The first break in the baseline indicates that the response had not returned to a constant rate until the 72nd day. At times during this period the animal did respond, but the response rates were only at, or slightly above, the operant level. It is to be noted that the cumulative latencies for the two higher intensities have shifted upward

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2 See Appendix for a glossary of animal designations and manner of treatment of each animal.

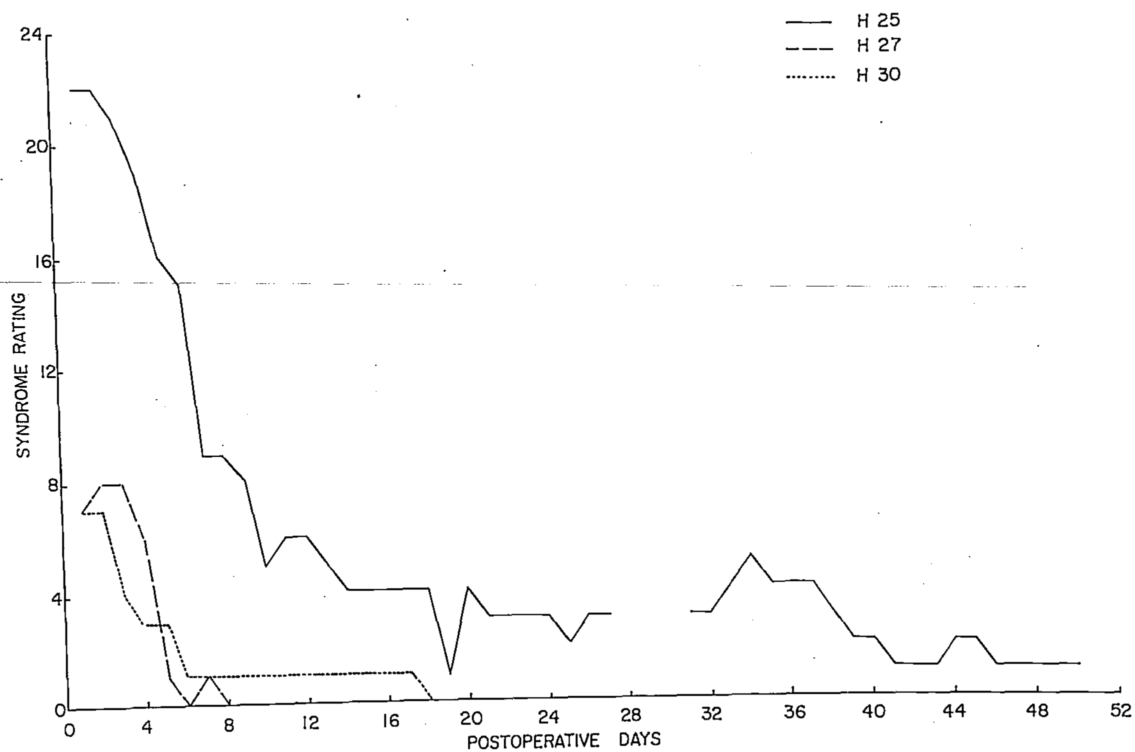

FIGURE 3

POSTOPERATIVE SYNDROME RATING, RATS: H 25, H 27, H 30

(The broken line indicates no ratings for days 28, 29, and 30)

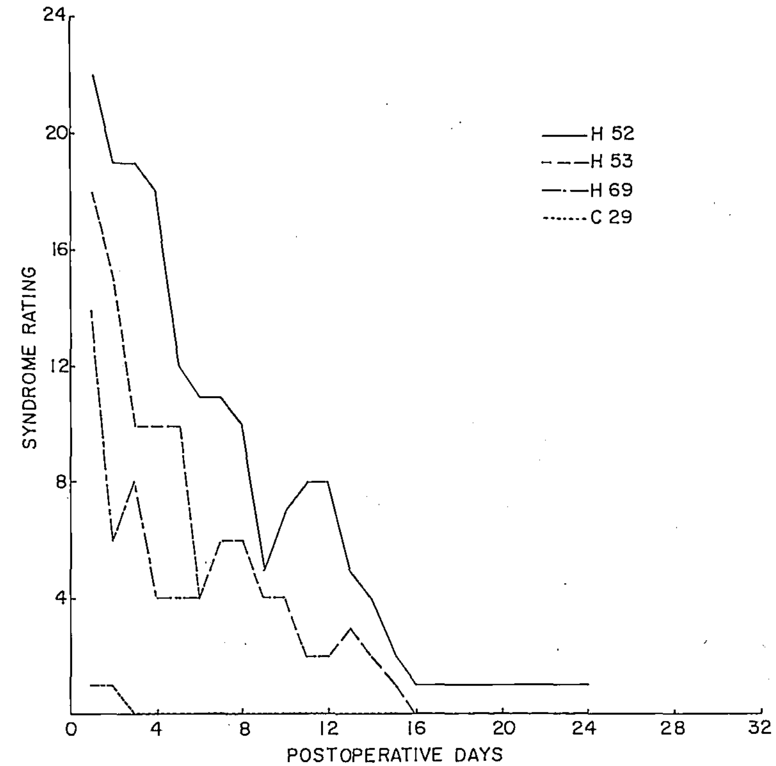

FIGURE 4
POSTOPERATIVE SYNDROME RATING, RATS: H 52, H 53, H 69, C 29

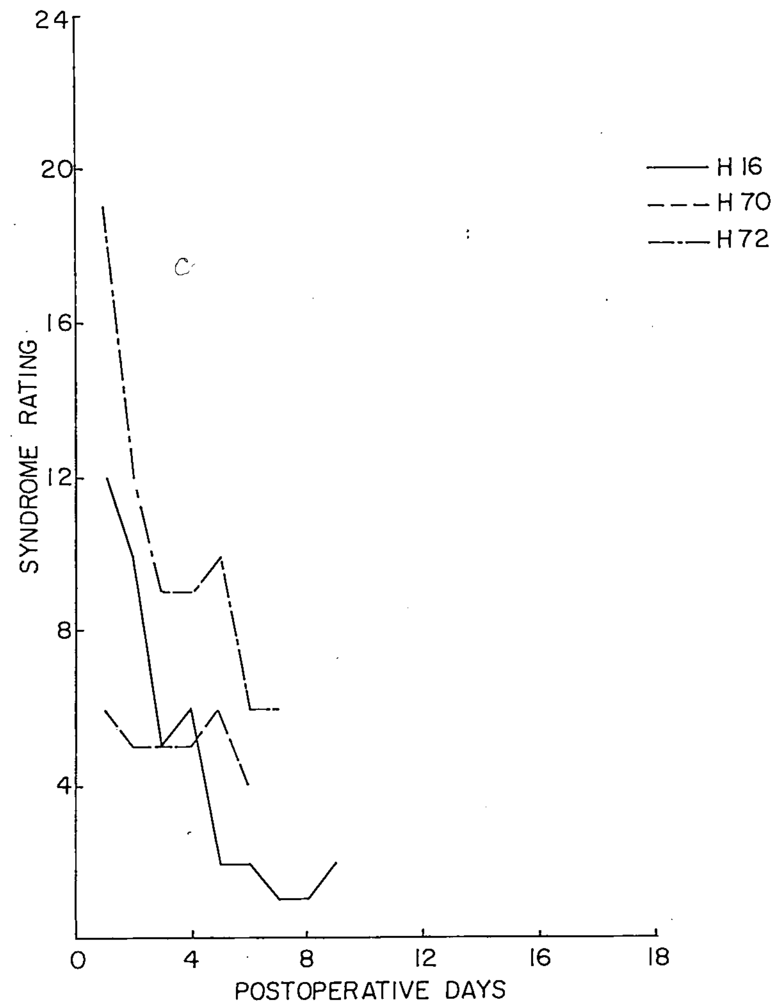

FIGURE 5
POSTOPERATIVE SYNDROME RATING, RATS: H 16, H 70, H 72

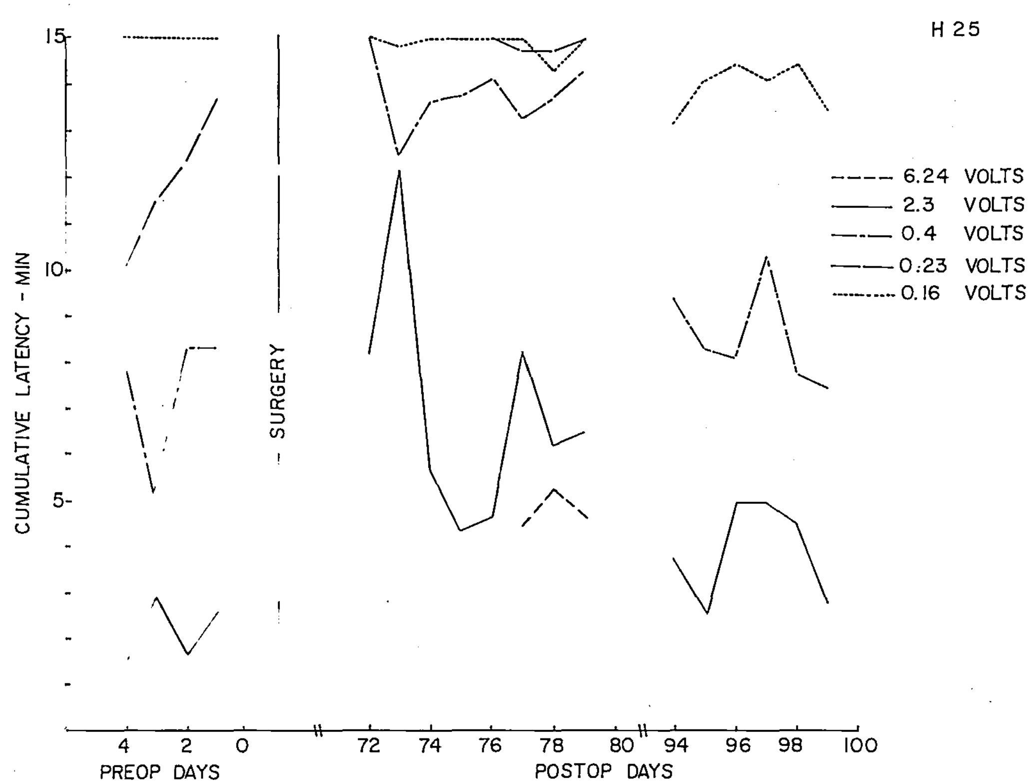

FIGURE 6
CUMULATIVE LATENCIES FOR SEVERAL NOISE INTENSITIES, RAT: H 25

to the vicinity of the lowest intensity. From the 72nd day until the 99th day there is a gradual drop in the cumulative latencies for these two intensities. The three latencies had resumed discriminable differences by about the 94th day. (It was decided to terminate the 0.23 voltage intensity in the interests of economy of time.) On the 77th, 78th, and 79th days a much higher voltage intensity was used to ascertain if it would decrease the cumulative latency time. Significantly, this did occur. This supplements the evidence of a general shift of the critical intensity upward. Although the higher intensity did not reduce the latency time to the level of the highest preoperative level, presumably a still higher intensity would have done so.

Tables I, II, and III present the data for animals H 25, H 27, and H 30. It is to be noted with H 27 that by the 67th day cumulative latency times had returned to their approximate preoperative levels for the three noise intensities. H 30 was run for only four postoperative days. It is, however, quite obvious that these data are in general agreement with the other two animals in the experiment, viz., that there is a shift upward in the critical noise intensity required for the animal to make the escape response.

<u>Control animals</u>

The two animals serving as controls for the retention of the motor act of pressing the lever showed no impairment in this respect following

TABLE I

CUMULATIVE LATENCY FOR FOUR INTENSITIES PRE- AND POSTOPERATIVELY: H 25

(Cumulative latency expressed in minutes)

	Intensities (Volts)				
Days	6.24	2.3	0.4	0.23	0.16
4		1.58	7.92	10.08	15.00
3		2.90	5.13	11.58	15.00
2		1.62	8.33	12.33	15.00
1		2.60	8.33	13.75	15.00
Surgery					
72		8.17	15.00		15.00
73		12.17	12.50		14.75
74		5.68	13.67		15.00
75		4.34	13.87		15.00
76		4.68	14.15	15.00	15.00
77	4.42	8.34	13.30	14.72	15.00
78	5.25	6.20	13.75	14.72	14.43
79	4.67	6.50	14.33	15.00	15.00
94		3.75	9.42		13.17
95		2.58	8.33		14.15
96		5.00	8.13		14.50
97		5.00	10.33		14.15
98		4.50	7.75		14.50
99		2.75	7.50		13.50

TABLE II

CUMULATIVE LATENCY FOR FOUR INTENSITIES PRE- AND POSTOPERATIVELY: H 27

(Cumulative latency expressed in minutes)

	Intensities (Volts)				
Days	6.24	2.3	0.4	0.23	0.16
4		3.55	10.00		14.50
3		2.50	10.83		13.08
2		2.07	8.33		10.25
1		4.12	8.08		13.58
Surgery					
30	5.00	13.33	15.00		15.00
37		4.88	12.58		14.15
38		4.67	13.00		12.00
49		9.08	12.73		13.87
53		13.17	13.87		12.75
54		13.00	14.43		15.00
66		2.05	11.30		13.17
67		2.13	9.50		13.30
68		3.17	5.28		14.72
69		3.25	9.33		14.50

TABLE III

CUMULATIVE LATENCY FOR FOUR INTENSITIES
PRE- AND POSTOPERATIVELY: H 30

(Cumulative latency expressed in minutes)

	Intensities (Volts)				
Days	4.16	2.3	0.4	0.23	0.16
3		4.77	11.50		15.00
2		5.38	12.25		15.00
1		4.80	12.72		14.72
Surgery					
54	7.00	15.00	14.72		15.00
55	6.17	14.08	12.50		14.15
56	7.50	11.42	13.83		15.00
57	12.00	15.00	15.00		15.00

the septal lesion. Figure 7 shows the actual pre- and postoperative food-maintained response curves for H 53. The data for another animal (H 52) was virtually identical, so it is not reproduced here. H 53 regained his preoperative response rate within a few days after surgery. The return of the response rate while recovering from the effects of surgery is obvious.

In figure 8 we have presented a section of actual pre- and postoperative noise-maintained response curves for C 29, the anesthesia and surgical control animal. A record was taken for only one noise intensity. The slope and the frequency of the small vertical bars on the cumulative response curve are indices of the rate. The difference between the two rates, as judged by inspection, is within the day by day variation for this measure. So, we can conclude that the effect of the anesthesia, the placement of burr holes in the skull, and a minor lesion in the cortex apparently had no effect on the noise maintained response.

The results for the noise-discrimination control animal, H 69, are shown in figure 9. The discrimination between noise and no-noise, which is obvious preoperatively, is not modified by surgery after one postoperative day. The numerical values for H 69 and H 25 are listed in tables IV and V respectively. Although H 25 was not run on this discrimination test preoperatively, he was started on this schedule on the 42nd postoperative day. The discrimination was rapidly formed. This discrimination was

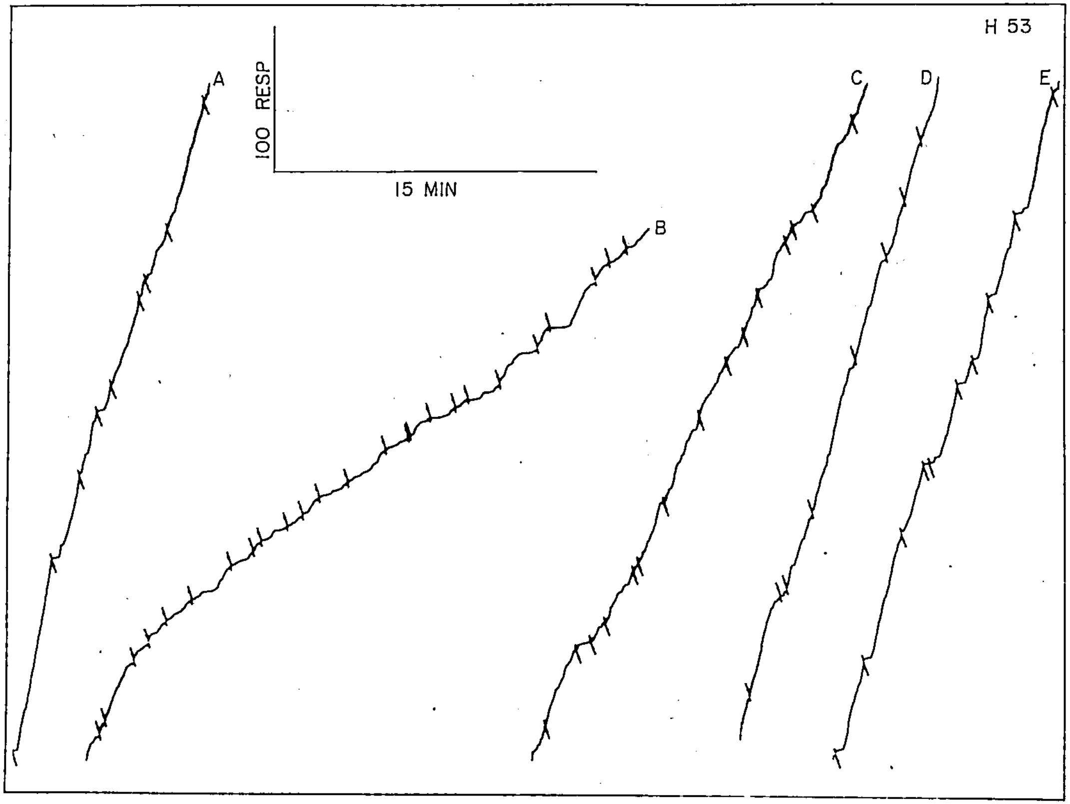

FIGURE 7
PRE- AND POSTOPERATIVE FOOD-MAINTAINED RESPONSE CURVES
A: One Day Preoperatively. B: One Day Postoperatively. C: Three Days Postoperatively. D: Five Days Postoperatively. E: Seven Days Postoperatively, RAT: H 53

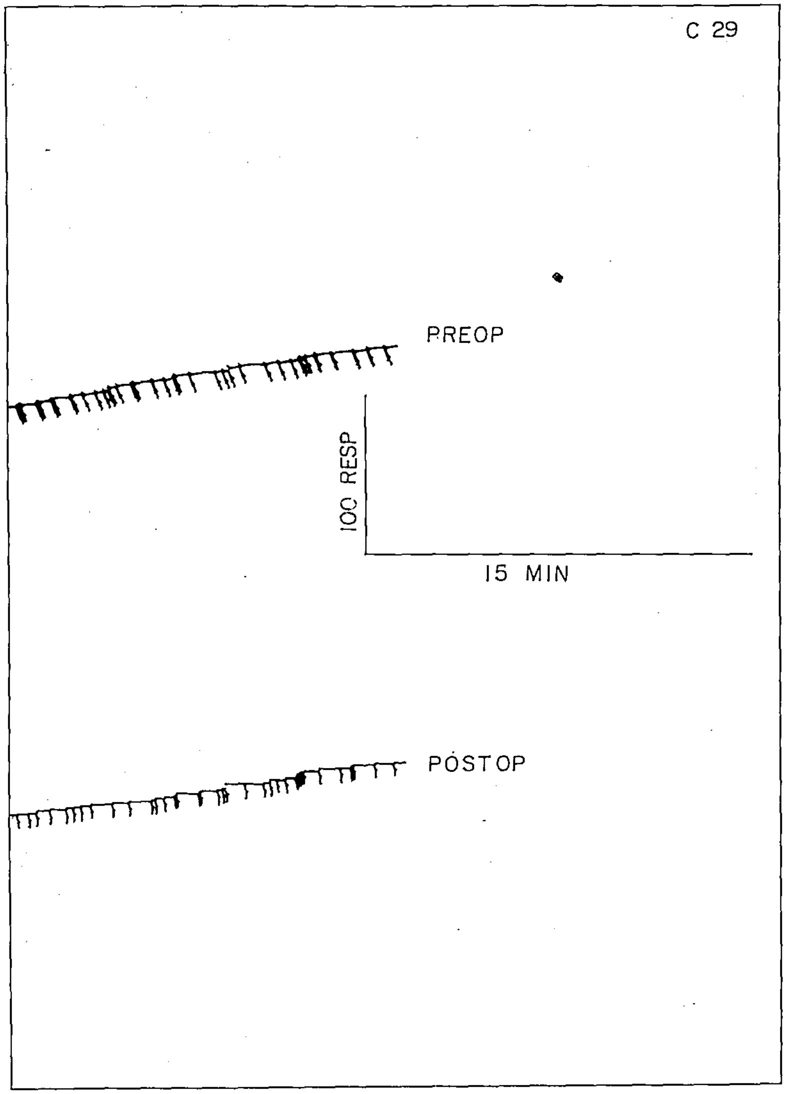

FIGURE 8
PRE- AND POSTOPERATIVE NOISE-MAINTAINED RESPONSE
Preoperative: One Day Before Surgery.
Postoperative: Five Days After Surgery. RAT: C 29

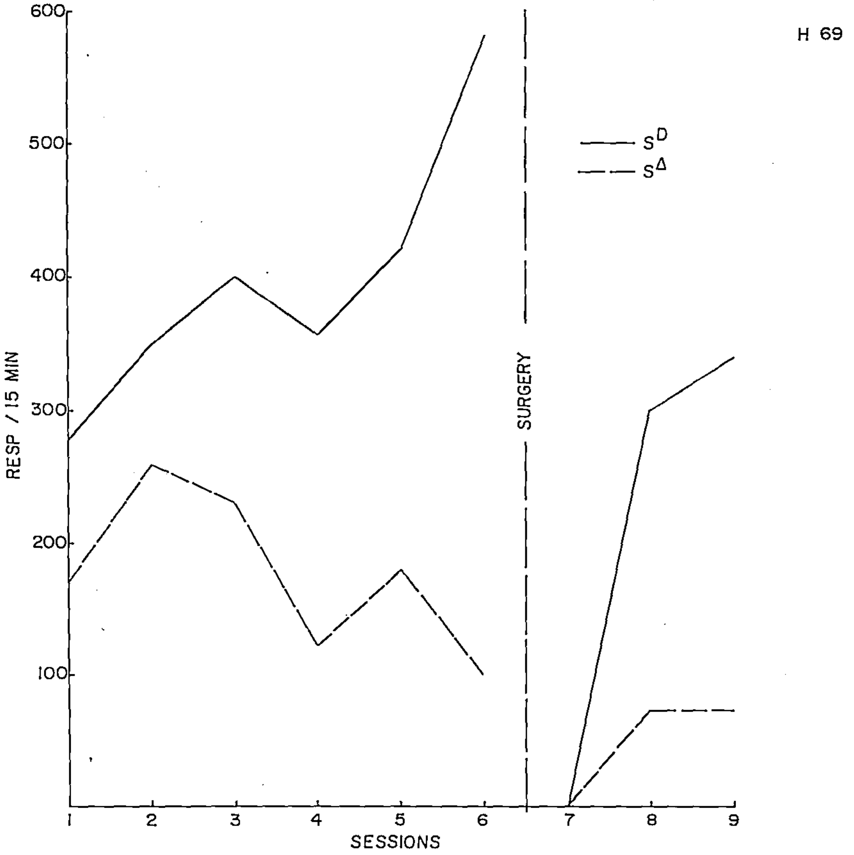

FIGURE 9
NOISE DISCRIMINATION RESPONSE RATES, RAT: H 69

TABLE IV

S^D, S^Δ DISCRIMINATION PRE- AND POSTOPERATIVELY: H 69

Session	S^D	S^Δ	Intensity (Volts)
1	280	170	0.68
2	350	260	0.68
3	400	230	0.68
4	360	120	0.68
5	420	180	0.68
6	580	100	2.30
Surgery			
7	0	0	0.68
8	300	70	0.68
9	340	70	2.30

TABLE V

POSTOPERATIVE S^{D}, S^{Δ} DISCRIMINATION: H 25

Session	S	S	Intensity (Volts)
1	460	290	0.16
2	550	375	0.16
3	500	240	0.16
4	420	120	0.40
5	475	240	0.40
6	400	180	0.68
7	510	360	0.68
8	650	330	2.30

maintained over a range of noise intensities to which the animal had worked under the escape conditions.

Experiment II: The Noise Interference Experiment

In table VI the time required for the surgical animals to regain their preoperative operant rate is given. H 18 did not show the syndrome. Consequently he was not run postoperatively, and is not included in the table. Rats H 13 and H 21 showed unusually long surgical recovery periods and corresponding losses of the syndrome. Figures 10 and 11 are two curves representing the rate of responding under the 2.3 voltage intensity as a percentage of the no-noise response rate for H 16 and H 14. It may be noted that for both animals adaptation to the noise was essentially unaffected by the lesion. H 14 was an operated animal which did not exhibit the syndrome. He thus served as a control for H 16, an animal with the typical set of symptoms.

Figures 12 and 13 are thenoise-interference curves for animals H 16 and H 72. Animal H 16 had adapted to the interfering noise stimulus before surgery. H 72 had been run only one day preoperatively and had not adapted to the effects of the noise. The significant finding is, of course, that neither animal demonstrated any suppressive effects following the septal lesion on their food-maintained behavior. Table VII gives the pre- and postoperative response rates for all the animals, except H 18, for experiment II.

TABLE VI

RECOVERY TIME FOR RATS OF EXPERIMENT II

(Postoperative days required to regain preoperative operant rate)

Rat	Days Postoperative
H 13	11
H 14	4
H 16	4
H 21	14
H 70	5
H 72	7

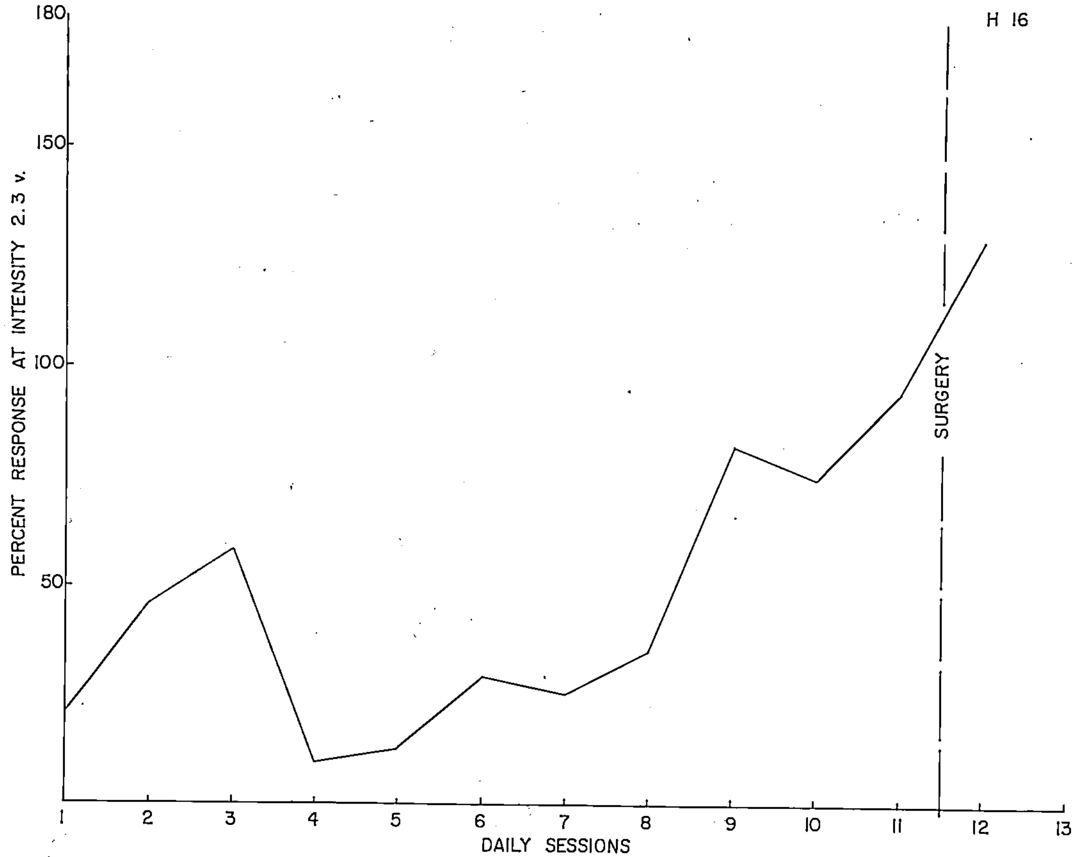

FIGURE 10
RESPONSE RATE UNDER THE 2.3 VOLTAGE INTENSITY
AS A PERCENTAGE OF THE NO-NOISE RESPONSE RATE, RAT: H 16

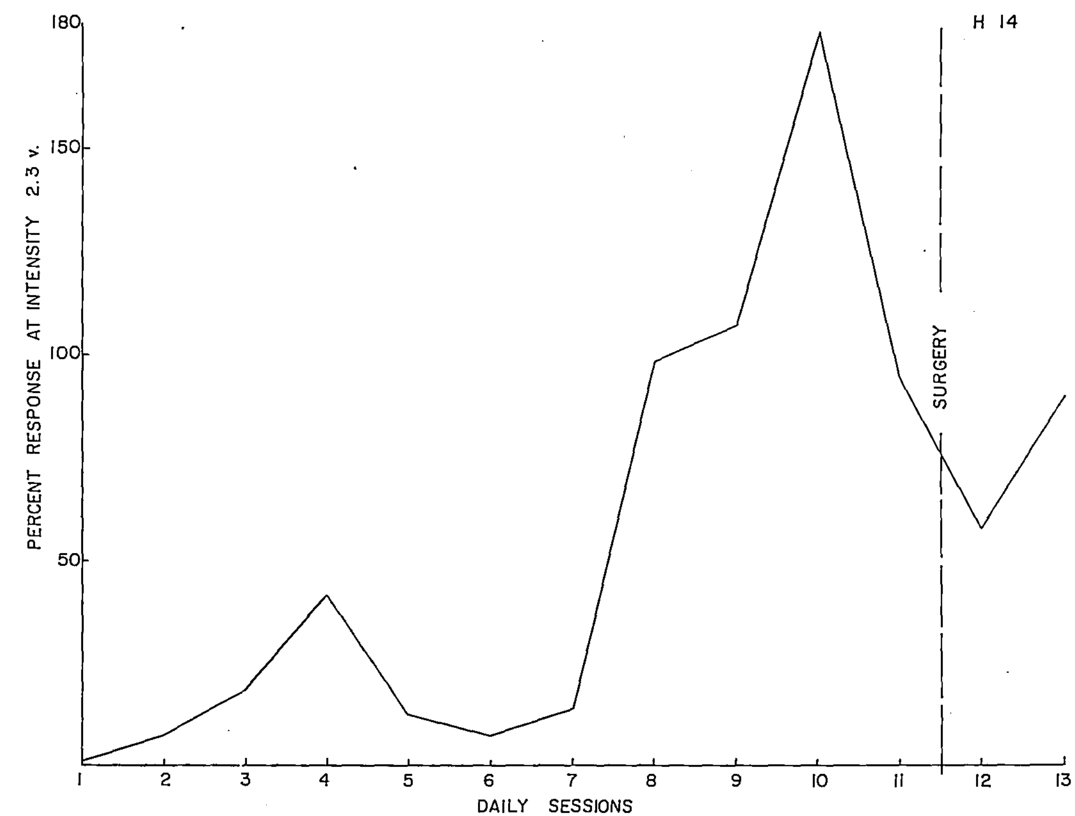

FIGURE 11
RESPONSE RATE UNDER THE 2.3 VOLTAGE INTENSITY
AS A PERCENTAGE OF THE NO-NOISE RESPONSE RATE, RAT: H 14

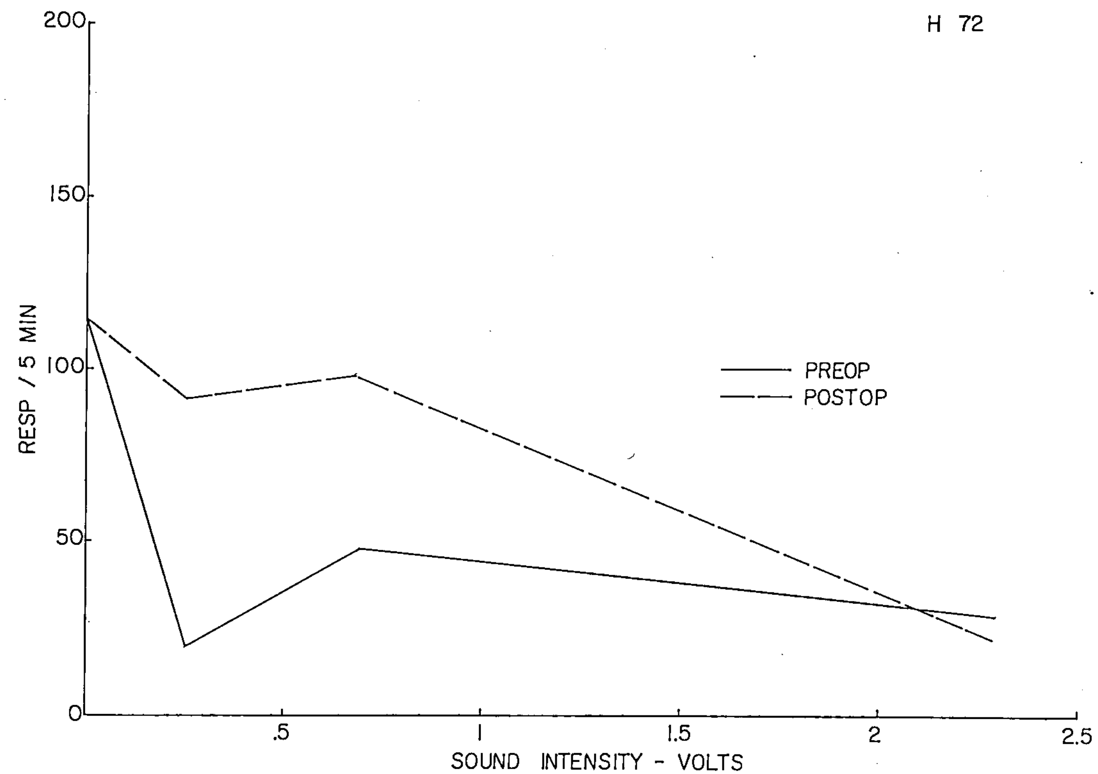

FIGURE 12
EFFECTS OF INTERFERING NOISE PRE- AND POSTOPERATIVELY, RAT: H 72

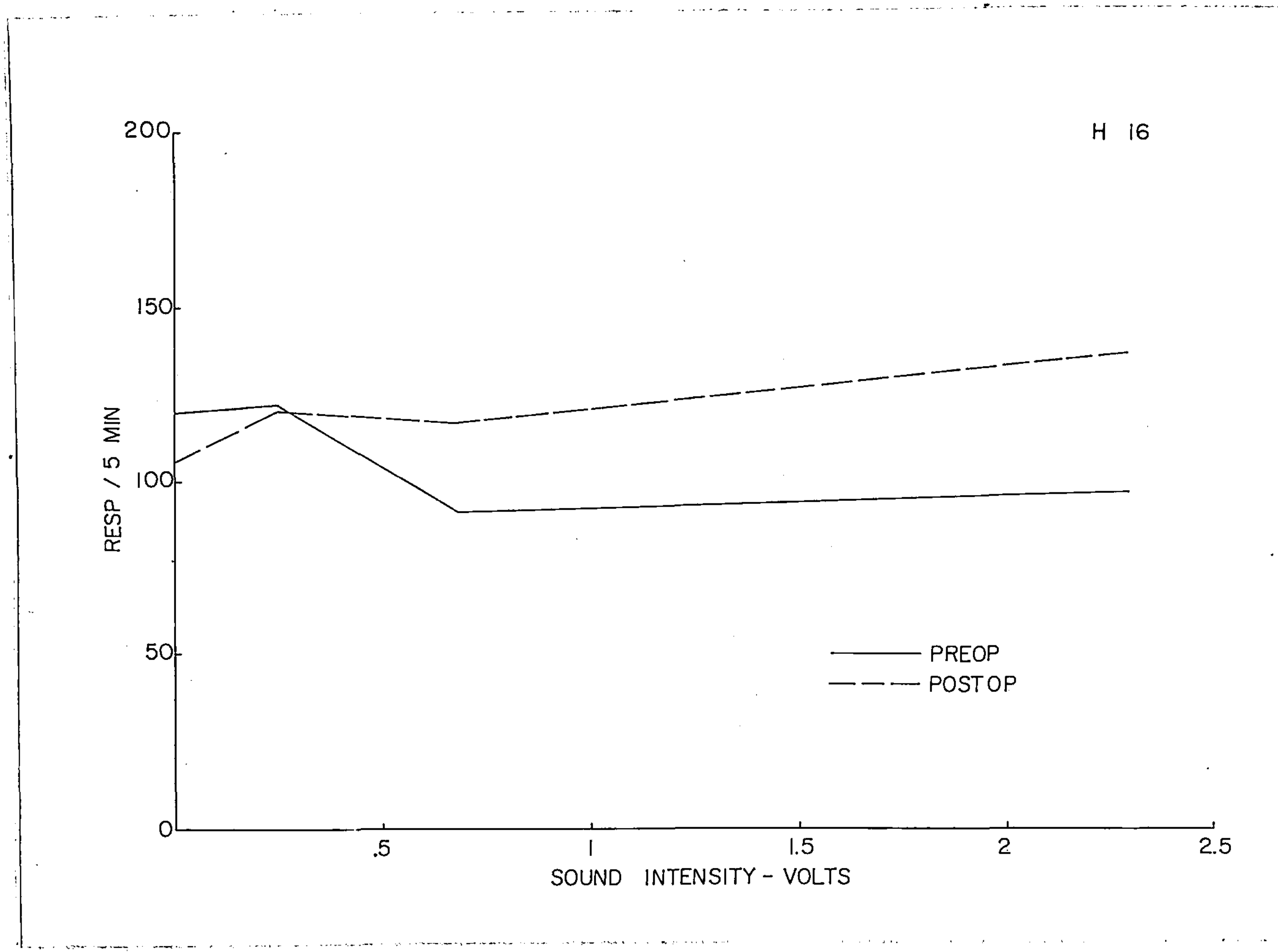

FIGURE 13

EFFECTS OF INTERFERING NOISE PRE- AND POSTOPERATIVELY, RAT: H 16

TABLE VII

FOOD MAINTAINED RESPONSES UNDER THREE INTERFERENCE INTENSITIES—5 MINUTE SESSIONS

Rat	H 13				H 14				H 16			
Intensity (Volts)	0	0.25	0.68	2.30	0	0.25	0.68	2.30	0	0.25	0.68	2.30
Sessions	94	77	79	46	210	8	3	5	145	151	125	31
	Surgery				269	130	75	20	145	149	130	67
	165	160	181	172	266	90	81	49	182	140	117	106
					300	178	145	170	150	110	76	13
					250	181	192	33	185	135	63	22
					260	224	154	17	170	120	84	47
					225	180	115	31	165	86	65	40
					200	301	285	195	130	110	130	44
					285	275	325	285	145	120	120	119
					195	213	265	347	125	122	109	92
					185	190	169	174	135	138	143	127
					Surgery				Surgery			
					160	85	107	92	105	120	117	137

Rat	H 21				H 70				H 72			
Intensity (Volts)	0	0.25	0.68	2.30	0	0.25	0.68	2.30	0	0.25	0.68	2.30
Sessions	145	204	180	145	98	88	69	9	115	20	47	31
	172	150	158	170	Surgery				Surgery			
	185	209	226	196	104	147	39	26	115	91	97	23
	140	166	151	185								
	Surgery											
	144	181	193	218								

Histological Study

The primary lesion in all animals which manifested the behavior syndrome consisted of the obliteration of tissue centered around the genu of the corpus callosum and extending ventrally and caudally into the upper third of the septum. All animals sustained extensive damage of the medial cortex over the rostral quarter of the corpus callosum and forward toward the tip of the hemisphere. The forward quarter of the corpus callosum was usually degenerated or completely obliterated. The fornix longus and the rostral end of the induseum greseum were also obliterated or degenerated in all animals. Damage to the septal nuclei, the primordial hippocampus, and the forward continuation of the hippocampus was present only in some animals. (See table VIII.)

Damage to the principal hippocampal system was present in only some of the animals which showed the behavior syndrome. In rats H 25 and H 27 the descending fornix columns, the precommissural fornix, the ventral hippocampal commissure, and the fornix superior were completely degenerated. In animals H 30, H 53, and H 72 damage to these structures was either absent or minimal. The hippocampus and dentate fascia appeared to be normal in all animals.

In animal C 29 the lesion consisted merely of two bilateral stab-like lesions which penetrated the cortex, corpus callosum, and the upper quarter of the caudate nucleus.

A summary of the lesions of each of the critical animals is given in table VIII.

TABLE VIII

SUMMARY OF OPERATIVE LESIONS

Rats	Rat.	V.H.C.	F. Sup.	Col. F.	P.C.F.	L.S.N.	L.F.S.	M.F.S.	F.C.H.	P.H.
H 25	22	2	2	2	2	2	2	1	2	2
H 52*	22	0	1	L0	L1	L1	2	L1	2	1
H 72	19	0	0	0	0	1	2	1	1	1
H 53	18	0	0	0	0	1	1	1	1	1
H 69	14	1	2	2	2	2	2	2	2	1
H 16	12	1	2	1	2	2	2	2	2	2
H 27	8	2	1	2	2	1	0	1	0	0
H 30	7	0	0	0	0	0	0	0	1	1
H 70	6	1	0	0	0	1	1	2	1	1
C 29	1	0	0	0	0	0	0	0	0	0

0 indicates less than 10% primary damage or degeneration, 1 indicates between 10% and 90% damage, and 2 indicates more than 90% damage or degeneration. Beh. Rat: behavior rating. V.H.C.: ventral hippocampal commissure. F. Sup.: fornix superior. Col. F.: columns of the fornix. P.C.F.: precommissural fornix. L.S.N.: lateral septal nucleus. L.F.S.: lateral fine septal fibers. M.F.S.: medial fine septal fibers. F.C.H.: forward continuation of the hippocampus. P.H.: primordial hippocampus.

*L indicates that the damage is on the left side. On the right side the structures were obliterated.

**Because of technical difficulties it was impossible to completely read the slides for H 14 and H 18.

CHAPTER IV

DISCUSSION OF RESULTS

The primary question asked in this study was whether rats with lesions in the septal region would show greater sensitivity to noise stimulation than they had preoperatively. Sensitivity was defined in terms of the intensity of noise necessary for a lever-pressing contingency, and the rate of lever pressing to a given noise. It was found that septal animals consistently showed less sensitivity in the experimental situation than they had preoperatively. For the three animals on a noise-maintained behavior schedule there were long delays before responding postoperatively. The shift for critical noise intensities was upward. The cumulative latencies were greater than they had been preoperatively.

The lever pressing response did not return for weeks after the symptoms had disappeared for all three animals. This suggests that the noise-maintained response is a more sensitive measure of changes in behavior in the septal animal. Of course, the effects of lesions in various other parts of the brain, particularly in subcortical areas, needs to be explored thoroughly for more adequate control of the differential influence of different areas on this type of response. The surgical control animal ruled out the possible effects of the anesthesia, the burr hole, and a small amount of neocortex damage. What, if any, effects lesions in other regions of the brain may have on noise-maintained behavior cannot be answered without another major experiment.

The experiment reported here developed from the cage observations of the septal animal. The animal's responses to noise were considered characteristic of hypersensitivity to auditory stimuli. The experimental results were unexpected in light of the cage observations and the original formulation of the study.

Basically this may reflect nothing more than a question of how sensitivity is defined. The resolution of the problem is to consider the animal's exaggerated reaction to noise in the cage as a different class of behavior from the lever-pressing response to escape a noise. The exaggerated startle, frequent squealing, and freezing observed in the septal rat may be classified as essentially reflexive in nature. On the other hand, the act of pressing a lever to turn off a noise may be considered as falling in that general class of responses called instrumental. From this point of view we may state that whereas the rat is more sensitive to noise in terms of certain reflex response measures in the cage situation, it is less sensitive to noise insofar as the instrumental lever pressing response to noise is concerned. Hence, although the two response classes do not fall in the same general class, another response measure is now available for the study of the changes following the placement of septal lesions.

Insofar as the anatomy is concerned, it appears to be fairly clearly established that sectioning the hippocampus proper does not result in the typical behavior syndrome which has been described in this paper. This is in general agreement with Swann (24) who found no change in the general behavior of rats with up to 75% bilateral destruction of the hippocampus together with varying amounts of damage to the induseum greseum, fornix, and cingular gyrus. Bard (3) removed nearly the entire hippocampi in two cats. Postoperatively, neither animal showed any significant changes in cage behavior or to nocioceptive stimulation. A slight increase in "tameness" was reported. Allen (2) found no change in the behavior of dogs following the placement of lesions in the hippocampi. In general, the results of the present study agree with Brady and Nauta (4) in emphasizing the importance of the septal region. As has been already noted, Spiegal et al (23) found symptoms in cats somewhat similar to Brady and Nauta's following lesions of the fornix column and septum.

Insofar as extrapolation of findings from one species to another is permitted, it appears likely that these results may have been due to the damaged septum. Green and Arduini (10), in work with rabbits and cats, reported that ten to thirty days following the placing of electrolytic lesions in the septal region of rabbits these animals appeared "hyperesthetic and unusually alert and fearful." These writers suggest that afferent connections to the hippocampus are mediated through the septum by way of precommissural and dorsal fornix fibers. Study of these areas in our animals does not substantiate the importance of severance of the dorsal or precommissural fornix in the production of the symptoms. Two of our animals (H 72 and H 53) manifested the syndrome with minimal or no damage to these structures.

In reviewing table VIII, no single area can be singled out as critically involved in the behavioral syndrome. It appears that if a more specific critical area is to be designated it will be necessary to study the effects of more precisely placed lesions. The stereotaxic instrument may be advantageously used in such an experiment.

In attempting to explain the lessened sensitivity of the septal animal to noise in the noise escape experiment several possibilities may be presented. First of all, amnesia for the lever pressing response following the septal lesion is ruled out by the quick return of the food-maintained response in H 52 and H 53. The possibility that freezing might have delayed the return of the lever-press escape contingency would seem unlikely inasmuch as the noise interference animals showed no postoperative noise suppressive effects. Also, the noise had no suppressive effect on H 69 and H 28 under the discrimination conditions. Gross deafness, too, can be eliminated by these latter data. The question of permanent hearing loss for certain high frequencies is impossible in the light of the eventual return of the critical intensities to their preoperative level in H 27. The problem of the necessary and sufficient lesion to produce the effect of delaying the response recovery and raising the critical intensity level remains to be solved as with the cage behavior syndrome.

It is possible, however, to offer suggested directions for further experimentation which will shed more light on the problem. A next step might be in the direction of systematic exploration of tactile sensitivity in an instrumental escape situation similar to the one described in this dissertation. Escape from tactile stimulation of a particular surface of the rat's body would be made contingent on a specified response. Inasmuch as the bottom of the rat's feet might be one area to be studied, a lever-pressing response would probably not be appropriate. There are, however, many other classes of responses to choose from in selecting a dependent variable.

The investigation of what is lost in audition in the animal with a septal lesion is, of course, an equally important one. A careful scrutiny of the nature of the loss might begin with an exploration of the use of higher intensities of noise than those employed in the present study. At what point the animal will begin to respond postoperatively when higher noise intensities are used needs to be ascertained. The possibility of temporary loss of sensitivity to specific sound frequencies is a problem which may turn out to merit consideration in the light of future data.

CHAPTER V

SUMMARY AND CONCLUSIONS

The experiments reported here were conducted to ascertain if albino rats subjected to lesions in the septal forebrain region became more sensitive to noise stimulation. This problem developed from the observation that animals with lesions in the rostral part of the hippocampus and the septum manifested characteristic symptoms which suggested hypersensitivity to auditory and tactile stimuli.

The primary purpose of the investigation was to study the sensitivity of individual rats to noise pre- and postoperatively under experimental conditions. A second purpose of the study was to ascertain if the septal area was the critical area involved in the production of the symptoms and to attempt to further delimit the nerve pathways and nuclei involved.

A modified Skinner box was used to obtain the experimental data. A lever-pressing response was the instrumental act recorded on a cumulative recorder. This response was contingent upon noise escape in the experimental animals. For certain controls several animals were run under food maintained lever-pressing conditions. A total of 15 male albino rats were used in the experiments.

Using a critical noise intensity level and the cumulative latency time to turn off a noise as dependent variables, it was found that each of the three experimental animals postoperatively were less sensitive to the noise than they had been preoperatively. It was also found that they required periods ranging from 30 to 75 days after surgery before they recommenced the noise-maintained response. Direct effects of the surgical procedure per se on the lever-pressing response was ruled out by control animals.

Freezing to the noise was tested by subjecting septal animals on a food schedule to an interfering noise of similar intensities to that employed with the noise-maintained response animals. The noise did not effectively interfere with or freeze the animals on the food schedule. Control animals demonstrated that they could still make a discrimination between noise and no noise on a food reinforcement schedule. This made an hypothesis of tempor*ar*y deafness untenable.

The question of why the rat appears to be hypersensitive to noise when observed under home cage conditions and less sensitive in terms of the dependent variable under experimental conditions is explained by a basic difference in the nature of the two classes of responses. The animal may be described as hypersensitive when certain reflexive responses are studied in the cage situation. On the other hand, the animal was less sensitive when the instrumental act of turning a noise off was involved. Significantly, the instrumental lever-press for food was not affected by the septal lesion.

Insofar as the anatomy is concerned, the results strongly indicate that sectioning the hippocampus proper does not result in the typical behavioral syndrome described in the paper. This is in general agreement with the available literature. In general, the results agree with Brady and Nauta in emphasizing the importance of lesions in the septal region in producing the syndrome. A more precise designation of the specific pathways and nuclei involved was not warranted after histological study.

APPENDIX

Glossary of Animal Designations and Manner of Treatment

Experiment I:

H 25	Pre- and postoperative noise-maintained behavior. This animal also was trained in a postoperative noise discrimination situation.
H 27, H 30	Pre- and postoperative noise-maintained behavior.
H 28	Preoperative noise-maintained behavior. This animal died three days postoperatively.
H 52, H 53	Pre- and postoperative food-maintained behavior.
H 69	Pre- and postoperative noise discrimination schedule.
C 29	Surgical control animal. Pre- and postoperative noise-maintained behavior.

Experiment II:

H 13, H 70, H 72	Noise interference animals. Not adapted to noise preoperatively.
H 14, H 16, H 18, H 21	Noise interference animals. Adapted to noise preoperatively.

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Changes in Noise-Maintained Behavior Following Septal Forebrain Lesions in the Albino Rat

Abstract of a Dissertation

Submitted in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
1956

Boston University Graduate School

by

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ABSTRACT

Recent work by Brady and Nauta demonstrated that lesions in the septal region of the albino rat was followed by rather typical behavior. The characteristic syndrome described by these investigators included the following symptoms: an exaggerated startle response to auditory and tactile stimuli, squealing and biting if handled, freezing after a startle reaction, a peculiar hopping with a rabbit-like gait, a so-called magnet-reaction to an object rotated in front of its nose, and squealing when the fur of its dorsal surface was manipulated. The appearance of the syndrome following surgery was only a matter of hours, and it was dramatically different from the preoperative behavior of the animal. Brady and Nauta rated the animals daily for the presence of the symptoms, and found that the duration of the syndrome ranged from about 12 to 60 days. In a preliminary study in the Boston University laboratory it was found that if the hippocampus was bilaterally severed in its caudal aspect the characteristic behavioral symptoms did not appear. However, if the lesion included the rostral tip of the hippocampus and the septal region the typical syndrome appeared. With Brady and Nauta's findings corroborated to this extent, it was decided that it was necessary to study objectively certain features of the syndrome, and to attempt to further delimit the site of the lesion.

Inasmuch as the cage behavior of the animal indicated hypersensitivity to noise it was decided to set up an experiment which would enable one

to quantify sensitivity to noise stimulation pre- and postoperatively. The Skinner box technique was selected as an appropriate one for obtaining constant data before and after surgery. With this technique it is possible to train animals to a lever pressing response which is under stimulus control. It has been a common practice to establish a lever pressing response contingent on a food reinforcement. Various reinforcement schedules may be employed, and constant response rates may be obtained. Through the use of discriminative stimuli it is possible to condition the animal to respond differentially to various schedules. Sidman and Ferster, among others, have independently reported conditioning rats to make avoidance responses (using a lever pressing response) to avoid an electric shock. In the Boston University laboratory we have found in preliminary experiments that rats may be conditioned to turn off a noise by pressing a lever. This method was adopted for the basic experiment to be reported here. In order to further test the findings of this experiment a second experiment was utilized. This latter experiment consisted of measuring the interfering effect of a noise stimulus, of several intensities, on a food-maintained lever pressing response.

The subjects in the experiment consisted of 15 male albino rats.

The apparatus was a modified Skinner box. The inner dimensions of the box were 18 1/2" x 13 1/2" x 26 1/2". Adjacent to the food cup was a response lever. A University "Tweeter" loudspeaker was mounted at the top of the box for the reproduction of the auditory stimulus. On the outside of the box, but in the same room, was an automatic feeder. An Ampex tape recorder #600 was used as a source of limited white noise for the auditory stimulus. This stimulus was a tape recording of a hissing air jet. The noise reaching the animal consisted principally of high audio frequencies, i.e., 1000 to 15,000 cy/sec. The intensity of the signal could be regulated by the dial setting on a Concord Amplifier. In an adjacent room there was a relay control unit, a cumulative response recorder, and a program timer. An electronic timer recorded the total time the noise was on.

All rats were classified both pre- and postoperatively for the presence or absence of symptoms. The three animals in experiment I (the noise-maintained behavior animals) were conditioned preoperatively to press a lever to terminate the noise. Using the cumulative latency time required to turn the noise off as a dependent variable, and empirically selecting three different noise intensities, three discriminable intensity-latency functions were obtained. Two animals on a variable interval reinforcement schedule served as controls for the retention of the motor response of pressing the lever postoperatively. Another animal trained to noise-maintained behavior served as a surgical control. Two more animals were conditioned to a food, no-food discrimination situation. Food was available when the discriminative stimulus, a noise of the same character as that used in the noise experiment, was present. This was a control for possible postoperative deafness. One of these animals was trained to this discrimination preoperatively.

The animals in experiment II (the noise interference experiment) were subjected to three noise intensities, of approximately the same intensity as that used in experiment I, while they were making food-maintained lever-pressing responses. Some of these animals were run daily until they adapted to the suppressive effects of the interfering noise, i.e., they responded at the same rate as when noise was not present. Others were not run for a long enough time for adaptation to occur. The purpose of this experiment was essentially to ascertain if a noise would have a greater suppressive or freezing effect on a septal rat than on the normal animal. This question was raised by experiment I when it was found that the response of these animals was not occurring with the noise on. It was reasoned that if the postoperative experiment I animals were "freezing" to the noise, then those septal animals which had preoperatively adapted would show marked postoperative suppression of the food response. Also, it seemed that those animals which had not adapted would show greater postoperative suppression of response than their preoperative level.

The aim of surgery was to make a bilateral lesion which would be sufficient to sever both septal and fornix fibers. Histological study was used to define the general site of the lesion and to state precisely the areas involved.

Postoperatively, it was found that the three experiment I animals required periods ranging from 30 to 75 days before they recommenced the noise-maintained response. When they did begin responding again at a constant rate the critical intensity, or aversive threshold, had shifted upward for each of the three animals. That is, the cumulative latency times for suprathreshold intensities were much higher than they had been preoperatively. It was found that the introduction of a stimulus of higher intensity than any used preoperatively served to lower the cumulative latency time. Loss of the lever-pressing response, freezing, and gross deafness were ruled out by the control animals and experiment II. Continued running of two of the rats for an extended period of time revealed an essentially clearcut return of the intensity-latency function to its preoperative level, i.e., a lowering of the critical intensity level, in one animal, and a definite tendency in the same direction by the second animal (after 65 and 93 postoperative days respectively).

In experiment II the noise had no specific suppressive effect on the food-maintained behavior of both the adapted and the non-adapted animals following the septal lesion. This experiment demonstrated not only that the animals did not freeze, but also that they continued to adapt when the noise was introduced; i.e., the food rate increased with the prolonged occurrence of the interfering noise.

Anatomically, the primary lesion in all animals which manifested the behavior syndrome consisted of the obliteration of tissue centered around the genu of the corpus callosum and extending ventrally and caudally into the upper third of the septum. All animals sustained extensive damage of the medial cortex over the rostral quarter of the corpus callosum and forward toward the tip of the hemisphere. The forward quarter of the corpus callosum was usually degenerated or completely obliterated. The fornix longus and the rostral end of the induseum greseum were also obliterated or degenerated in all animals.

In general, the results agree with Brady and Nauta in emphasizing the importance of lesions in the septal region in producing the syndrome. However, a more precise designation of the specific pathways and nuclei involved in the production of the syndrome was not warranted after histological study. In agreement with the literature, lesions in the hippocampus proper were not critical for the appearance of the syndrome.

Behaviorally, the question of why the septal rat was hypersensitive to noise when observed under home cage conditions and less sensitive under the experimental conditions may be explained by a basic difference in the nature of the two classes of responses. From this point of view we may state that whereas the septal rat is more sensitive to noise in terms of certain reflex response measures in the cage situation, it is less sensitive to noise insofar as the instrumental lever pressing response to noise is concerned.

Suggested directions for further experimentation were offered. These include the study of possible differential loss of sensitivity to specific sound frequencies, the effect of the use of higher noise intensities than those employed in the reported experiment, and changes in sensitivity to tactile stimulation following septal lesions.

AUTOBIOGRAPHY

The candidate was born in Willimantic, Connecticut on August 13, 1919. His parents were William and Katherine Tracy. He obtained his elementary school education in public schools in Connecticut. He was graduated from Windham High School, Willmantic, in 1937. In 1941 he received the Bachelor of Science degree from the University of Connecticut. He was granted the Master of Arts degree in psychology from Boston University in 1945. In 1946 he was matriculated into Boston University as a Ph. D. candidate in psychology. From 1945 to 1946 he was employed as a psychologist at the Gardner State Hospital in Gardner, Massachusetts. From 1946 to 1950 the candidate worked at the Norfolk House Centre in Roxbury, Massachusetts as a group worker and personal counselor. In 1950 he accepted a position as acting chief psychologist at the Governor Bacon Health Center in Delaware City, Delaware. He remained there until September, 1953, at which time he returned to the Boston University experimental psychology laboratory.

PHOTOGRAPH OF THE CANDIDATE