

THE UNIVERSITY OF MICHIGAN  
COLLEGE OF LITERATURE, SCIENCE, AND THE ARTS  
Department of Psychology

Final Report

HIPPOCAMPAL ABLATION AND BEHAVIOR

Robert L. Isaacson

ORA Project 05425

under contract with:

OFFICE OF THE SURGEON GENERAL  
U.S. ARMY MEDICAL RESEARCH AND DEVELOPMENT COMMAND  
GRANT NO. DA-MD-49-193-63-G75  
WASHINGTON, D.C.

administered through:

OFFICE OF RESEARCH ADMINISTRATION      ANN ARBOR

February 1964



## ABSTRACT

1. The University of Michigan
2. Hippocampal Ablation and Behavior
3. Robert L. Isaacson
4. 33 pages, 19 illustrations, February 4, 1964
5. Grant No. DA-MD-49-193-63-G75
6. Supported by: Office of the Surgeon General  
U.S. Army Medical Research and Development Command  
Washington, D.C.

Research was conducted on the behavioral effects of bilateral ablation of the hippocampal formation. Generally this involved making lesions by aspiration in the rat, although cats were used in one phase of the work. Control lesions of posterior-lateral isocortex were also used. The results can be summarized as follows:

1. Hippocampectomized animals tested for retention of a preoperatively acquired successive discrimination developed response fixations in both an original experiment and its replication. Neocortically damaged Ss also showed severe deficits in retention.
2. Animals tested in spontaneous alternation problems do not tend to alternate responses, or response-produced proprioceptive feedback. The significance of this fact for understanding the behavior of brain-damaged animals is discussed.
3. Hippocampectomized Ss are not "distracted" by the introduction of irrelevant cues as are normal animals.
4. An attempt to develop antibodies for specific areas of the cat brain was not successful.
5. Hippocampectomized Ss were not able to inhibit their responses so as to master a 20-sec delay operant-conditioning problem.



FINAL REPORT ON GRANT NO. DA-MD-49-193-63-G75

This formal report will be divided into six sections. Each section will deal with an aspect of the research undertaken during the course of this grant. The sections are named as follows: (1) Retention of a successive discrimination problem by hippocampectomized and neocorticate rats. (2) Studies in cues used by animals in alternation behavior. (3) The distractibility from behavioral problems of hippocampectomized rats. (4) The development of antibodies specific to the hippocampus and the caudate nucleus in the cat. (5) The inability of hippocampectomized animals to operate effectively on a 20-sec delayed-response schedule. (6) Preliminary results.



## SECTION 1

### RETENTION OF A SUCCESSIVE DISCRIMINATION PROBLEM BY HIPPOCAMPECTOMIZED AND NEODECORTICATE RATS

In the interim report of the project (April 18, 1963), an experiment was reported which was an attempt to study the post-operative retention of a successive discrimination problem acquired in two types of mazes. Essentially, animals were trained in the successive discrimination problem in a Y maze or a maze shaped like an arrowhead ( $\uparrow$ ). While hungry, subjects ran down a single alley to a choice point where they could turn right or left. The angle of the turns at the choice point was the only differentiating feature of the two mazes. The  $\uparrow$  maze required a much sharper turn than did the Y maze. On any given trial the walls of both of the maze arms following the choice point were either black or white. If they were both black, the animal had to turn down the other arm for the reinforcement.

After acquisition of the discrimination problem, animals received either bilateral hippocampal lesions, neocortical lesions, or sham operative procedures. Then, all animals were retrained in the problem following a post-operative recovery period of from 10 to 19 days.

In our previous report we indicated the following results:

1. Faster preoperative acquisition by animals trained in the  $\uparrow$  shaped maze than in the Y shaped maze.
2. A post-operative debilitation of the neodecortical animals in post-operative training.
3. A severe post-operative depression of behavior of animals with bilateral hippocampal lesions that differed between the two mazes. Animals trained in the Y maze showed greater impairment than the neodecorticate animals. Hippocampectomized animals trained in the  $\uparrow$  maze developed a response fixation toward one side or the other of the maze.

The experiment was replicated during the period of the grant. Animals received preoperative acquisition training on one of the two mazes. The animals then were operated upon, receiving hippocampectomies or lesions of the neocortex overlying the hippocampal formation. No sham operates were used in the replication study.

The results obtained in the second study were similar to those of our first study in that:

1. Animals trained preoperatively in the † maze acquired the successive discrimination problem faster than those trained in the Y maze.

2. Neodecorticate animals showed severe impairment in retention and relearning of the problem.

3. The hippocampectomized rats showed severe impairment and retention of the successive discrimination problem. All hippocampally ablated Ss showed no sign of learning in the first six days of post-operative training. Following this a fixation of response developed in both mazes. This is the point of variance from the results obtained in our initial study. In the former study only the animals trained in the † maze showed fixated behavior. In the second study animals trained in both mazes developed fixated behavior patterns.

The major difference between the first and second studies may lie in the difference in the rooms used to conduct the study. The extramaze visual cues (room cues) were more figural in the first study than in the second, although it is difficult to determine just how these cues could influence the outcome of the experiments. In any case, the development of fixated responses seems to be a certain outcome of our studies of the retention and relearning of the difficult successive discrimination problem in the hippocampectomized rat but not in ones suffering neodecorticate damage, despite the fact this latter group has difficulty with the problem.

This may be explained by one type of explanation which has been offered for the behavioral effects of frontal isocortical lesions (e.g., Mishkin, Prockop, and Rosvold, 1962) as well as subcortical lesions (e.g., McCleary, 1961). This explanation proposed that hippocampectomized animals have difficulty in changing the dominant response in any given situation. This difficulty may be due to a deficiency in those processes necessary for the inhibition of responses.



## SECTION 2

### STUDIES IN CUES USED BY ANIMALS IN ALTERNATION BEHAVIOR

Our interest in the cues used by normal and brain-lesioned animals in the spontaneous alternation situation was aroused by the work of Daniel P. Kimble (1963), and Leonard Lash in their theses. Kimble found that the hippocampectomized rat had difficulty in acquiring a successive discrimination problem in the Y maze. His lesioned animals, however, had no difficulty in learning a simultaneous discrimination problem in the same maze. At that time it looked as though the hippocampectomized rat had difficulty in solving this type of psychological problem. Subsequently, Lash in his thesis showed that the hippocampectomized rat could learn the successive discrimination problem if the physical situation of the maze was altered. Lash showed that the ease of learning the discrimination problem was related to the ability of the physical apparatus to alter nonrewarded alternation behavior (measured before the discrimination study was undertaken). In other words, the more animals showed response alternation, that is, alternated right and left turns on consecutive nonrewarded trials before the discrimination problem was undertaken, the more likely it was that both normal and hippocampectomized animals would learn the discrimination. Lash's evidence suggested that the brain lesioned animals alternated different cues than did normal animals. This led us to undertake a series of experiments which attempted to more fully understand the nature of spontaneous alternation in both the normal and the brain damaged animals. Previous work had not been sufficient to identify adequately cues which are alternated by animals.

On two consecutive nonrewarded trials in a two choice situation, such as a T maze, a rat will usually visit the arm of the T maze on the second trial that is different from the one first visited. This alternation behavior is called spontaneous since it occurs in the absence of special training or rewards for responses to one or the other of the arms of the T maze. It is thought to be a miniature instance of exploratory behavior. Although many attempts have been made to determine what cues are being alternated by the rat on two consecutive choices in the T maze none of them have been very helpful to us with the exception of the study by Walker, Dember, Earl, and Karoly (1955). These authors reported that rats alternated their behavior to the following cues (listed in their order of effectiveness in eliciting alternation behavior): intramaze, or alley, cues; stimuli from outside the maze (room cues); and finally feedback from the response itself (response-produced cues). It has generally been assumed that most nonresponse cues which are alternated by animals are visual.

However, Dember and Roberts (1958) showed that blind animals alternated T maze choices as much as normal animals and showed that this was not due to an increase in alternation of response-produced cues. This suggests that either nonvisual cues are more important than was suspected or that an animal will alternate whatever cues are available. Since Lash had argued that hippocampal Ss could not use response-produced cues as well as normal Ss, we have undertaken a number of studies of alternation phenomena in the hope of learning of the role of response-produced cues. In the first study (Appendix A) a method of determination of chance levels of alternation is described. This is important because a precise measure of chance responding is a necessary baseline for the determination of changes in behavior induced by alteration in the experimental conditions. The second study (Appendix B) shows that responses, or response-produced cues, are not alternated by rats in the T maze situation to any measurable degree. In the third paper (Appendix C) we show that even brightness and pattern cues along the cross-arms of the T maze are not alternated by normal animals. In the same paper we present evidence that certain cues associated with the structure of the floor appeared to be alternated at a high rate. We are now trying to isolate this "floor cue" and are continuing work on the problem. Floor cues could be tactual, olfactory, or mediated by the auditory sense. This last possibility receives support from the work of Professor (Emeritus) John Shepard of The University of Michigan who has for thirty years or more been investigating the role of situational cues in complex maze learning in the rat and in the human. It is his opinion that floor cues convey important information to the rat through vibrations relayed to the auditory system by air and by means of bone conduction through the limbs.

At present we are revising the three papers included as Appendices A, B, and C for submission for publication. Also, Mr. Robert Douglas is extending our research into the possible effects of olfactory cues in alternation behavior through surgical and behavioral techniques as part of his doctoral dissertation.

## SECTION 3

### THE DISTRACTIBILITY FROM BEHAVIORAL PROBLEMS OF HIPPOCAMPECTOMIZED RATS

After we had found that hippocampectomized animals were not deficient in their ability to form an active avoidance response (Isaacson, Douglas, and Moore, 1961) but were impaired in their ability to form a passive avoidance response (Isaacson and Wickelgren, 1962), we became interested in the possibility that animals with bilateral hippocampal ablation might be deficient in their ability to inhibit other sorts of responses. We were especially interested in the suppression of responses by other means than punishment. This led us to an investigation of the effects of introducing stimuli which would affect the behavior of normal animals in such a way that inhibition would be a likely mechanism responsible for the change. We used a simple runway situation. Hippocampectomized, neocorticate, and sham operated animals were trained to run from one end of a linear runway to the other for a food reward. After the latencies (time required to exit from the starting box) and running speeds had stabilized on the seventh day of training, irrelevant stimuli were placed along the floor of the runway. The effects of this change in the experimental situation was as expected. The sham operated animals and the animals with the neocortical lesions showed elevations of running speeds and latencies. This suggested that the additional irrelevant cues acted as a distracting stimulus and this, in turn, produced an inhibition-like effect. The hippocampally ablated animals, on the other hand, showed no effect from the additional stimuli. Our report on the results of this experiment has been published in Nature. (Wickelgren and Isaacson, 1963.) Reprints of this article have been forwarded to the U.S. Army Medical Research and Development Command.

After completing the study we have undertaken a replication of this study under somewhat altered conditions including other varieties of limbic system lesions. It now appears that our original data have been replicated, and that similar results can be obtained with lesions in the septal area but not with lesions in certain other areas of the limbic system.

## SECTION 4

### THE DEVELOPMENT OF ANTIBODIES SPECIFIC TO THE HIPPOCAMPUS AND THE CAUDATE NUCLEUS IN THE CAT

During the past year we attempted to replicate a study by Mihailović and Janković (1961) in which they reported the development of antibodies which would eliminate the electrical activity of selected sites in the nervous system.

Tissue from the hippocampus and from the caudate nucleus was removed from a cat by aspiration into clean and separate containers. This material was combined with Freund's adjuvant and repeatedly injected subcutaneously into different rabbits over the period of one month. Later, serum from the blood of the rabbits was injected into the lateral ventricles of cats in which chronic bipolar electrodes had been inserted a month or more before. The electrode placements were in the hippocampus (bilateral), caudate nucleus (bilateral), and the neocortex. The electrical activity in all these locations was monitored during the intraventricular injection of the serum and thereafter intermittently monitored for a month or longer.

We have concluded our efforts in this area and representative records are presented below. Generally, we failed to obtain the abolition of electrical activity in either hippocampus or caudate nucleus following injection of anti-caudate or anti-hippocampus serum. Histological examination showed no change in the cellular composition of these locations when examined by the optical microscope. This corroborates the results of Dr. Way (personal communication), Department of Anatomy, University of Iowa, who looked for neuronal changes following the injection of supposedly specific antibodies for brain tissue.

Our failure to replicate the results of Mihailović and Janković should not be taken as conclusive for although their procedures were followed, it may be that unknown factors of procedure and preparation may have prevented our demonstration of the reported phenomena.

#### Cat 1

Figure 1 shows the electrical activity before and immediately following injection of the anti-caudate antibody. The animal was anesthetized with sodium pentobarbital and hole had been drilled through the skull to allow the stereotoxic implantation of a cannula into the right lateral ventricle. As

can be observed, a burst of large show-wave activity was seen in the recording from left caudate nucleus, the recording across the left and right caudate nucleus, and the right hippocampus. This could be the result of the tissue reaction to the antibody or merely a reflection of the distortion of the brain produced by the intraventricular injection of .5 cc of fluid. Periodic changes in the electrographic activity in these sites was obtained over the next several minutes (Fig. 2). By an hour and one-half after the injection, even greater irregularities could be observed in the records (Fig. 3).

Over the next two months, the cat continued to show diminished electrical activity in the left and right caudate leads, see "pedestal recordings" (Fig. 4). Before the cat was sacrificed, the wires from the electrodes were detached from the pedestal on the head and recordings were obtained directly from the wires, themselves.

The potentials from the right caudate nucleus and the hippocampus show diminished electrical activity at this time whether recorded from the pedestal or from the wires leading to the electrodes. This diminished level of activity was the only instance in which the results of Mihailović and Janković were found. Even here, however, the activity recorded from the electrode in the right medial portion of the hippocampus seemed to be due to impaired electrical continuity, because the electrode located more laterally in the structure was not diminished (see top record, Fig. 4). Records from either the left or right caudate nucleus do seem reduced, however.

#### Cat 2

Like the other cats in this series, this animal had chronic electrodes implanted about one month previous to the injection of the antibody. In this case, anti-hippocampal serum was injected by cannula stereotaxically inserted into the left lateral ventricle. The animal was anesthetized with pentobarbital. Figure 5 presents records obtained from the anesthetized cat before and after insertion of the cannula.

The injections of about .5 cc of anti-hippocampus serum were made. A general slowing of all records was observed and this was especially prominent in the left hippocampus (Fig. 6). About 7 min following the second injection the heart rate began to falter and the electrical records were very slow with a dome-like appearance. Adrenalin was administered to support the heart rate of the animal. This increased the heart rate temporarily and the electrographic records improved in tone, but soon diminished and periods of quiescence and bursts of activity alternated in the brain recordings (Fig. 7). Figure 8 shows a burst of seizure-like activity which appeared before the animal succumbed.

The possibility the animal's death and the abnormal electrical activity could have resulted from a generalized neural reaction to the antibody can be discounted since other animals in this series did not have the same difficulties. More likely the animal's death could have resulted from cardiac and respiratory failure induced by the barbiturate used as a hypnotic. Such failures do occur, although rare. It is my opinion that this animal represents one of the unfortunate instances of such failures.

#### Cat 3

This animal was prepared in the same manner as the others in the series. Records obtained before and after the insertion of the cannula (hypodermic needle) into the left lateral ventricle are shown in Fig. 9. Injection of .5 cc of the anti-hippocampal serum failed to produce any discernable effects in the electrical recordings (Fig. 10). A second injection of the serum was given and this also failed to alter the electrical activity of the brain sites from which we were recording (Fig. 11).

Recordings from this animal made a month later failed to indicate any lasting alteration in the electrographic potentials (see Fig. 12, N. B. Variable recording speeds).

#### Cat 4

This animal received intraventricular injection of anti-caudate serum. Records made prior to administration of the serum are presented in Fig. 13. Figure 14 shows the records made immediately following injection of 1.0 cc, the anti-caudate serum (slower recording speed). Figure 15 illustrates records made 20 min later. This pattern was observed over the next month and longer.

Histological examination of the brain of this animal revealed that the electrodes intended for the hippocampus did not descend far enough to reach the hippocampus and were located in the white matter over the lateral ventricles. In any case the caudate nucleus, the target area of the antibody remained unchanged in its activity.

## Cat 5

Cat 5 received intraventricular injection of anti-hippocampus serum. Preinjection recordings of various brain sites are presented in Fig. 16. These were obtained under anesthesia produced by sodium pentobarbital. Records obtained immediately following injection are presented in Fig. 18, and records obtained three weeks later without anesthesia are presented in Fig. 19. Once again, no demonstrable change in the electrographic as a function of intraventricular injection of the antibody was observed.

## SECTION 5

### THE INABILITY OF HIPPOCAMPECTOMIZED ANIMALS TO OPERATE EFFECTIVELY ON A 20-SECOND DELAYED-RESPONSE SCHEDULE

Clearly the most prominent behavioral correlate of hippocampal destruction is the inability of animals to withhold responses. This has been demonstrated by many studies in our laboratory and in studies originating elsewhere. Following this general operational principle, we have looked for new experimental techniques which would allow the presumed behavioral deficiency to manifest itself in other ways.

One direction we have investigated is the attempt to establish an enforced delay between bar presses in the operant conditioning situation. It is possible to train animals to withhold their responses in a bar press situation for various intervals of time. If our hypothesis about the effect of hippocampal ablation was correct, we would expect that hippocampally ablated animals would have difficulty in withholding their responses. Therefore we began an experiment in which animals with hippocampal and neocortical lesions, as well as sham operates, were first trained under a continuous reinforcement schedule (reinforcement delivered following each bar press) and then were switched to what is called the 20-sec delay schedule (DRL-20). The DRL-20 schedule means that after each rewarded bar press an animal must wait 20 sec before pressing the bar again in order to attain another reinforcement. Presses which occur in less than the 20-sec interval following the last reinforcement act only to reset the governing mechanism such that another 20-sec period is started. Animals were maintained on a water deprivation schedule and were given water as a reinforcement in the operant conditioning chamber.

As expected, the hippocampectomized animals performed very poorly when the delay procedure was started. Under the continuous reinforcement schedule which preceded the delay schedule, the response rates of the hippocampal operates were slightly lower than that of animals in the other two groups. At the onset of the delay schedule, the hippocampally operated group's response rate increased far beyond that of the other animals. It remained high throughout the remainder of the experiment and this resulted in a very low number of reinforcements.

A report of this experiment is included as Appendix D. This paper has been submitted to the Journal of the Experimental Analysis of Behavior. Further experiments along in this area have been undertaken and are described in Section 6.



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the runway performance of animals with lesions in the hippocampus, septal region, and neocortex was undertaken. The lesions of the hippocampus were of three kinds: (a) the large bilateral type most often used in our work (Isaacson, Douglas, and Moore, 1961), (b) small lesions of the dorsal extent of the hippocampus made by aspiration, and (c) electrolytic lesions. While the results are not completely analyzed it appears safe to conclude that the differences between hippocampal operated and other groups of animals cannot be explained on the basis of motivational variables and that septal lesions mimic most, but not all, of the hippocampal effects found in the runway before. In addition the behavior of animals with lesions in the hippocampus made by D. C. fulguration is different from that made by aspiration.

The activity levels of animals was studied in the exercise wheel. This measure of activity showed the hippocampally ablated animals were less active than control groups in both quiet and noisy environments. We are extending this line of research by use of multiple methods of recording activity and by extending our limbic lesions into other areas. Also we are studying the adaptation of hippocampally lesioned animals to new environments.

GRADUATE STUDENTS SUPPORTED BY THIS GRANT

ROBERT J. DOUGLAS

CAROL VANHARTESVELDT CLARK

LEONARD SCHMALTZ

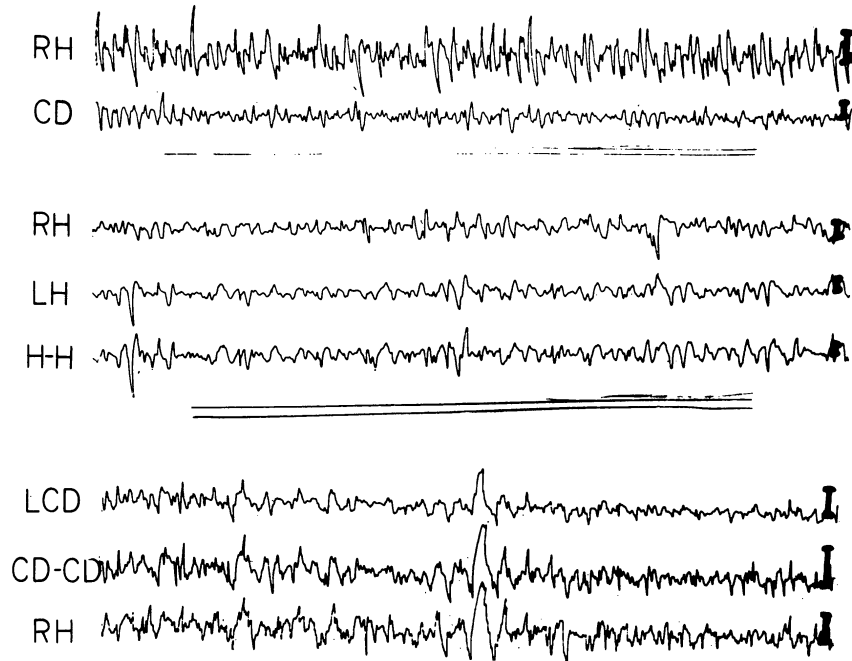
DANIEL R. SNYDER

LINDA PIERCE

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CAT I BEFORE INJ



35 SEC AFTER  
INJ OF ANTICAUDATE SERUM

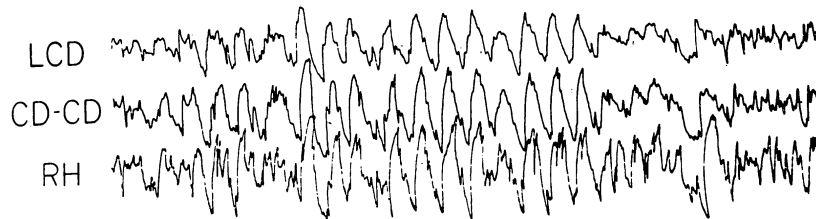
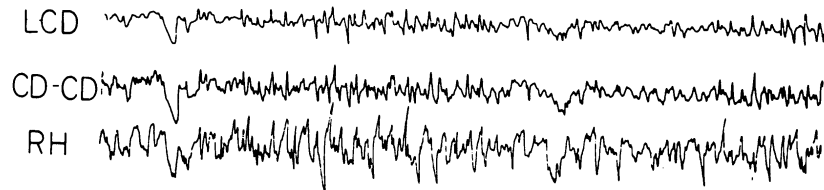
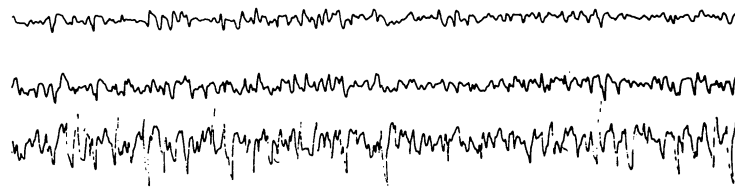


Fig. 1. Electrographic records obtained from selected brain sites of anesthetized cat before (top) and 35 sec after (bottom) injection of anti-caudate serum into lateral ventricle. RH = right hippocampus vs. ground (gnd); CD = caudate nucleus vs. gnd; LH = left hippocampus vs. gnd; H-H = potential difference recorded between left and right hippocampi; LCD = left caudate nucleus vs. gnd; CD-CD = potential difference between caudate nuclei. Vertical calibration = 100  $\mu$ V. Recorded at paper speed of 25 mm/sec.

CAT 1  
2 MIN POST INJ



6 MIN POST INJ



11 MIN POST INJ

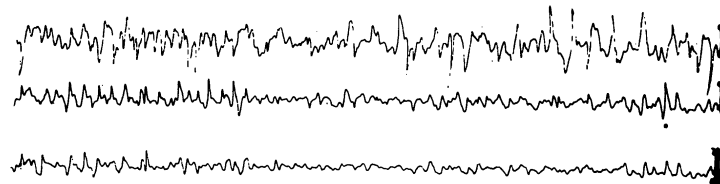
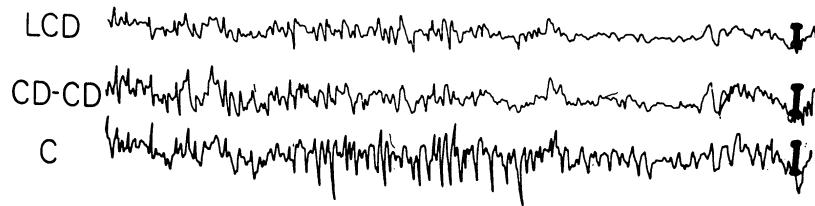
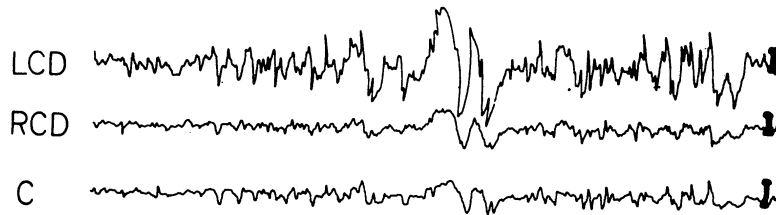


Fig. 2. Electrographic records obtained at subsequent periods from cat 1. Brain locations as given in Fig. 1. Records taken at 6- and 11-min post-injection from sites indicated 2-min post-injection. Calibration = 100  $\mu$ V.

CAT 1  
20 MIN POST INJ



1 HOUR POST INJ



1 HOUR 20 MIN POST INJ

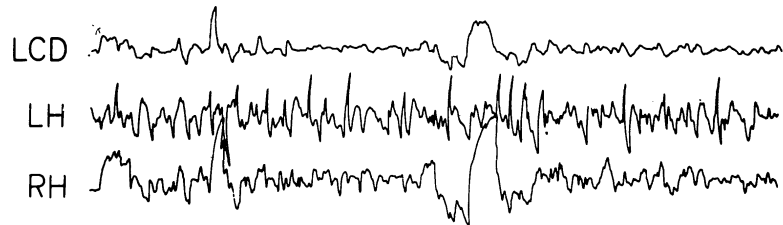
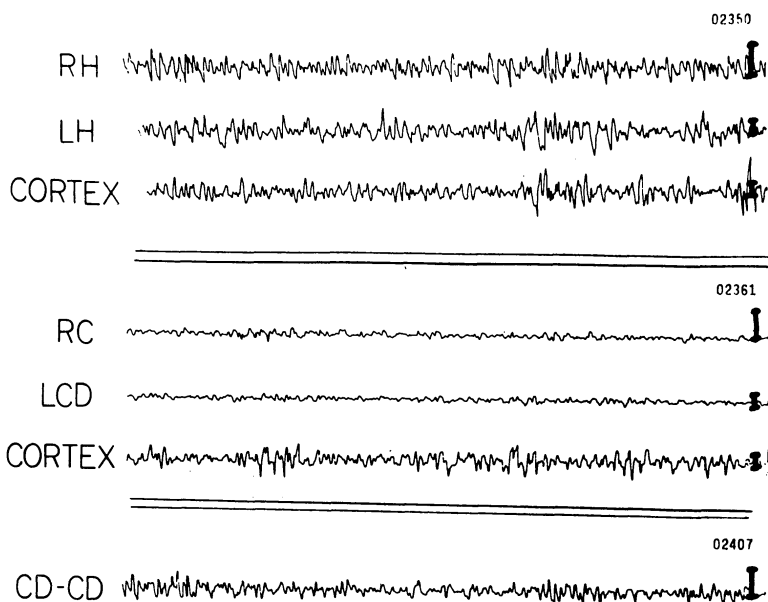


Fig. 3. Electrographic records obtained at later periods from cat 1. Brain locations as indicated in Fig. 1. RCD = right caudate nucleus vs. gnd. Calibration = 100  $\mu$ V.

CAT I  
PEDESTAL RECORDINGS



RECORDS FROM WIRES

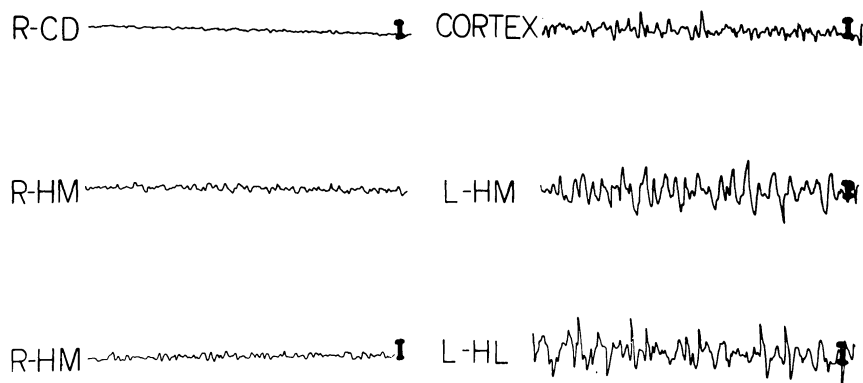
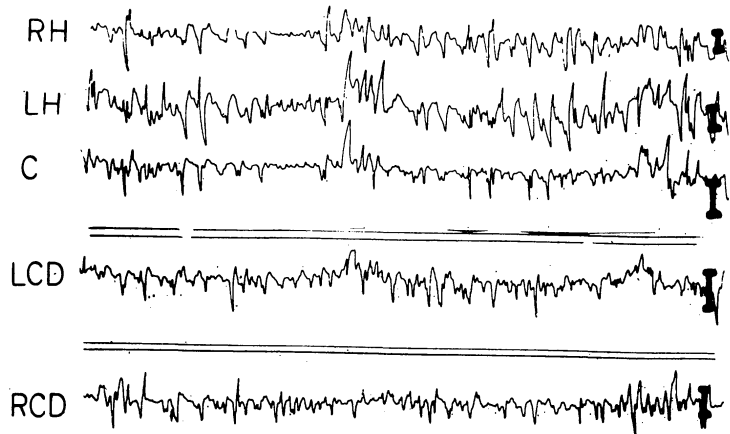


Fig. 4. Recordings made from cat 1 under sodium pentobarbital anesthesia about six weeks after injection of the anti-caudate serum. Upper portion made from electrode pedestal. Bottom portion made from wires from electrodes to pedestal. Designation of brain locations as given in Figs. 1 and 3 with the following changes. CORTEX = recording from stainless steel screw implanted over lateral gyrus of cat vs. diffuse gnd; RC in upper records = right caudate nucleus; RHM = recordings from the more medially placed electrode of the two placed into right hippocampus; L-HM = recordings from the medially placed electrode of the two placed into the left hippocampus; L-HL = recordings from the laterally placed electrode of the two placed into the left hippocampus. Calibration = 100  $\mu$ V.



CAT 2  
UNDER NEMBUTAL.



AFTER INSERTION OF CANNULA

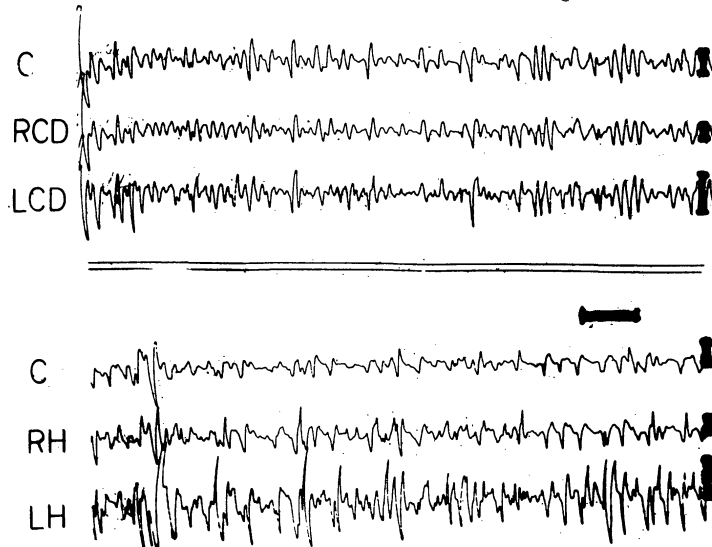
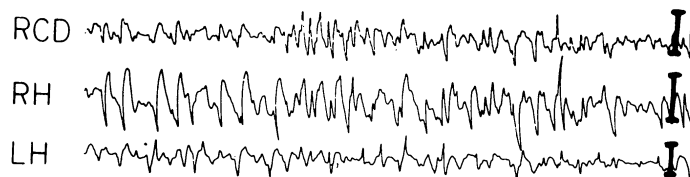


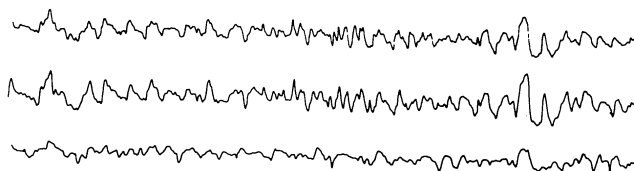
Fig. 5. Electrographic records obtained from selected brain sites of cat 2. Animal under sodium pentobarbital before and after insertion of cannula into lateral ventricle. Symbols RH, LH, LCD, RCD as given in Figs. 1 and 3. C = records obtained from stainless steel screw over lateral gyrus and diffuse gnd. Vertical calibration = 100  $\mu$ V. Horizontal calibration = 1 sec.

CAT 2

40 SEC. POST INJ.

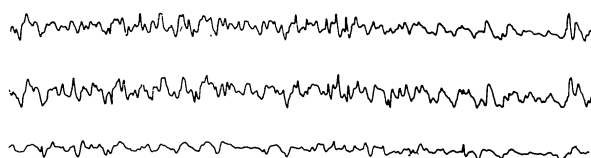


8 MIN 40 SEC POST INJ



2ND INJ: 9 MIN 20 SEC AFTER 1ST INJ.

1 MIN AFTER 2ND INJ



4 MIN AFTER 2ND INJ

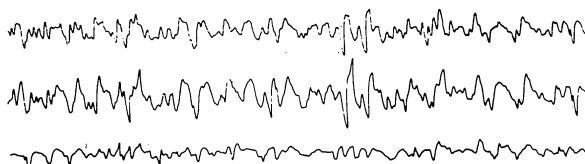
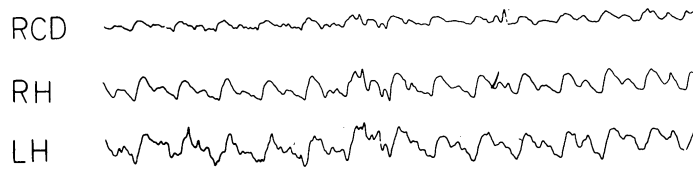


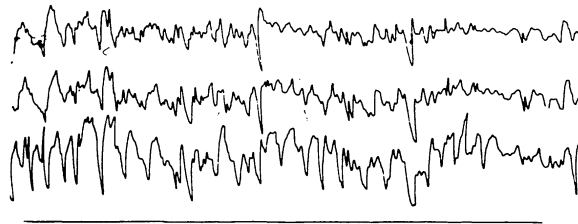
Fig. 6. Records obtained from cat 2 at various times after injection of anti-hippocampus serum. Symbols as given in Figs. 1 and 3. Vertical calibration = 100  $\mu$ V.

CAT 2

7 MIN 20 SEC AFTER 2ND INJ.



ADRENALINE GIVEN-19MIN AFTER 1ST INJ.



1 MIN AFTER ADRENALINE

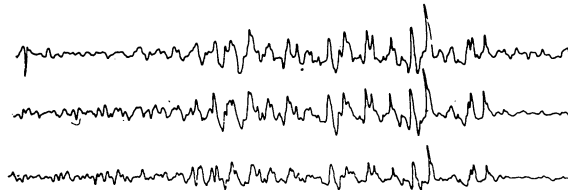


Fig. 7. Records obtained from cat 2 at various times after second injection of anti-hippocampus serum and after injection of adrenaline. Symbols as given in Figs. 1 and 3. Calibration as given in Fig. 6.

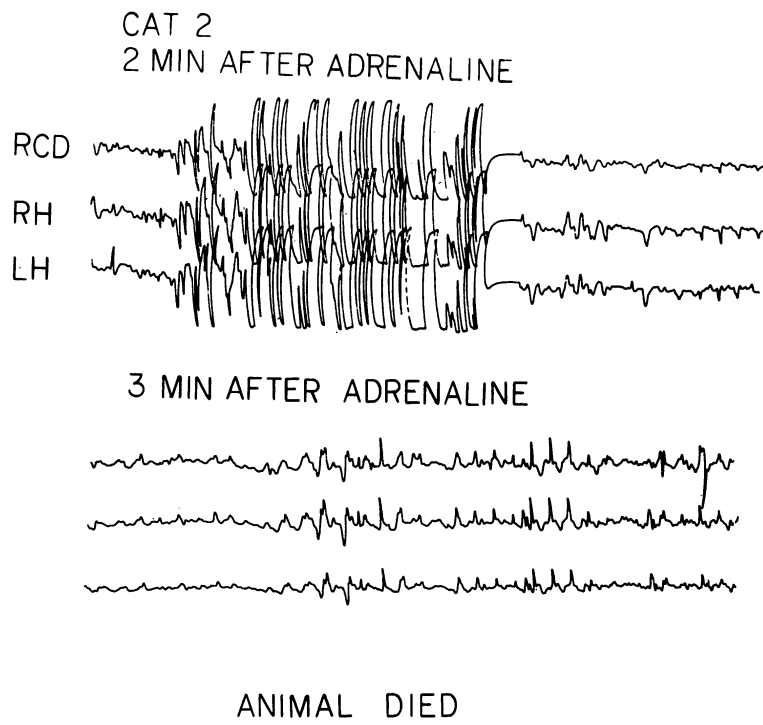
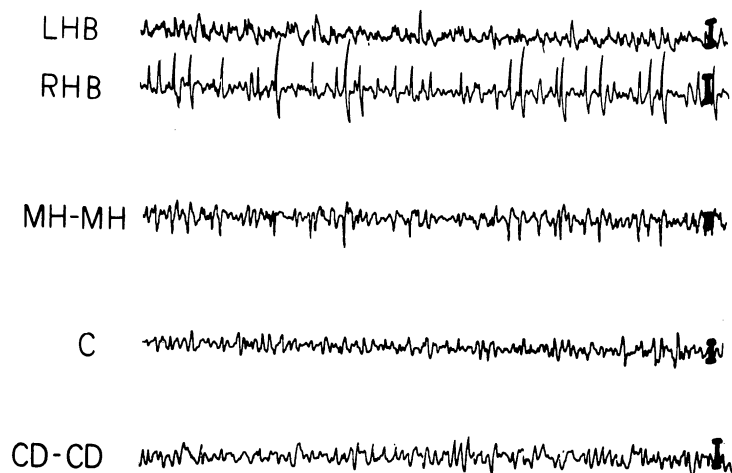


Fig. 8. Records obtained from cat 2 at later periods following administration of adrenaline. Symbols and calibration as given before.

CAT 3



NEEDLE INTO VENTRICLE

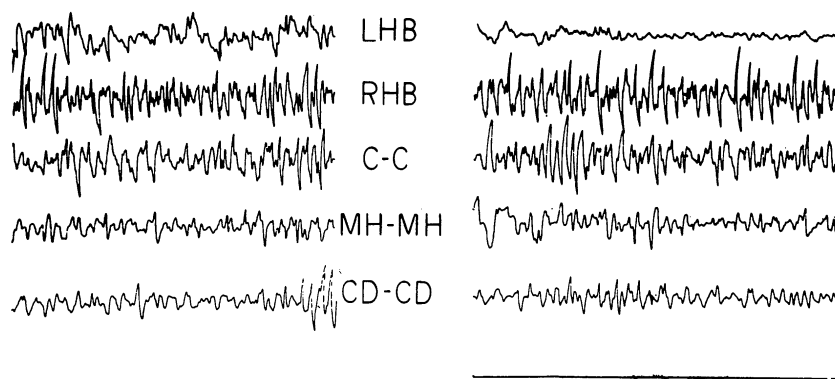


Fig. 9. Top records: records obtained from brain sites of cat 3 before injection of antibody. Bottom records: records obtained from brain sites while animal was anesthetized immediately after introduction of hypodermic needle (cannula) into lateral ventricle. LHB = bipolar recording of activity in left hippocampus; RHB = bipolar recording of activity in right hippocampus; MH-MH = records of potential difference between the more medially placed electrodes in left and right hippocampi; C and C-C = records obtained from stainless steel screw in skull over lateral gyrus vs. diffuse gnd; CD-CD = records of potential difference between left and right caudate nuclei. Vertical calibration = 100  $\mu$ V. Paper speed: 25 mm/sec.

CAT 3 20 SEC AFTER INJ.

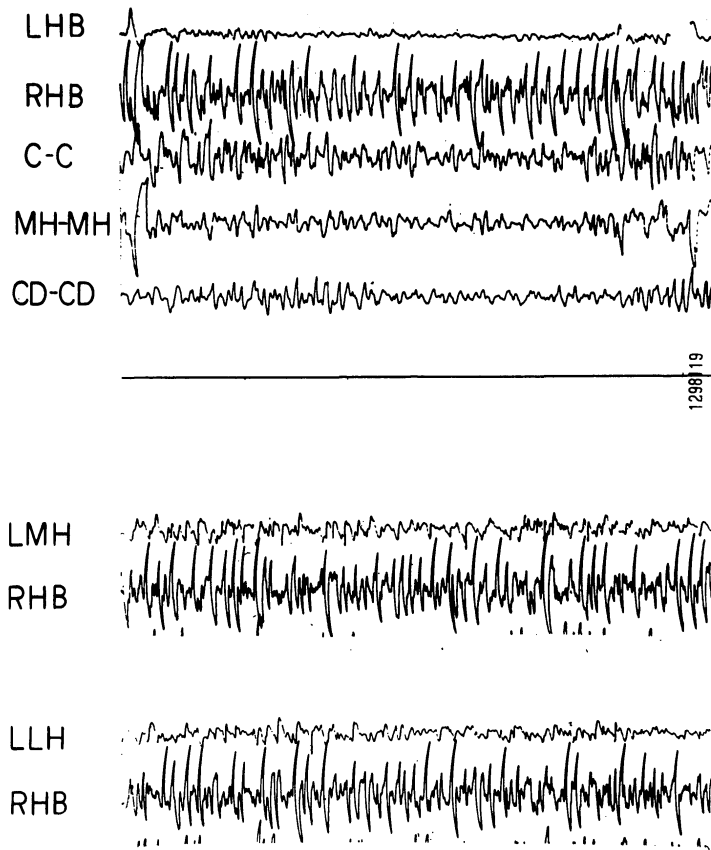
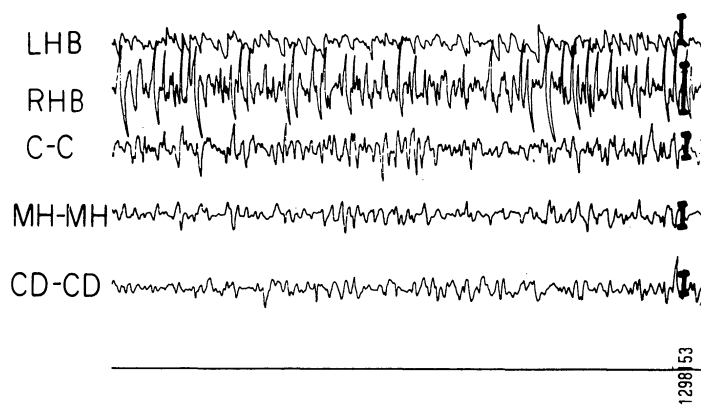


Fig. 10. Further records from cat 3 following intraventricular injection of serum. Symbols as in Fig. 9. LLH = records from laterally placed electrode in left hippocampus vs. diffuse gnd.

CAT 3

1 MIN AFTER 2ND INJ



2 HOURS AFTER 1ST INJ.

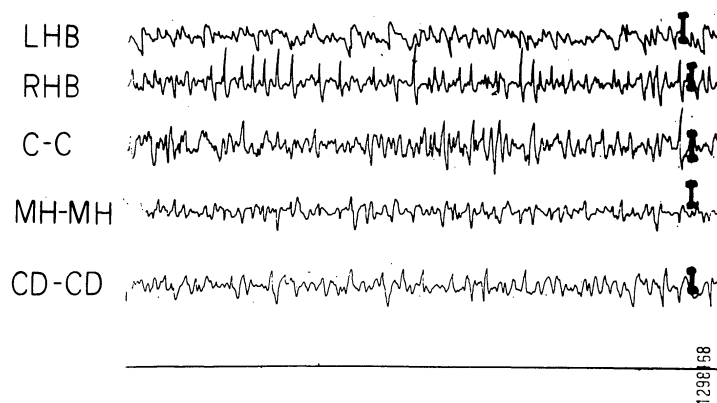


Fig. 11. Later records from cat 3. Symbols as given in Fig. 9. Vertical calibration = 100  $\mu$ V.

CAT 3

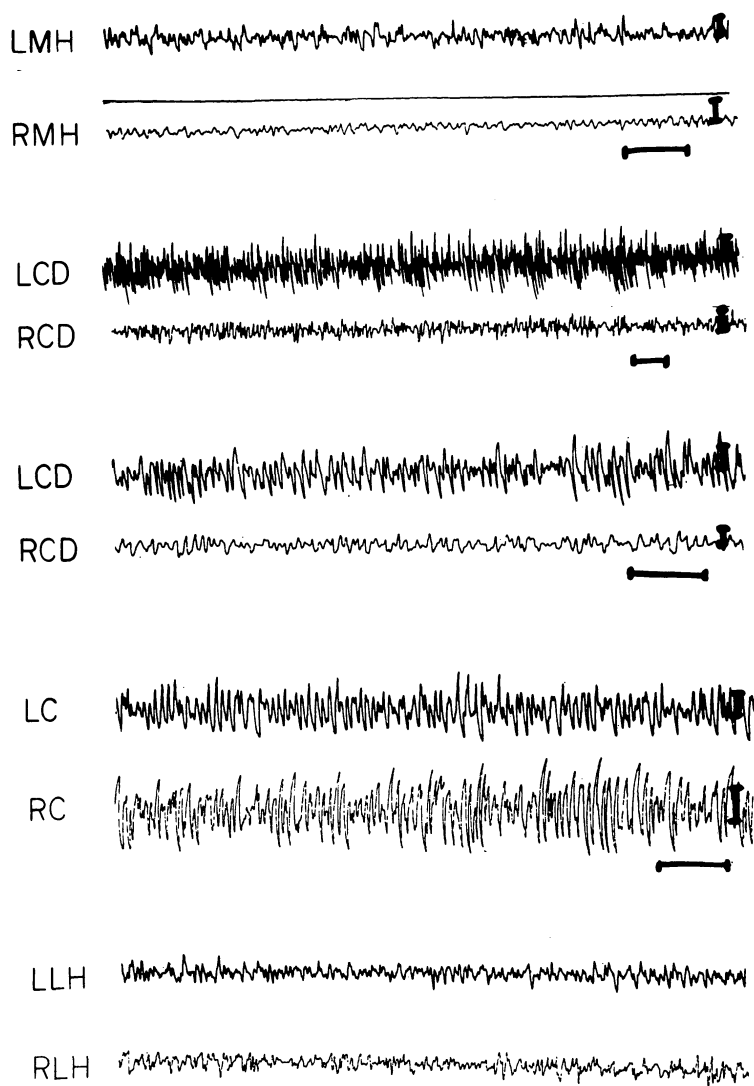


Fig. 12. Records from cat 3 about one month following injection of antibody serum. Preparation unanesthetized. Symbols as given before. Note difference in paper speeds. Vertical calibration = 100  $\mu$ V. Horizontal calibration = 1 sec.



CAT 4

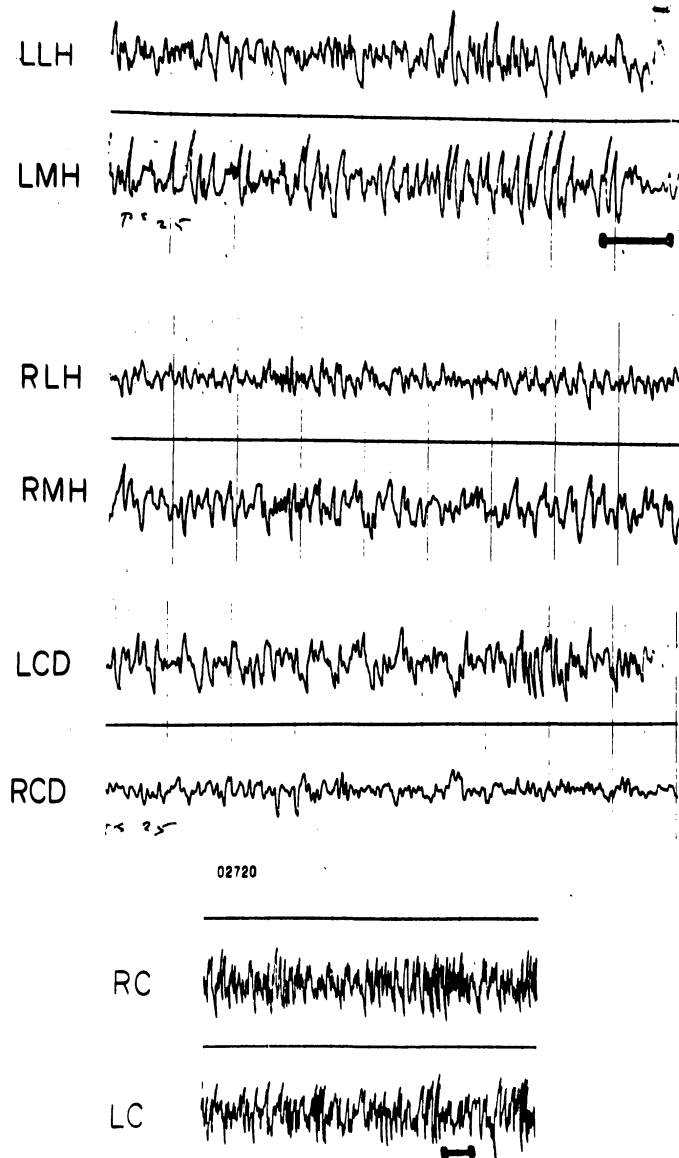


Fig. 13. Electrographic records from various brain sites of cat 4. Preparation was unanesthetized. LLH = lateral electrode in left hippocampus vs. diffuse gnd; LMH = medial electrode in left hippocampus vs. gnd; RLH and RMH = comparable to LLH and LMH only in right hippocampus; LCD and RCD = left and right caudate nuclei vs. diffuse gnd, respectively. RC and LC = contrast in potentials recorded from stainless steel screws in skull over left and right lateral gyri. Horizontal calibration = 1 sec. N. B. lower records recorded at slower speeds.

CAT 4 RIGHT AFTER INTERVENTRICULAR INJ.

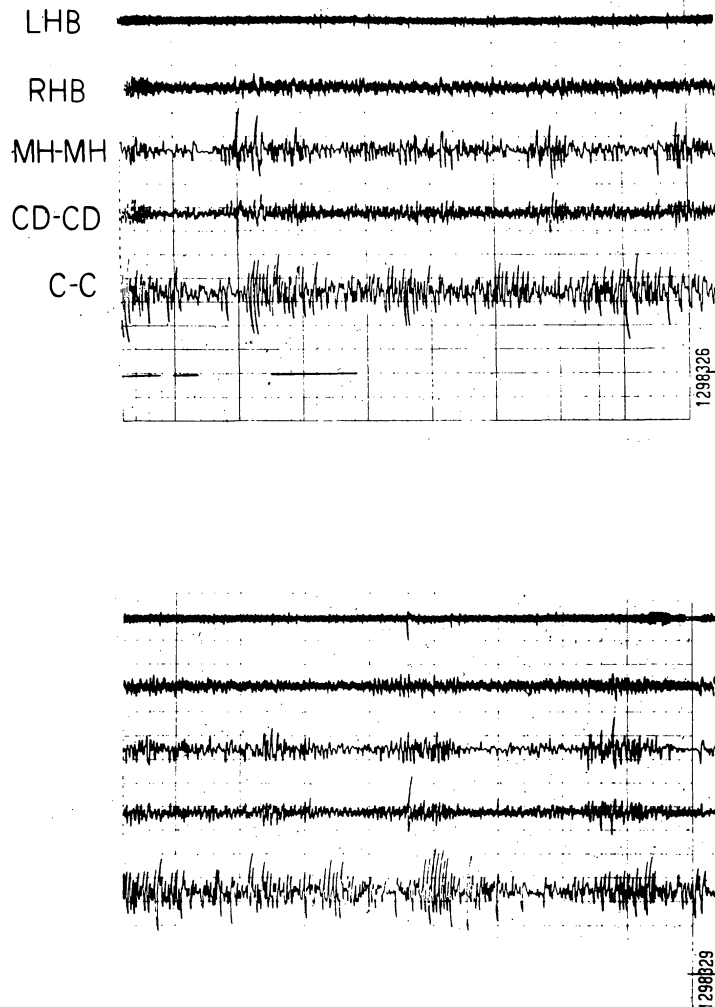


Fig. 14. Records obtained from cat 4 while anesthetized and following intraventricular injection. Electrodes intended for hippocampi were found to be too high and terminated in white matter overlying lateral ventricles. Thus, LHB = bipolar recording from white matter on left; RHB = bipolar recording from white matter on right; MH-MH = transcallosal recording between white matter of two sides; CD-CD = recording of potential difference between left and right caudate nuclei; C-C = recording of potential difference between left and right neocortical placements. Lower records obtained from sites given in upper records.

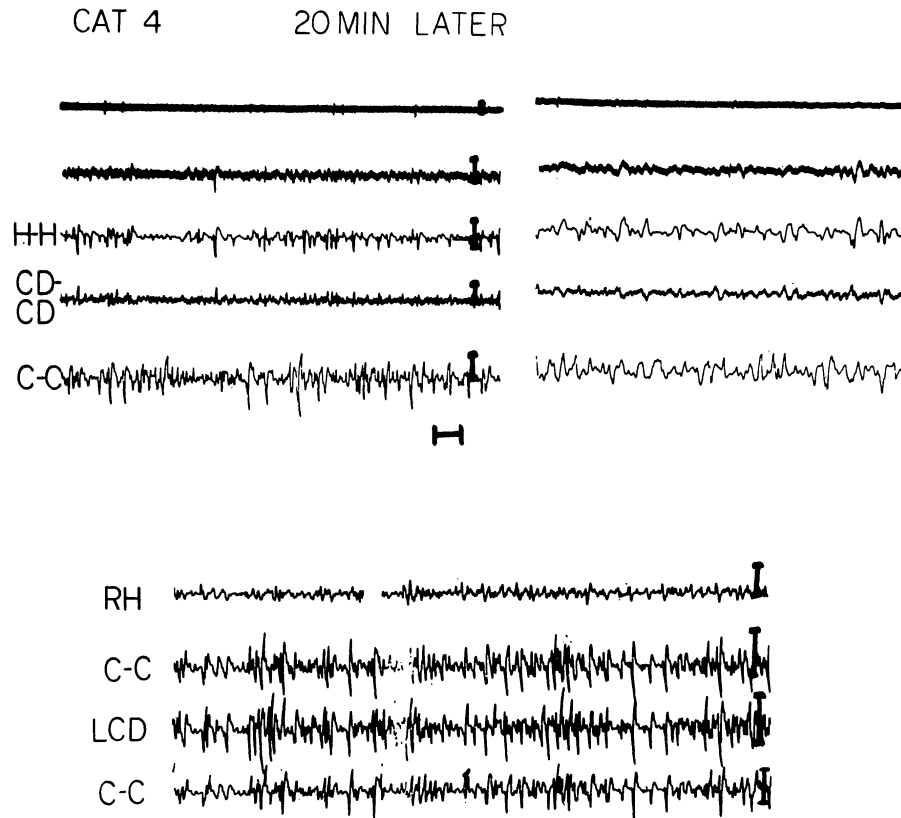


Fig. 15. Further records from cat 4 following intraventricular injection. Symbols as in Fig. 14, except that H-H = MH-MH; RH = RHB. Vertical calibration = 100  $\mu$ V. Horizontal calibration = 1 sec. Lower records made at faster speed (25 mm/sec) than upper (10 mm/sec).

CAT 5

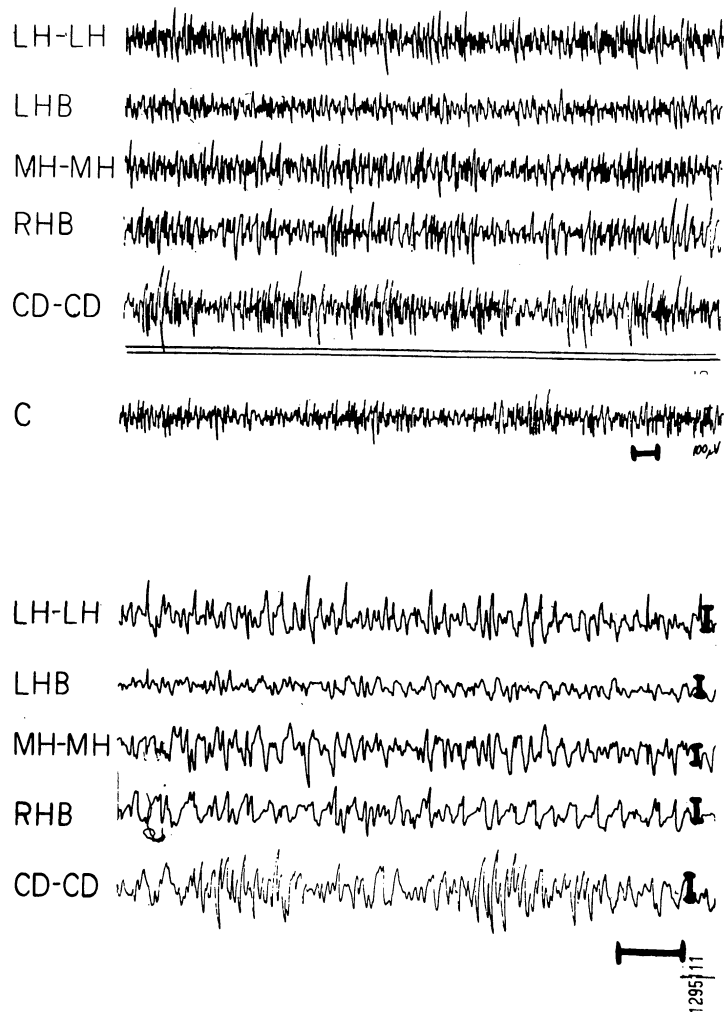
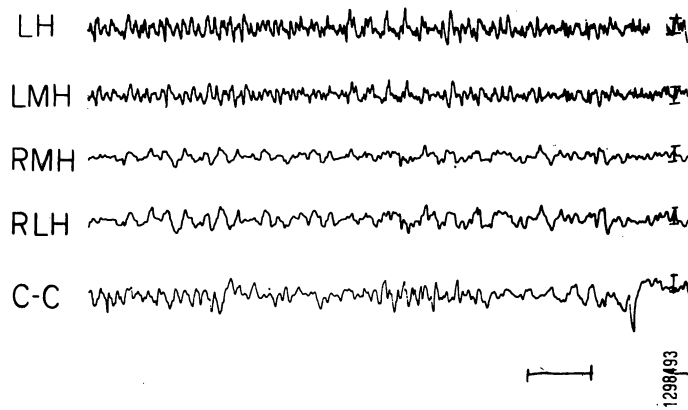


Fig. 16. Records obtained at two speeds before operation for intraventricular injection of serum. Preparation unanesthetized. Symbols given in Fig. 14 except for: C = stainless steel screw over lateral gyrus vs. diffuse gnd. Vertical calibration = 100  $\mu$ V. Horizontal calibration = 1 sec.

CAT 5  
IMMEDIATELY FOLLOWING INJ. OF ANTIBODY



17 MIN. POST INJ.

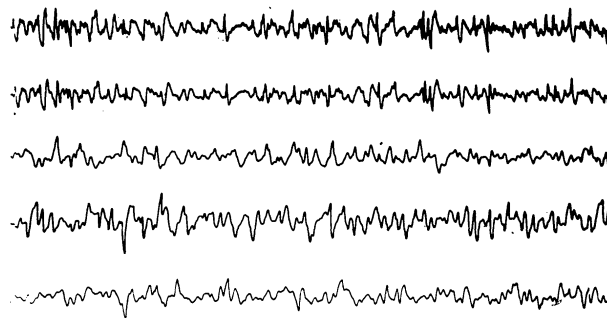
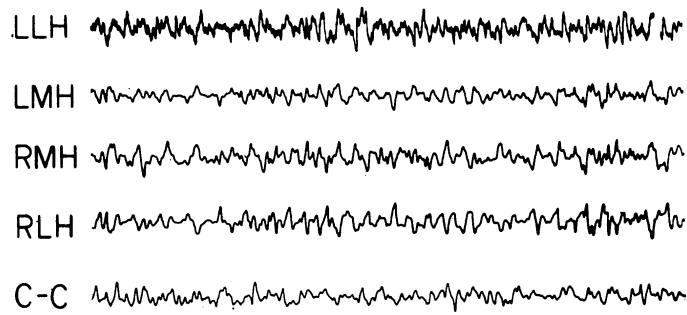


Fig. 17. Further records from cat 5 following injection of serum.  
Symbols as given in Figs. 15 and 16.

CAT 5  
FOLLOWING FURTHER INJECTION OF ANTIBODY



1295049

1 HOUR 30 MIN. POST INJ.

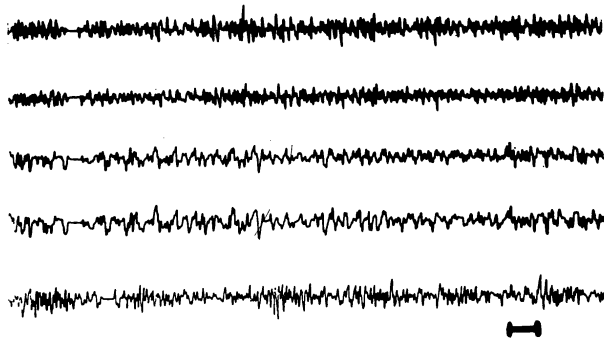


Fig. 18. Further records from cat 5 following injection of serum. Symbols are given in Figs. 15 and 16.

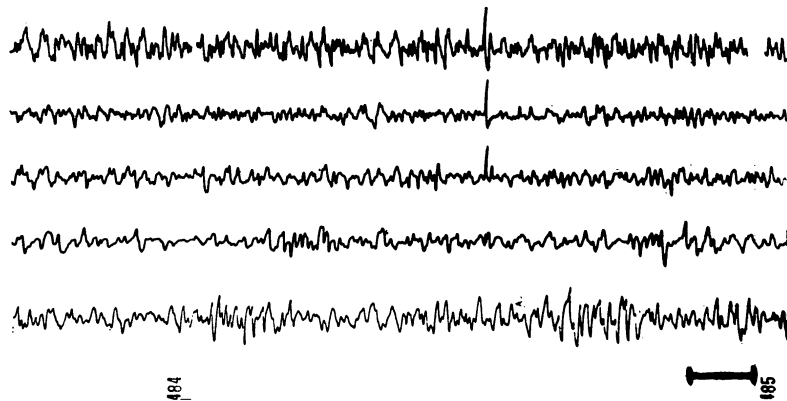
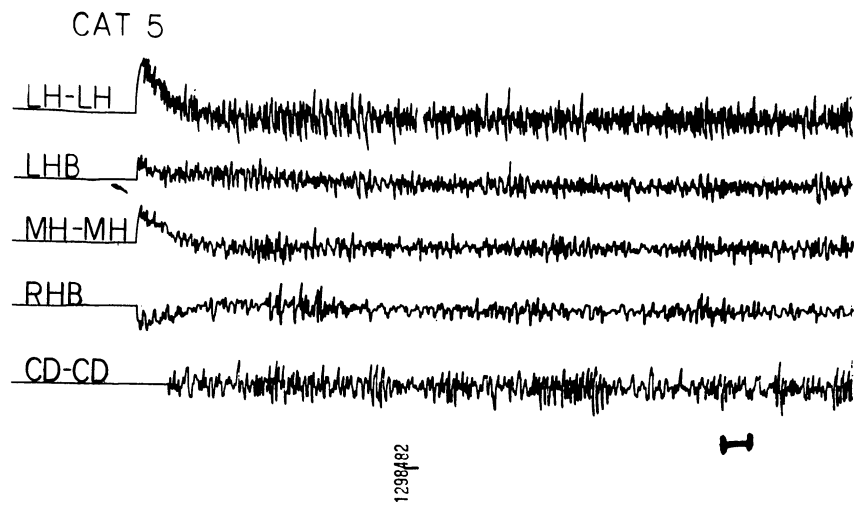


Fig. 19. Records obtained from cat 5 three weeks following injection of serum. Symbols as given in Figs. 15 and 16.





APPENDIX A

THE SOURCE OF SPONTANEOUS ALTERNATION CUES



# THE SOURCE OF SPONTANEOUS ALTERNATION CUES<sup>1</sup>

Robert J. Douglas and Robert L. Isaacson  
Department of Psychology  
The University of Michigan

## ABSTRACT

Rats were run in situations in which they could spontaneously alternate either brightness cues, visual pattern stimuli, or floor cues. Although the animals had a definite "preference" for black versus white, they did not alternate to these or to other visual cues. When only cues associated with the floor could be alternated, the rats spontaneously alternated at a very high rate. It was suggested that the cues to which rats spontaneously alternate are possibly olfactory, tactile, or auditory in nature.

On two consecutive unrewarded trials in a T maze a rat rarely visits the same side twice in a row: he spontaneously alternates. The precise cues to which an animal alternates have never been revealed, although Walker, Dember, Earl, and Karoly (1955) separated them into three classes: extramaze stimuli, intramaze cues, and response feedback. Of these three classes, response produced stimuli have been shown to have very little or no effect in producing alternation (Douglas and Isaacson, 1963). The other two classes would seem to be primarily visual. Extramaze light sources have been reportedly alternated even by the worm (Wayner and Zellner, 1958), and

intramaze stimuli have been commonly thought of as primarily visual in nature. T mazes used in alternation studies typically have black and white differentiation of the cross alleys in order to "help" the rats to distinguish them. In a study widely held to explain spontaneous alternation as an approach to change, Dember (1956) demonstrated that rats usually enter the T maze alley that has been changed in brightness from a previous trial in which the animal could see into both alleys, but was restrained from entering them. Thus, visual stimuli would appear to be an important source of alternation cues.

However, Dember (1958) reported that peripherally blinded rats spontaneously alternate to maze stimuli at about the same rate as normal animals. This suggests that either normal rats usually alternate to non-visual, non-response produced cues, or they alternate whatever cues are available, and removal of one source of cues (e.g., visual) only results in alternation to the remaining stimuli at an equal rate.

Three experiments were carried out in order to test these alternative hypotheses. In all three, the plan was basically the same: the animal would be provided with only one set of alternation cues at a time, either visual or non-visual. All observed alternation could thus be in response only to these cues. This was accomplished by using two separate T mazes with one trial being run in each maze. Only one set of cues was held constant for both trials. The principle of this system is that an animal cannot alternate to a given cue unless he has two opportunities to respond to that cue. As all other stimuli appeared only once, they could not possibly be alternated. In the first experiment, the constant cues were the black and white differen-

tiation of the alleys of both mazes. In the second experiment, both cross alleys of both mazes were of equal brightness, but were differentiated by visual pattern stimuli. The right alleys of both mazes were covered with either stars or circles, with the left alleys covered with whichever pattern was not used in the right alley. In the third experiment, the mazes had no fixed bottoms and were alternately placed over the same outlined area on a piece of heavy paper, which was taped to the asbestos tile over concrete floor. In this way, only cues associated with the floor were constant. In these three experiments, spontaneous alternation to visual brightness and pattern stimuli and to floor cues could be tested without confounding the stimuli.

## METHOD

### EXPERIMENT 1

Subjects were 40 male hooded rats bred at The University of Michigan laboratory, and between the ages of five and seven months. All had been handled frequently and were well gentled. The two mazes, which differed in proportion and construction, have been described elsewhere (Douglas and Isaacson, 1963). Despite differences, both were standard T mazes. Both mazes had either their right or their left cross alleys lined with black cardboard inserts, with the opposite alley lined with white. The mazes were placed at right angles to each other in the same room, and the tops of both were covered with dark opaque paper in order to minimize extra-

maze cues. The room was darkened during the experiment.

Each rat was run two trials a day for two consecutive days. On one day a subject would have its first trial in, say, maze I and the next trial in maze II. On the following day, it would be maze II before maze I. Each rat was run once with the right alleys of both mazes black, and once with the left alleys black.

On the first trial a subject was placed in the starting box of one of the mazes and, after being detained for five seconds, was allowed access to the maze. When the rats' entire body had entered one of the cross alleys, a sliding door was lowered and the animal detained for about ten seconds in that alley. The subject was then removed and placed in the starting box of the other maze and the second trial begun.

## EXPERIMENT 2

Twenty-four rats of about the same age and experience as those of experiment 1 were used as subjects. The same two mazes were used, and the procedure was identical to that of the first experiment except that black cardboard stars or circles on white cardboard backgrounds replaced the plain black and white inserts. The figures were constructed so that they were equal in area. For a given session with a given subject, the walls of the right alleys of both mazes would be covered with stars and the left alleys with circles, or vice versa.

## EXPERIMENT 3

The same subjects from experiment 2 were used. Two different T mazes

were constructed of equal sizes and proportions but without bottoms. The main stem and the cross alleys were all about 18 in. in length. The walls of one maze were yellow while those of the other were black. The experimental procedure was similar to that of experiments 1 and 2 except that the two mazes were alternately placed over the same spot on a piece of heavy paper which was taped to the floor of the room. The room floor was constructed of asbestos tile over concrete. A black outline of the maze was drawn on the paper in order that the mazes could be placed in the same location. The tops of the mazes were covered in order to minimize extramaze cues, but had an open patch of screening over the choice points so that the subjects could be observed. A hooded 7-1/2 watt light bulb was placed over the choice point and the room was darkened. Each rat was run for one trial in each maze. Between trials the animal was removed and placed in a waste basket while the maze was being removed and the other maze placed in the vacated area for the second trial. The whole process of changing mazes took only a few seconds. On the following day, a subject was run first in the maze that had been second on the previous day.

#### CALCULATION OF RANDOM OR CHANCE SCORES

In order to state that alternation did not occur, an estimate must be made of what random behavior would be in that same situation. If an animal is neither alternating or repeating responses, its behavior on the second trial should be determined by the same variables that influence first-trial performance. Random alternation is not 50 percent since it has been estab-

lished that rats in this laboratory have an initial right side preference of about 67 percent (Douglas, 1963). In addition, rats "prefer" black to white in the T maze, and this fact must enter into the calculations. Other experiments in this laboratory indicate a black preference of about 80 percent if the right alley is the black one, and 60 percent if the left alley is black. Therefore, if the animals in experiment 1 behave "true to form" in their biases, the probability of alternating by chance alone is the average of the probabilities in the two possible situations or:

$$\text{Pr(Alt)} = (1/2) \left\{ [\text{Pr}(R_b L_w) + \text{Pr}(L_w R_b)] + [\text{Pr}(R_w L_b) + \text{Pr}(L_b R_w)] \right\}$$

where:

Alt = alternation of maze alleys or turns

$R_b$  = right turn when right side is black

$R_w$  = right turn when right side is white

$L_b$  = left turn when left side is black

$L_w$  = left turn when left side is white

or:

$$\text{Pr(Alt)} = (1/2) \left\{ [(.80 \times .20) + (.20 \times .80)] + [(.40 \times .60) + (.60 \times .40)] \right\} \text{ or } .40.$$

In experiments 2 and 3 unless some unexpected side preference occurs, the probability of a random alternation response is simple the sum of the probabilities of a left-right and a right-left sequence of turns with the two trials independent, that is:  $(.67 \times .33) + (.33 \times .67)$  or 44 percent.



## RESULTS

### EXPERIMENT 1

The black-white cues were alternated only 38.5 percent of the time. Since the observed black preference did not differ much from the expected preference mentioned earlier, random alternation would be about 40 percent. None or very little of the behavior of these animals could be attributed to alternation or repetition tendencies. Even though the alternation rate was near that expected to occur at random, behavior as a whole was far from being "random." The subjects had a definite tendency to visit the black alley as is shown in Table 1.

A difference this large in the distributions would occur less than 1 percent of the time by chance ( $\chi^2$  test). Therefore a rat is capable of a strong response to a stimulus without alternating to that stimulus.

### EXPERIMENT 2

The subjects alternated to the stars and circles at a rate of 50 percent. There was no significant preference for either the stars or the circles, and the observed right turn tendency did not differ significantly from the expected 67 percent (it was 60 percent) usually observed in homogeneous-colored mazes ( $\chi^2$  test). Since fewer animals did go to the right on the first trial, however, random alternation would be  $(.60 \times .33) + (.40 \times .67)$  or 47 percent (see Douglas, 1963 for details). In addition, the animals that alternated on the first day were no more likely to alternate on the second day than those that repeated turns on the first day. For this reason, it is doubtful that

some individuals are "visual alternators" while others are not. Thus, there was no suggestion that any of the rats' behavior could be attributed to alternation of visual pattern stimuli.

### EXPERIMENT 3

Animals having each trial in a separate maze, but with the same floor used for both mazes, alternated alleys at the rate of 85.4 percent. Since the observed right side preference was very close to 67 percent, a random rate of alternation would be about 44 percent. This difference between the observed alternation and the random rate is significant at the .01 level ( $\chi^2$  test), and is shown in Table 2.

The results of all three experiments are summarized on Table 3.

### DISCUSSION

These results indicate that, contrary to the popular belief, visual cues are not spontaneously alternated. It would appear that floor cues are the major source of stimuli which are alternated. It cannot be established at this time just what these floor cues are. Possibly the animal is merely avoiding his own odor trail on the floor, or it could be that the important cues are tactile in nature. Shepard (1959) has reported that kinesthetic cues are not a major source of information used by rats in maze learning, and he believes the cochlea to be the sensory organ which mediates the use of floor cues. A more exact determination of the sensory modality (or modalities) relevant to spontaneous alternation remains a task for the future, although

vision and kinesthesia have now been eliminated.

These results make the "approach to change" theory of alternation (December, 1956) less plausible. Even though his animals showed a definite attraction to a changed stimulus, that does not imply that alternation is also an approach to a changed stimulus. The present study demonstrates that visual stimuli can have a considerable degree of "attractiveness" and yet not be used as alternation cues.

A possible criticism of this study could be that proper controls were not used in the first two experiments. The rats should have been given two consecutive trials in each maze in order to show that they would alternate significantly in a normal situation. However, rats of the same strain, prior experience, and age have been run in these mazes many times. These well-tamed animals have always alternated at higher than usual rates (85 to 90 percent). The present subjects probably did not become progressively tamer as the experiment proceeded, as they were very "unemotional" to begin with. Few fecal boli were ever found in any of the mazes. This is an important point, as emotionality results in reduced alternation (Douglas, unpublished data).

Finally, it might be argued that in experiment 3 the two mazes were so similar that the animals were unable to distinguish them, and the high alternation rate resulted from an inability to discriminate. In order to rule out this possibility the present authors re-ran the rats used in experiment 3 with the two similar mazes placed on two different areas of the floor. The result was random alternation. If the two mazes were not "con-

fused" in this situation they probably were not in experiment 3 either.

While it is still possible that a rat will alternate to stimuli in another sensory modality when the "usual" cues are missing, it is impossible to state in which modalities this could occur. At the present time, vision would appear to be eliminated.

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Table 1. Preference for the black alley.

	No. Turning Right	No. Turning Left
Right side black	31	9
Left side black	17	23

Table 2. Floor cue alternation: observed behavior vs. expected random behavior.

	No. of Alternation Responses	No. of Repetition Responses
Random expectancy	20	28
Observed behavior	41	7

Table 3. Summary of results.

Exper.	Alternation Cues	Number of Observations	Random Alternation Rate	Observed Alternation Rate	Sig. of Difference ( $X^2$ Test)
1	Visual black vs. white	80	40%	38.5%	not sig.
2	Visual stars vs. circles	48	47%	50.0%	not sig.
3	Floor cues	48	44%	85.0%	p < .01



FOOTNOTE

<sup>1</sup>This research was supported in part by Grant DA-MD-49-193-63-G75 from the Office of the Surgeon General, U. S. Army.



APPENDIX B

RESPONSE ALTERNATION: THE MYTH AND THE METHOD



# RESPONSE ALTERNATION: THE MYTH AND THE METHOD<sup>1</sup>

Robert J. Douglas and Robert L. Isaacson  
Department of Psychology  
The University of Michigan

## ABSTRACT

A group of rats was given one unrewarded trial in each of two separate T mazes. This would allow them to spontaneously alternate turning responses without interference from any other stimuli to which they might otherwise alternate. They were found to behave in a random manner, suggesting that response alternation does not occur as a behavioral phenomenon. When the animals were provided with other alternation cues by running them for two trials in the same maze, they alternated at a very high rate. Contradictory results in the literature were explained as due to differences in interpretation of the data.

It has generally been assumed that turning responses are spontaneously alternated to some degree. However, there has been a gradual lowering of the importance attributed to the response itself as the methods of measurement have been more refined. In 1948 Solomon, for example, considered spontaneous alternation in the T maze to be entirely caused by a response decrement. But a single T maze cannot be used to differentiate between alternation of a turn-

ing response and alternation of maze stimuli or goal boxes. When this maze is modified by the addition of another approach alley on the opposite side, the subject can be made to enter the choice point area from two different directions on two consecutive trials. The starting alley which is not used on a given trial is blocked off so that at any one time the maze is still essentially a T, although it looks like a  $\pm$ . In the  $\pm$  maze the subject must repeatedly visit the same alley and goal box in order to alternate turning responses, and must repeat the turning response in order to alternate side alleys. Glanzer (1953) and Montgomery (1951) independently used this method to demonstrate that turning responses were alternated less often than were maze stimuli.

Walker, Dember, Earl, and Karoly (1955) added the refinement of rotating the  $\pm$  maze in the room between trials so that the contribution of extramaze cues to alternation could be evaluated. They found that response alternation occurred less frequently than alternation of extramaze cues, which were, in turn, alternated less often than intramaze cues.

The  $\pm$  maze also has an inherent weakness. It cannot be used to differentiate alternation of one stimulus class and repetition of another. For example, if a rat "decides" to visit the same goal box twice in succession, his behavior is scored as an alternation of responses or of extramaze cues. In order to remedy this defect a situation was created in which the subject could either alternate turning responses or not alternate at all. This was accomplished by using two separate and distinct T mazes with the subject given one trial in each maze. Since it is not logically possible to alternate with

respect to anything that does not occur at least twice, all alternation could be then attributed to the response itself. In this way a purified, absolute measurement of response alternation was made possible, without confounding it with repetition of some other cue.

## METHOD

### SUBJECTS

Subjects were 24 male hooded rats bred in The University of Michigan Psychology Laboratory. They varied in age from about five to seven months. All had been handled frequently and were well-tamed.

### EQUIPMENT

Two T mazes were used: Maze I and Maze II. Maze I had white cardboard inserts in both cross alleys, a wooden floor and a two-foot long stem. Maze II was painted gray, had a brass grid floor and a one-foot stem. Maze I was illuminated by two 7-1/2 watt light bulbs near the centers of the cross alleys, while Maze II had a single bulb over the choice point. Both mazes had cross alleys of about three feet in length with sliding doors at the entrances, and enclosed starting boxes. Both mazes were covered with dark paper in order to minimize extramaze cues, and the room was darkened during the experiment. The two mazes were in the same room and at right angles to each other.

### PROCEDURE

The animals were run under four conditions. In two of these the same maze was used twice, and in the other two both mazes were used. Half of the

time maze I preceded maze II, and half of the time maze II was used first. On any one day six rats were run on each of the four conditions: I-I; I-II; II-II; II-I. Each animal was run under one condition a day for four days, so that all rats had all four conditions.

Running procedure consisted of placing a subject in the starting box of one of the mazes and after a five second delay raising the sliding door to the main alley of the maze. When an animal's entire body had entered one of the cross alleys a sliding door was lowered and the response scored as a right or left turn. The subject was detained for ten seconds in that alley and then placed in either the same starting box or the starting box of the other maze. The second trial was begun after another five second delay, and the procedure was the same as that of the first trial.

## RESULTS

When both trials were run in the same maze 89.6 percent of all second trial responses were alternations of the first trial responses. When one trial was given in each maze, alternation of responses dropped to 41.7 percent. This difference is significant beyond the .01 level (Sign Test). The results are shown in more detail in Table 1.

In order to determine whether any alternation has occurred, a chance level of alternation must be calculated. Random or chance alternation is that alternation which would occur even if the subjects' behavior on both trials were independent: That is, if behavior on each trial is determined by



side preferences, if any, without respect to the alley previously visited. In this laboratory rats have been found to have a 2:1 right side preference in T mazes (Douglas, 1963), and these animals were no exceptions. In maze I 69 percent of the rats went to the right on their first trial, and in maze II it was 71 percent. Since these figures do not differ significantly from the established 67 percent, the random rate of alternation would be  $Pr(RL)+Pr(LR)$  or about  $(.67 \times .33) + (.33 \times .67)$  or .44. This is very slightly higher than the observed rate of .42 when two mazes were used. Therefore the subjects were alternating response-produced cues at only a random rate.

Since rats do not alternate when over four hours elapses between trials (Walker, 1956) an "empirical" chance score can also be estimated by counting the frequency of alternation of first trial responses from one day to the next. This procedure results in an estimated random rate of 47 percent, once again slightly higher than the observed rate.

## DISCUSSION

It might still be argued that under the appropriate circumstances alternation of response-produced cues might be demonstrated. Possibly the handling of the subjects between trials disrupted the response stimuli. If the animals had not been squeezed, bent and mauled the pure turning feedback might have been put to use by the rats.

The present authors have already tested this possibility in the following way. An extension alley was added to the base of a T maze, at right angles to the main alley. The extension alley joined the main alley at the

point where the starting box normally is located. The starting box was re-located at the far end of the extension. Two of these extensions were built, so the subjects could be made to make either a forced left or a forced right turn in order to enter the main alley from the extension and proceed to the choice point. In this way the subjects would be able to alternate turns without having the continuity of their performance interrupted, and without the intervening handling. The rats were found to behave as if the forced turn had not even been made: eight of twelve subjects turned to the right at the choice point after a forced left turn, but eight out of twelve rats also turned to the right after just making a forced right turn. These 24 rats were later shown to have the usual 2:1 right preference in the "T" part of this modified maze. Thus, handling probably did not prevent response alternation from occurring in the two-maze situation. It is a more likely supposition that response alternation would not have occurred anyway.

These results would appear to contradict those mentioned in the scoring system used in the  $\pm$  maze. Even when a rat is allowed to alternate to all possible cues (for example in a stationary T maze) it does not always do so. Typically, rats alternate about 80 percent of the time. Yet in the  $\pm$  maze every possible response by the rat is scored as an alternation of some cue or other. It may well be possible that the reported "response alternation" in the  $\pm$  maze represents the lack of alternation of other cues, since failure to alternate to one stimulus is scored as an alternation of another.

If response alternation does not occur, as these results indicate, then

the inability of many researchers to increase its rate is readily understandable. The one study which does report an increase in response alternation is that of Walker, Dember, Earl, Fawl, and Karoly (1955). In that study, a maze was used in which the rats were forced to twist and climb in order to reach the goal boxes. This maze was much like a  $\pm$  maze in that it had two opposite starting points and only two goal boxes. The subject's behavior was also scored as if they were in a  $\pm$  maze. However, the maze has two separate choice points and the animal is thus not really forced to make the same decision twice in a row. At either of the choice points the rat must "decide" which of two different pairs of ascending alleys to enter, even though they lead to the same goal boxes. One might expect less alternation of maze stimuli in this situation than in the  $\pm$  maze because there are far fewer constant stimuli to alternate. Because of the scoring system which was used, this hypothetical decrease in alternation of maze stimuli would be scored as if it were an increase in response alternation. It is impossible to use this explanation to cover the fact that spontaneous alternation to all cues occurs at a higher rate in the sidwinder maze than in an orthodox T maze. This phenomena may be due to causes other than the addition of figural response cues, however. There is no independent evidence that the figural response was the reason for the higher rate of alternation in the sidwinder maze. Thus, the present report does not contradict the data of earlier studies, but only questions their interpretation.

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Table 1. Results under all conditions.

Condition		Percent Alternation	Mean Percent
Same maze	I-I	91.6	89.6
	II-II	87.5	
Differ- ent mazes	I-II	41.7	41.7
	II-I	41.7	

FOOTNOTE

<sup>1</sup>This research was supported in part by Grant DA-MD-49-193-63-G75 from the Office of the Surgeon General, U. S. Army.

APPENDIX C

RANDOM BEHAVIOR IN THE 'T' MAZE





# RANDOM BEHAVIOR IN THE 'T' MAZE<sup>1</sup>

Robert J. Douglas  
Department of Psychology  
The University of Michigan

## ABSTRACT

Several large groups of rats of different types were shown to have a 2:1 right turn tendency on their first trials in homogeneously colored T mazes. It was reported that whether an individual rat turned left or right on its first trial in the maze, it has a .67 probability of turning to the right on future trials in the maze if several days elapse between trials. Several methods of calculating random or chance rates of spontaneous alternation were discussed.

"Spontaneous alternation" is said to occur when an animal visits both sides of a T maze on two consecutive unrewarded trials. Subjects usually do not alternate all of the time, and spontaneous alternation can be positively demonstrated only if it can be shown that it occurs at a rate higher than expected by chance alone. Yet there is no data presently available which reveal exactly what constitutes random or chance behavior in the T maze. The present study is an attempt to fill that gap in our knowledge.

In spontaneous alternation, an animal's second response is highly depend-

ent on his first one. Random alternation can therefore be considered as the rate of alternation that would occur if the subject's two responses were independent of each other. Some alternation would be expected to occur even if all subjects had no "memory" of their previous trials. The problem is, how much is some alternation? Since the present author operationally defines random alternation as the alternation rate predictable from a knowledge of the subjects' behavior on a single trial, the problem of calculation of this random rate hinges on a precise determination of response biases or stimulus preferences, and an understanding of what these represent. This problem has often been resolved in the past by assuming that the probability of a right or left turn is 50%, and thus the probability of alternation by chance is  $\text{Pr}(\text{RL}) + \text{Pr}(\text{LR})$  or  $(.25 + .25)$  or .50, if the two trials are independent. However, rats typically do not have a 50-50 turn or side bias.

It has repeatedly been observed in The University of Michigan laboratories that when homogeneously colored T mazes are used, about two thirds of our rats go to the Right side on their first trial. The cause of this 2:1 Right preference has not been determined, but it has been observed in male, female, albino, and hooded rats, as well as in rats with hippocampal, neocortical, and fornix-septal area lesions (see Table 1).

Furthermore, the same 2:1 Right preference has been found in a wide variety of T mazes, so that it is not dependent on some idiosyncrasy of a particular maze. This preference may be reversed in some groups of rats or be due to the handedness of the experimenter (Walker, E. L., personal communication), however any side preference can be treated in the same manner as

is being done in this paper. The exact figure of .67, even though based on exhaustive data, is used for illustrative purposes. Some side preference, however, can almost always be expected to occur. This side preference, for example a .67 right side bias, can be interpreted in at least three ways:

(1) Two-thirds of the rats are right handed and one-third are left handed with respect to their turns or choices. If an individual turns left on the first trial, he will continue to favor the left side (disregarding spontaneous alternation), and vice versa.

(2) Subjects are homogeneous in their preferences. If two-thirds of the animals go right, then each and every rat has a .67 right side preference. In the future, it will continue to choose right on two-thirds of the trials (again, disregarding spontaneous alternation).

(3) Subjects are mixed. While some have a definite preference, others behave as in no. 2 above.

These alternatives were tested by running twenty-four rats on five separate occasions separated by several days between trials. Since Walker (1956) has shown that spontaneous alternation falls to its lowest rate after only four hours, these trials could all be considered as essentially "initial trials," as if the animal were repeatedly making first choices. If all rats making a right turn on the first day are placed in one group, and those making a left turn in the other, the following predictions would be made from the three interpretations of first trial behavior (see Fig. 1).

## METHOD

Subjects were 24 male hooded rats between five and seven months of age. All had been frequently handled and were very tame. Thirty-eight animals were run on the first day in order that 12 left turning rats could be obtained. Only the first 12 of the Right turning rats were used. The maze used was a conventional T maze with black inserts in both cross alleys. Experimental procedure consisted of placing a subject in the starting box of the maze. After five seconds, a sliding door to the main alley was raised and the animal allowed to proceed to the choice point. When the entire body of the rat had entered one of the side alleys, a sliding door was lowered and the animal confined there for about ten seconds. After this the subject was replaced in his cage and not used again for several days.

## RESULTS

The following graph shows the percent of right turns made by each of the two groups on all five days (see Fig. 2).

It can be seen that the points coincide with or lie very near those predicted from interpretation no. 2, that each animal has a 2:1 right preference. It is impossible to state that a true left or right turning "handedness" does not occur in some rats, but if it does, it is probably rare. Even fewer animals made all right or left responses than would be predicted by interpretation no. 2, as two were observed, but 2.6 would be predicted:  $((.67)^4 + (.33)^4) \times 12$ . This discrepancy favors no. 2, however, as more than

this would be predicted by either interpretation no. 1 or no. 3.

## DISCUSSION

These results favor the idea that the frequency of right turns made by a group of rats is a reflection of the magnitude of a right side (or turn) preference in each and every rat. This conclusion does not rest completely on the data presented here, as the present author has rechecked the data of literally hundreds of subjects that have been given alternation tests on more than one occasion. The data revealed that both left and right turning rats had about the same 2:1 right preference on future occasions. It should be noted that the physical basis of turn preference may be hereditary, and that some populations may be mirror images of these rats with respect to turn or side preferences. Several years ago, the rats in this laboratory were consistent left turners (Walker, E. L., personal communication). The present animals represent a considerably different genetic population. In addition, the earlier experimenters in question were all left handed, while the present one is not. But the observation that these side preferences persist, as shown in this experiment, does not depend on these speculations.

## CALCULATION OF RANDOM ALTERNATION

Calculation of the alternation rate expected to occur by chance alone depends on whether a prediction is being made before the first trial has been run, or whether the first trial (or both trials) have been run and the

data used in the calculations. For example, if the subjects are to be run in a homogeneously colored T maze, the following percentage of the group would be expected to make the following sequences of behavior by chance alone:

RR: (.67) (.67) 100; 45%	}	44% random alternation
RL: (.67) (.33) 100; 22%		
LR: (.33) (.67) 100; 22%		
LL: (.33) (.33) 100; 11%		

However, if the animals had already been run, it would be expected that their observed initial responses would vary somewhat from the theoretical 2:1 right preference because of chance fluctuations. This is especially true with small groups, and unless their behavior differs significantly from a .67 right preference, the latter figure should be used. If, for example, half of the rats turned right on the first trial, expected random alternation would be the probability of a left turn given a right, plus the probability of a right, given a left turn. This would be  $(.50 \times .67) + (.50 \times .33)$  or 50%.

There is yet another method of calculating random alternation which the present author calls the "empirical chance" method. If, in a spontaneous alternation experiment, the animals are given two trials a day for several days, one can merely count the alternation rate of their first trial choices from one day to the next. This method is best used when side preference is thought to differ from the 2:1 right preference, perhaps because of some nonhomogeneity of the maze. An example of this is

when one cross alley is darker than the other. It is well established that rats tend to enter the darker of two alleys (Walker, 1958), but the exact dark preference may depend on how dark the alley is in relation to the other alley. Furthermore, it does not overrule the right preference, but is probably in an additive relation to it. The present author (unpublished data) has observed that about 80% of his rats make right turns when dark black is to the right, and bright white to the left. About 60% go to the left side, if that side is the black one. But these figures are by no means well established and when in doubt, a balanced experimental design and the empirical chance method are perhaps the best insurances of determining a reliable level of random alternation.

#### SPONTANEOUS REPETITION

Now that a fairly reliable estimate of random behavior in the T maze is possible, how is less-than-chance behavior to be interpreted? If a group of animals alternate even less than expected on a random basis, then variability of behavior at a given session is less than the variability observed from day to day. This implies a degree of dependence of a trial on the immediately preceding trial, and is as much a real tendency as the opposite one: spontaneous alternation. Spontaneous repetition should not be confused with a habitual turning response, as the latter would be part of the data used to calculate "empirical chance" alternation. It is conceivable that under some conditions or following some brain operations, spontaneous repetition might be found.

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Table 1. Right preference in rats.

Group		Number of Observations	% Right Turns On First Trial
Normals	Male hooded	152	67.7
	Female hooded	28	67.9
	Male albino	27	74.1
Lesioned	Hippocampal	49	63.3
	Neocortical	50	66.0
	Fornix-septal area	20	70.0

## FIGURE CAPTIONS

Fig. 1. Predictions of future side preferences from the 3 hypotheses.

Fig. 2. Right turns made by each group on five separate occasions.

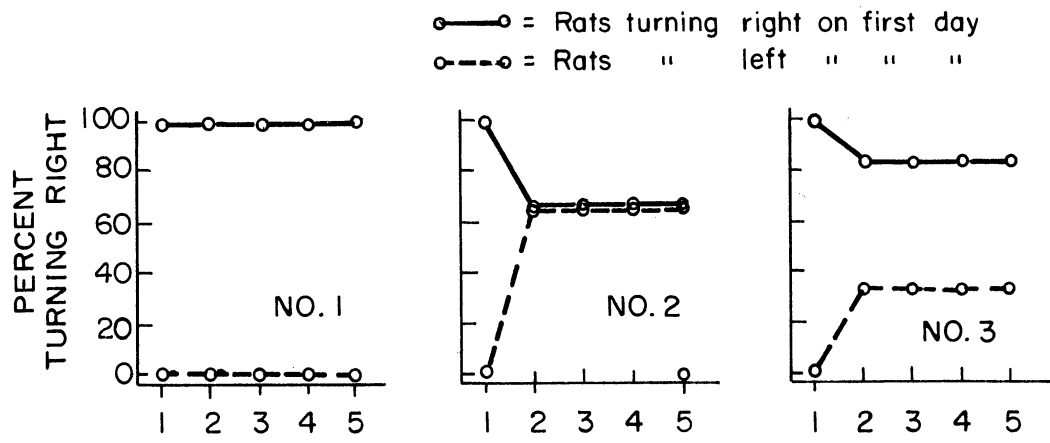


Fig. 1.

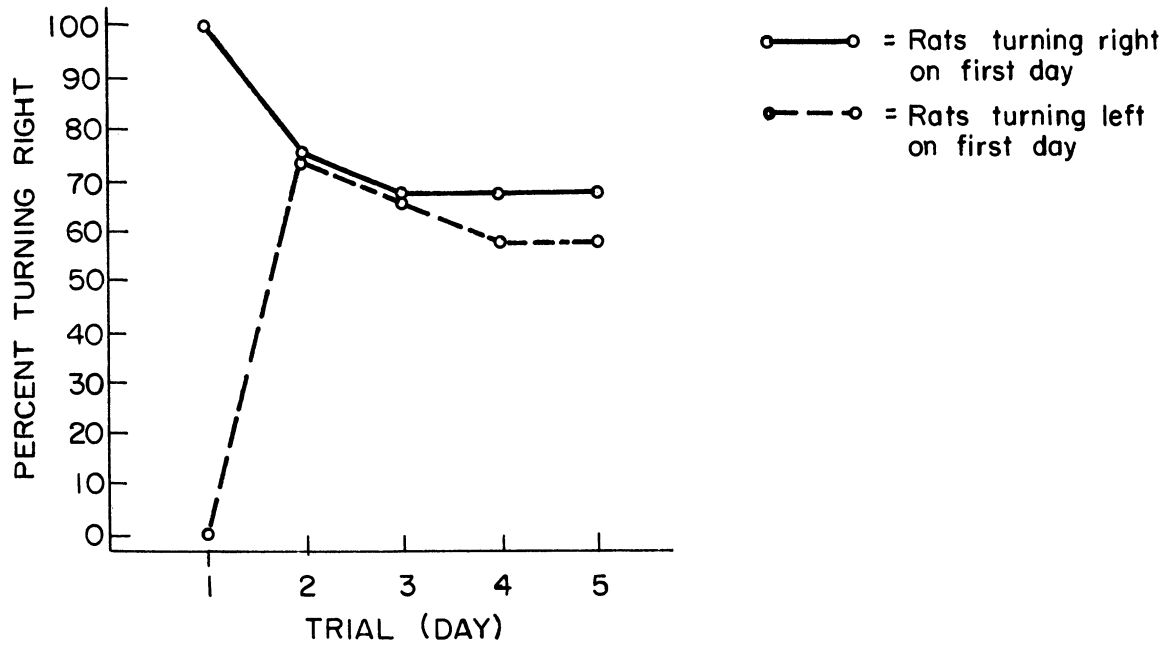


Fig. 2.

FOOTNOTE

<sup>1</sup>This research was supported in part by Grant DA-MD-49-193-63-G75 from the Office of the Surgeon General, U. S. Army.



APPENDIX D

EFFECT OF BILATERAL HIPPOCAMPAL ABLATION ON DRL PERFORMANCE





# EFFECT OF BILATERAL HIPPOCAMPAL ABLATION ON DRL PERFORMANCE<sup>1</sup>

Carol V. H. Clark<sup>2</sup> and Robert L. Isaacson

The University of Michigan

## ABSTRACT

Six animals with bilateral hippocampal lesions, six animals with neocortical destruction, and five normal animals were conditioned to bar press on CRF and then on DRL schedules of water reinforcement. In comparison with the neodecorticate and normal Ss, the hippocampectomized animals showed lower rates of responding under CRF, higher rates under DRL, and, therefore, a lower percentage of reinforced responses under DRL.

# EFFECT OF BILATERAL HIPPOCAMPAL ABLATION ON DRL PERFORMANCE<sup>1</sup>

Carol V. H. Clark<sup>2</sup> and Robert L. Isaacson

The University of Michigan

The present experiment investigates the behavior of rats with hippocampal lesions in an instrumental situation. Hippocampally-ablated animals are compared to cortical and unoperated controls with respect to the temporal patterning of their responses during differential reinforcement of low rates of responding (DRL). There is reason to expect that hippocampally ablated rats would have difficulty in acquiring the temporal discriminative required by a DRL schedule because of their apparent deficiencies in passive avoidance situations (Kimura, 1958; Isaacson and Wickelgren, 1962) and their greater resistance to extinction under certain experimental conditions (Isaacson, Douglas, and Moore, 1961; Jarrard, Isaacson, and Wickelgren, 1963; Niki, 1962).

## Method

Subjects: Subjects were 17 naive male hooded rats. All were 5 to 6 months old at the time of surgery. Six animals received bilateral hippocampal ablation, six received lesions of the cortex overlying the hippocampus, while five served as unoperated controls. Operated animals were allowed at least two weeks to recover before going on the deprivation schedule.

Apparatus: Behavioral equipment consisted of two operant conditioning boxes,

each 16-1/2 in. long x 7 in. deep x 8 in. high, constructed of wood with a glass panel across the front. A metal bar which activated a microswitch under 80-100 gm. pressure was mounted on the left side 3-1/2 in. from the floor. To the right of the bar was an aperture 3 in. high into which a left-handed Lafayette water dipper could be raised. Each box had its own fluorescent light. The boxes were partially soundproofed with cement brick and felt and were placed in a room removed from that housing the programming equipment. The experimenter could observe the Ss through a one-way mirror in the connecting wall. Timers, relays, and Harvard cumulative recorders were placed in the adjacent room where their noise would be inaudible to the Ss. The system could be adjusted so that Ss received reinforcement for each bar press (CRF) or so that a bar press would activate the dipper only after a delay of 20 seconds or longer from the previous bar press (DRL).

Surgery: Clean surgical technique was used. Subjects were anesthetized with sodium pentobarbital; they were not held in a stereotactic instrument during the operation. The general operative procedure has been described before (Isaacson, et al., 1961). The essential details were as follows. After a midline incision was made in the scalp, temporal muscles were freed from their dorsal and lateral insertions. Suitable holes were drilled in the skull and enlarged with rongeurs. The dura was then slit and the desired portion of the brain removed by aspiration. In the experimental group the hippocampus was first exposed and then removed. In making neocortical lesions, the hippocampus was similarly exposed but left intact. After bleeding had ceased Gelfoam was inserted in the wound, the temporal muscles replaced, and the scalp closed. The Ss received intramuscular injections of penicillin follow-

ing the operation and Tetracycline was added to their drinking water for three days postoperatively.

Conditioning: Following recovery from surgery Ss were put on a 22-1/2 hour water deprivation schedule one week before training. Subjects were run in groups of three animals (one hippocampally lesioned S, one cortically lesioned S, one unoperated S) to equalize the effect of extraneous stimuli and minor deviations from the experimental schedule. The barpress response was shaped and then reinforced under DRF for 8-14 days in order to establish a steady rate of bar pressing. Then, DRL-20 schedule was instituted for 45 min. sessions for 14 days (consecutive days as far as possible). There was no shaping of the response from lesser delays to the 20 sec. delay.

Histology: After the experiment, the Ss were sacrificed and perfused intracardially with 10 per cent formalin. The brains were embedded in paraffin and sectioned at 15  $\mu$ . The sections were stained with thionin. Reconstructions of the lesions in the six hippocampally ablated Ss at five cross-sectional areas are presented in Fig. 1. Similar reconstructions of the lesions in five of the six neocortically lesioned Ss are presented in Fig. 2. The sections for one neocortically lesioned S were lost during histological preparation. The external appearance of this brain before embedding was not dissimilar from the brains for whom histological reconstructions were made.

In general the lesions of the hippocampus in the animals shown in Fig. 1 were smaller than those reported by Isaacson, Douglas, and Moore (1961) or by Isaacson and Wickelgren (1962), ranging from about 20 per cent to 80 per

cent. However, all but one S had less than 50 per cent of the structure destroyed. The hippocampal damage which was constant for all animals was in its most dorsal extent. A comparison of the behavior of animals with most and least amounts of hippocampal damage fails to suggest a correlation between behavioral changes and degree of hippocampal destruction.

In three hippocampally ablated Ss thalamic gliosis was observed. This primarily involved the lateral nucleus, and was only extensive in one animal. The gliosis was not produced by direct damage to the thalamus but probably resulted from surgically induced infarction of blood vessels in the region. A comparison of the behavior of the Ss with and without thalamic gliosis did not suggest any effect of the gliosis nor have other behavioral alterations been found related to similar thalamic changes (Wickelgren and Isaacson, 1963).

## Results

The acquisition of the bar press response was successfully accomplished in all brain damaged and normal Ss under continuous reinforcement. Within three to four days all Ss were pressing the bar in a regular fashion for the water reinforcement. The speed of acquisition of a bar press response is difficult to measure and no plans were made to measure initial acquisition of the bar press response in this experiment. However, the authors' impression is that the hippocampally lesioned Ss established the response more readily than either the neocorticate or the normal Ss.

Figure 3 presents the average number of reinforcements given to each group of animals on the last six days of acquisition training, after the re-

sponse had been well established. Both the neodecorticate and hippocampectomized Ss show a lower rate of response (reinforcements) than the normal animals. The difference between the normal Ss and the others over these last six days of continuous reinforcement was statistically significant as evaluated by a Friedman 2-way analysis of variance ( $.01 > p > .001$ ).

Upon switching to the DRL-20 procedure, the hippocampectomized Ss responded much more frequently than did the other two groups. Figure 4 is a graphic presentation of the number of bar presses emitted by the three groups of animals during the daily DRL training. The difference between the hippocampectomized group and the cortically lesioned and normal animals is statistically significant (Friedman analysis  $p > .001$ ).

Figure 5 presents the per cent of the total responses which were reinforced following inter-response times greater than 20 sec. This represents an estimate of the Ss' efficiency in obtaining reinforcements during the DRL session. The difference between the hippocampectomized Ss and the other groups of Ss was significant beyond the .01 level as evaluated by the Friedman test.

#### Discussion

The result that hippocampally ablated Ss depress the bar more often and obtain fewer reinforcements under a 20 sec. DRL procedure than the neocortically lesioned or normal animals seems to be compatible with other evidence relating this part of the limbic system to perseverate behaviors. The earlier findings of Kimura (1958), Isaacson and Wickelgren (1962), Kimble (1963) and others seems to establish the fact that hippocampally lesioned animals show decreased

ability to inhibit certain kinds of responses. Furthermore, hippocampectomized animals have an increased resistance to extinction in a linear runway when the between trial interval is about 10 min. (Jarrard, Isaacson, and Wickelgren, 1963; Niki, 1962). In a related experiment, Wickelgren and Isaacson (1963) found the runway latencies of hippocampectomized rats to be unaffected by the introduction of a novel and irrelevant cue. In the present case, the increased number of bar presses could reflect a similar inability to inhibit responses in the delay period: simple extinction is a component process in the formation of the temporal discrimination required under DRL. This kind of explanation has been offered for changes in behavior of animals with lesions in other subneocortical regions of the brain (McCleary, 1961; Kaada, Rasmussen, and Kveim, 1962; Battig, Rosvold, and Mishkin, 1962) as well as neocortical lesions (Mishkin, Prockop, and Rosvold, 1962; Brutkowski and Dabrowska, 1963).

At the beginning of the DRL procedure, the response rates of all groups increased as can be observed by comparing the number of responses emitted before and after the onset of the delay procedures (Figs. 3 and 4), and the hippocampally lesioned animals increased most of all. However, since the hippocampally lesioned animals showed a lower rate of responding than the other groups of animals in the last six days of continuous reinforcement it would be difficult to account for the present results on the basis of a general increase in drive resulting from our deprivation conditions if the rate of response is used as an indicator of drive level.

The lower response rate of the hippocampectomized animals before initiation of the DRL schedule also makes it difficult to explain our results on

the basis of an over-all increase in activity, although increases in general activity levels have been reported (Kimble, 1963; Teitelbaum and Milner, 1963).

At present, therefore, high bar press rates and low efficiency of performance of the hippocampectomized animal in a DRL-20 schedule seems best explained on the basis of an inability to withhold responses during the delay interval. This may be due, in turn, to a greater resistance to extinction of these animals during the formation of a temporal discrimination. This interpretation is supported by the finding that the hippocampectomized animals show higher rates of responding than neodecorticate and normals following the transition from CRF to DRL. This hypothesis, however, does not account for the great increase in response rate when the delay period is begun. Certainly, further refinement of this general hypothesis may be needed as more data concerning the effects of hippocampal ablation are reported.



## FOOTNOTES

1. This research was supported in part by a grant from the Office of the Surgeon General, U. S. Army to R. L. Isaacson (DA-49-193-63-G120).
2. Now at the University of Rochester, Rochester, New York.

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## FIGURE CAPTIONS

Figure 1. Reconstructions of the lesions sustained by the six hippocampally ablated Ss.

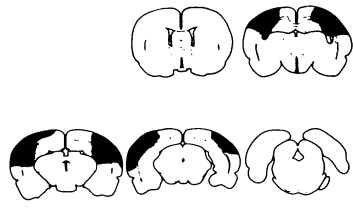
Figure 2. Reconstructions of the lesions sustained by five of the six neocortically lesioned Ss.

Figure 3. A graphic display of the number of bar presses emitted by the three groups of Ss while on CRF on the six days preceding the shift to the DRL-20 schedule. The day labeled day 1 is the sixth day preceding this shift in schedules.

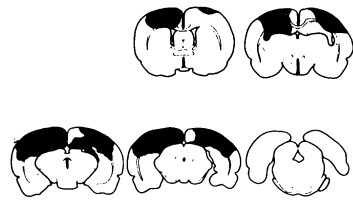
Figure 4. The total number of responses emitted by the three groups of Ss while on the DRL-20 schedule.

Figure 5. The ratio (x 100) of the number of reinforcements received to the number of bar presses for the three groups of Ss while on the DRL-20 schedule.

H1



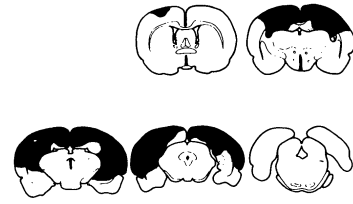
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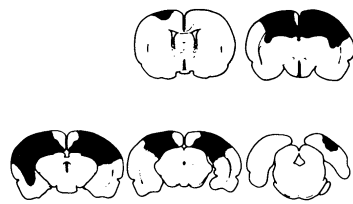
H2



H5



H3



H6

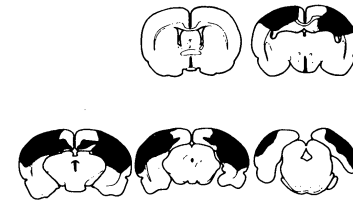
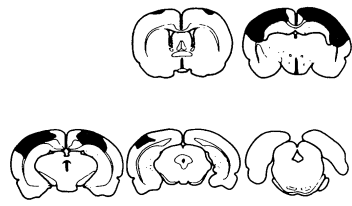


Fig. 1.

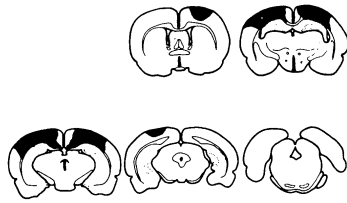
C7



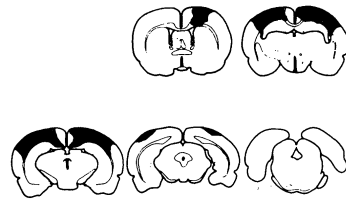
C10



C8



C11



C12

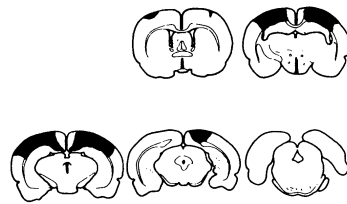


Fig. 2.

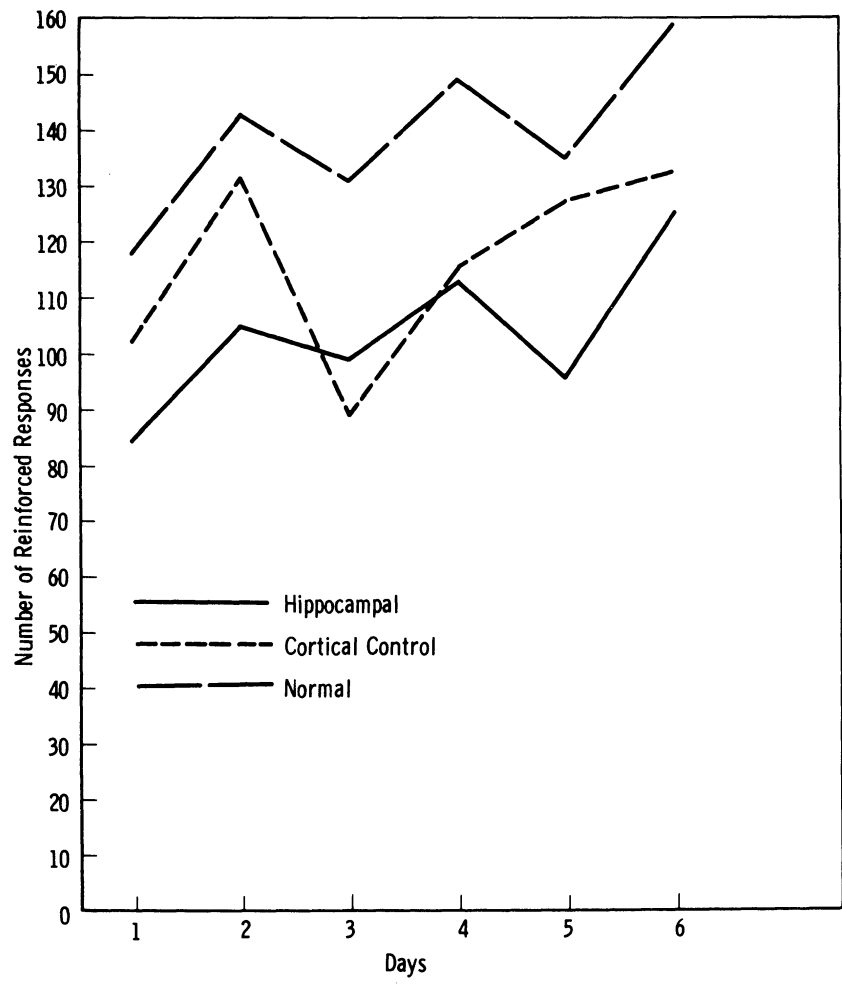


Fig. 3.

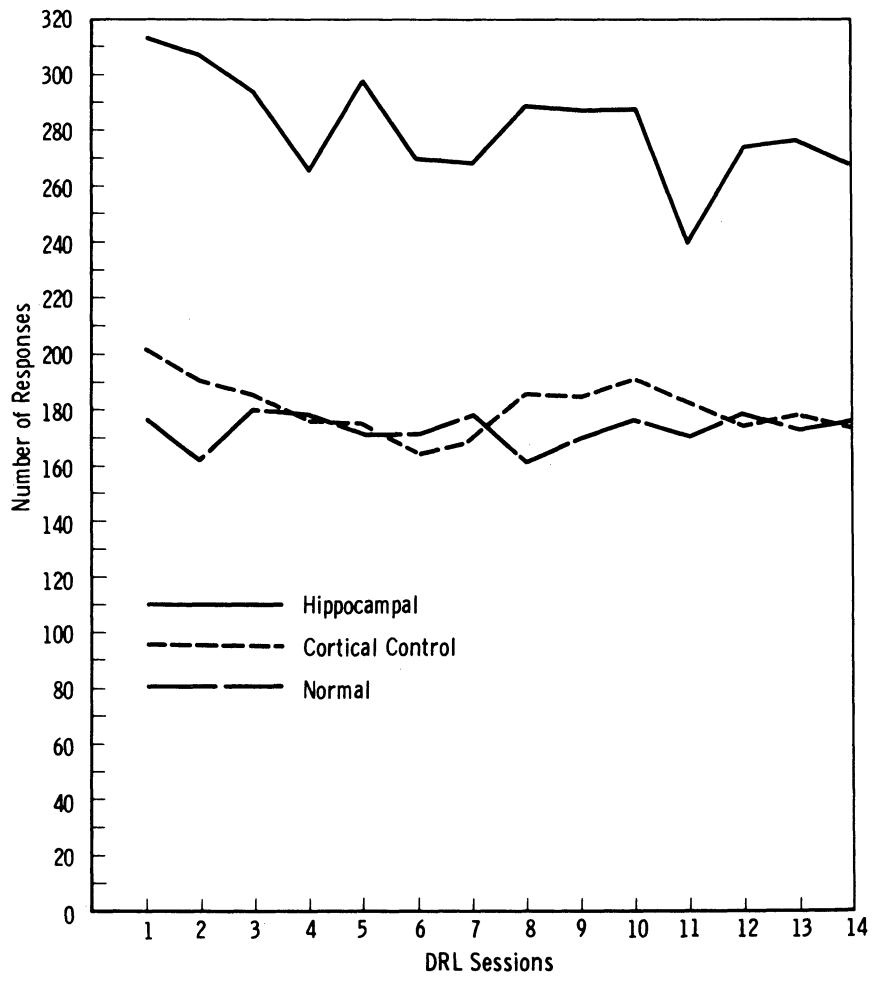


Fig. 4.

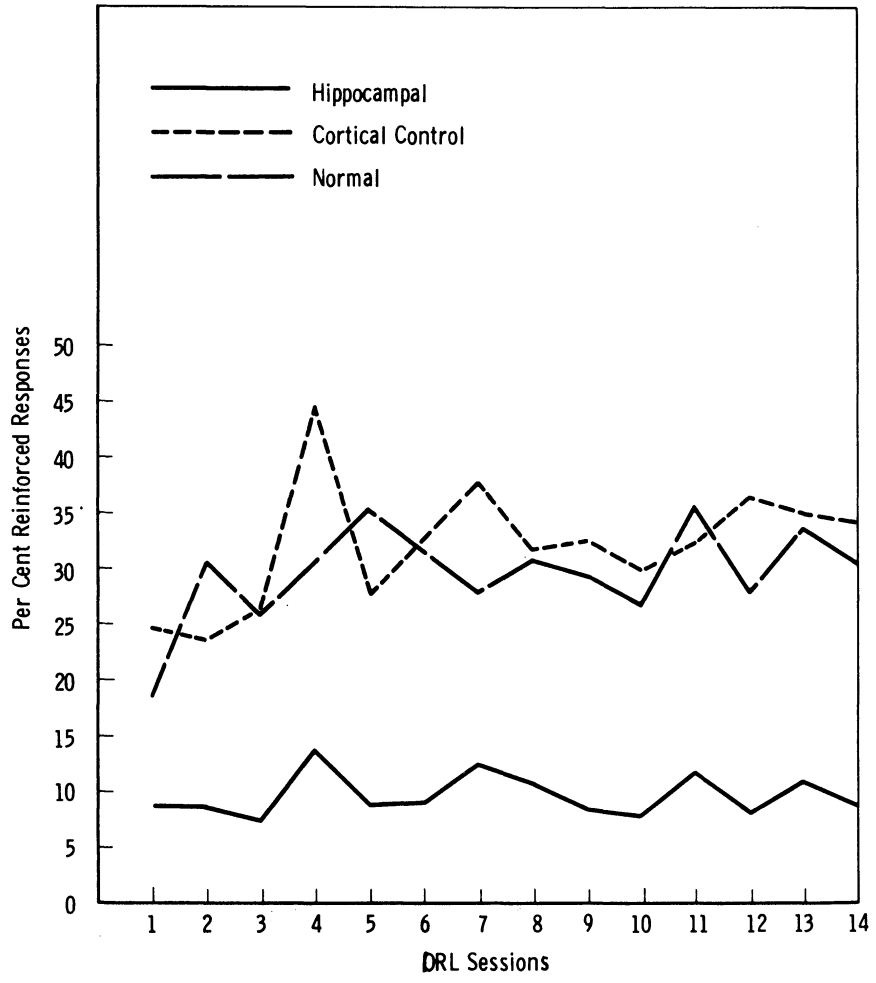


Fig. 5.





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