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The effect of hippocampal lesions on redundant relevant cue utilization in rats.

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THE EFFECT OF HIPPOCAMPAL LESIONS ON REDUNDANT RELEVANT CUE UTILIZATION IN RATS

by

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ABSTRACT

The present experiment was designed to test which of three proposed theories offered the most parsimonious explanation of the response perseverative behavior of hippocampal damaged animals.

Twenty-four male albino rats were subjected to either bilateral hippocampal lesions (HP group) or sham operations (SH group). Equal number of HP and SH animals were required to learn a redundant relevant discrimination in which brightness was made redundant and relevant with response alternation. After acquisition criterion was reached, all Ss were given brightness and alternation cue utilization tests with order of presentation counterbalanced.

Pretraining test trials found that both groups showed position preferences, but SH rats displayed more response alternation than HP rats. The HP animals acquired the redundant relevant cue task as easily as the SH control animals. Both groups acquired the brightness dimension and neither group acquired the alternation dimension. There was, however, a clear difference in the response pattern of the two groups. During the alternation test trials, HP Ss reverted to the originally preferred side of pretraining, while SH Ss did not reliably do so.

None of the proposed hypotheses could adequately explain the observed findings. The results were discussed

in terms of response perseveration being a function of minimal external cue discrimination. Small radiofrequency lesions in the posterior hippocampus appeared to be related to the ability to process information under ambiguous cue conditions.

PREFACE

This research is the result of the author's interest in the work of Dr. Jerome S. Cohen, Assistant Professor in the Department of Psychology, University of Windsor. His patience and guidance assisted in making this paper a reality for which the author wishes to express his grateful appreciation.

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Introduction

Statement of the Problem

Three major hypotheses have been proposed to explain the perseverative behavior of animals following hippocampal damage.

Kimble (1968) maintains that the hippocampus, along with arousal systems of the brain stem and thalamus, constitutes a co-ordinated system which is important in the production of Pavlovian internal inhibition. He presents both neuroanatomical and electrophysiological evidence to support this thesis, and posits that Ss with hippocampal lesions suffer from an inability to cease an ongoing motor response regardless of any external stimulus changes. This is an example of a deficit in internal inhibition. Douglas and Pribram (1966), on the other hand, maintain that the hippocampus acts to exclude stimulus patterns from attention through a process of efferent control of sensory reception which they call gating. Therefore, the Douglas-Pribram model would predict that animals with hippocampal lesions would be less able to ignore previously attended to stimuli no longer associated with reinforcement, and hence be less distractible than normal Ss. Douglas (1967) later termed this a deficit in stimulus habituation. A third interpretation, that of Winocur and Mills (1969) states that the perseverative

behavior is secondary to a fundamental deficit in the ability to integrate relevant sensory information. Damage to the hippocampus results in a deficiency in processing information about environmental changes.

It was the purpose of this study to further explore the relationship between hippocampal lesions and the above described hypotheses of response perseveration.

Background and Related Research

The hippocampal formation is a large and complex archipallial structure which takes up a considerable portion of the central section of each hemisphere. In the human brain the hippocampal formation extends from the septal region over the corpus callosum and ventrally into the rostral end of the temporal lobe.

The hippocampus proper (Ammon's horn, or cornu ammonis) consists of three layer cortex. It extends along the floor of the fourth ventricle and is covered by the ependymal lining of the ventricle and a sheet of myelinated fibers called the alveus. These fibers are continuous with the distinct fiber bundle called the fimbria which develops along the medial border of the hippocampus. The hippocampi of the two hemispheres are profusely interconnected through the hippocampal commissure. The dentate gyrus or fascia dentata is a narrow band of cortex which is almost entirely surrounded by the hippocampus and is continuous with the hippocampus in the hippocampal fissure.

The hippocampus in the rat is formed by the tight

interlocking of the hippocampus proper (Ammon's horn) and the dentate gyrus. The hippocampus receives direct connections from several regions of the limbic cortex (entorhinal area, the presubiculum, and septal area) and sends its efferent fibers out of the fornix to the mammillary bodies, the hypothalamus, the diffuse thalamic system, and the brain stem (Green, 1960).

Electrophysiological recording and stimulation have provided a technique for exploring the neuroanatomical circuits of the hippocampus. Green and Arduini (1954) observed an inverse relationship between hippocampal and neocortical activity. Neocortical desynchronization (fast low voltage activity, a sign of attending in the normal, awake animal) was accompanied by the appearance of high amplitude slow waves (4-7 c.p.s.) in the hippocampus. Conversely, when cortical spindle waves were recorded, hippocampal desynchronization was present. This inverse relationship between hippocampal and cortical activity was maintained during rest or sleep. The authors proposed that the slow waves of the hippocampus represented a specialized hippocampal arousal reaction. In support of this hypothesis, Holmes and Adey (1960) recorded activity from the hippocampus and entorhinal cortex in cats in a delayed response situation. The Ss attention was drawn to the baiting of one of two food containers, then, after a delay of 5-10 sec., a bridge was lowered to the cups. The slow-wave pattern in the hippocampus appeared just before the animals began to walk toward one of the goal boxes. The researchers suggest that the theta activity of the hippocampus might indicate a "readiness to act" since

it accompanies an alert state found in goal-directed activity. This view that theta (4-7 cps) wave activity in the hippocampus was an arousal reaction was further strengthened by the observation that it appeared as a result of stimulation of the reticular formation (Green, 1960).

The same electrophysiological phenomenon, i.e., the inverse relationship between hippocampal and cortical activity, received a very different interpretation from Grastyan (1959). He observed that cats stopped all ongoing behavior and oriented toward a moving object during electrical stimulation of the hippocampus. Furthermore, hippocampal stimulation alone, without specific sensory stimuli interrupted ongoing behavior. These observations led Grastyan to view the theta rhythm as an indication of hippocampal non-functioning, and that inhibition of attention was the result of hippocampal desynchronization.

Meissner (1966) found that the theta activity of the hippocampus could be influenced by stimulation of the septal and entorhinal areas. Stimulation of the septal region resulted in generation of theta rhythms in the hippocampus. Stimulation of the entorhinal region led to hippocampal desynchronization. He attributed his findings to two separate afferent paths to the hippocampus: 1) the septohippocampal circuit (SH) and 2) the temporoammonic circuit (TA). He concluded that the generation of the theta rhythm was linked to inputs from the medial septal region via the SH circuit. Desynchronization, on the other hand, was linked to inputs from the entorhinal area via the TA circuit.

Micro-electrode studies of single hippocampal nerve cells in the rabbit have shown that bursts of cellular activity tend to occur in synchrony with the grossly recorded theta thythm and can be evoked by all types of sensory stimulation (Green and Machne, 1955). Redding (1967) depressed cortical evoked potentials in both the auditory and visual modalities by concurrent stimulation of the hippocampus. He further reported that this depression of the cortical evoked potentials was opposite to the augmenting effect of reticular stimulation. Therefore, the hippocampus may exert an inhibitory effect on the reticular formation. In general, the electrophysiological data suggest a role for the hippocampus in the processes of arousal and attention. Although the exact nature of this role is as yet not clear, the above studies suggest that it is more likely to be a modulatory influence rather than primary control.

In human research the hippocampus has been implicated in short term memory function as well as a modulator of attention. The majority of animal hippocampal research was initiated by accidental clinical findings in human patients with temporal lobe lesions. Milner and Penfield (1955) found that after the hippocampus had been removed in humans, a deficit in recent memory occurred. Such patients could remember quite well events that happened weeks or months ago but could not recall immediate events such as what they had for breakfast. In support of the memory deficit theory, Talland (1968) reported that patients with Korsakoff's syndrome (a psychosis resulting from neural damage to the temporal lobe including the hippocampal system due to alcoholism) demonstrated dramatic deficits

on tasks requiring shifting of attention, although they were impervious to distraction by noise, or unscheduled incidents in their environment. Scoville and Milner (1957) showed that the deficit does not occur unless the hippocampus is included in the temporal lobe lesion. Although reliably demonstrated, the use of the term "recent memory loss" to describe the behavior of patients with hippocampal operations, has been misleading. The term has been used as an equivalent of "recent memory" implying a short-lived effect of a stimulus. By this definition, a recent memory loss would imply that the trace effects of a stimulus would be lost. This is not the case, however, as Penfield and Milner (1958) have demonstrated. They showed that the attention span is normal in patients with hippocampal damage, and that they could recall successfully for up to several minutes after exposure to the stimulus. Milner (1965) suggested that human subjects with bilateral hippocampal damage could sustain memory of current experience as long as no distracting stimuli were present. The deficit was considered to be a lack of consolidation of the trace effects of the stimulus into permanent memory. The "recent" part of the term refers to recently since the operation, not recently after the stimulus.

The experimental literature in animal research fails to consistently replicate human short term memory deficits observed after hippocampal damage. Jarrard, Isaacson, and Wickelgren (1965) trained hippocampal, cortical and unoperated control rats in a straight runway task. Response latencies and running times were recorded under two intertrial intervals (10 sec. and 10 min.). The "short-term"

memory hypothesis would predict that the larger ITI would produce a reduction in the acquisition performance of the hippocampal lesioned Ss. They found no difference in acquisition rates between the groups, and concluded that the integrity of the hippocampus was not essential for short-term memory. A similar finding was reported by Kimble and Pribram (1963) in monkeys under different experimental task conditions. An automated discrimination apparatus (DADTA), which could present 1-12 stimuli (numbers) at a time at different ITI's, on individual Lucite panels was used. In the first part of the experiment Ss responded by depressing consecutively the two panels which lit up in any order for a peanut reward. In a second part of the experiment an externally imposed correct order had to be maintained. On both tasks hippocampal Ss performed more poorly than controls demonstrating a deficit in behaviors of a sequential nature. However, the length of the ITI's had no effect even though some were extended up to 6 min. Lastly, Kimble (1963) trained hippocampal lesioned and cortical control rats on a black-white discrimination task with an 8 min. intertrial interval. The long ITI produced no significant differences in acquisition rate between the two groups. Furthermore, the experimental Ss showed good (70%) retention of the discrimination problem a week after acquisition. He concluded that a short-term memory concept could not account for these results. Hippocampal lesions did not seem to impair the acquisition and retention of learned tasks for relatively long periods

of time. Thus, the animal and human data appear to be inconsistent.

A possible resolution of these contradictions may be that the recent memory loss observed in man is a secondary effect of a different type of primary disorder. Another plausible explanation may be that the methods used to test for memory deficits in animals, such as ITI, may not be sensitive enough to detect the subtle memory disturbances that humans easily report verbally.

In animals, one of the more consistently observed effects of hippocampal damage has been a perseveration of ongoing or previously learned locomotor responses. Several behavioral measures have been used to demonstrate this effect.

One index of the relative incapacity of animals with hippocampal lesions to show normal behavioral variability has been found in non-reinforced alternation studies. Kirkby, Stein, and Kimble (1967) tested hippocampally damaged and control rats for spontaneous alternation after various lengths (50 sec., 10 min., and 50 min.) of confinement in the first choice arm of a Y maze. Only the hippocampal Ss failed to alternate as expected. Roberts, Dember, and Brodwick (1962) allowed hippocampectomized and neocortically lesioned rats to explore a T-maze, with one arm painted black and the other white (to facilitate discrimination). The number of spontaneous alternations was recorded. The hippocampal damaged group habituated more slowly to new

environments and lost their tendency to alternate sooner.

Deficits similar to those in spontaneous alternation have also been observed in learned or forced alternation studies. Racine and Kimble (1965) gave water deprived rats three trials per day of alternation training (i.e., reward followed an alternating response). Surgery was then performed to produce a hippocampectomized and cortical control group. All cortical Ss reached their pre-operative level of alternation while none of the hippocampal Ss did.

Position reversal shift learning has also been employed to demonstrate response perseveration following hippocampal lesions. Kimble and Kimble (1965) trained hippocampal and control rats to run five consecutive times to one then to the other side of a Y maze for a food reward. If hippocampectomy interefers with the inhibition of previously learned response patterns (i.e., impairs the S's "behavioral flexibility") then the hippocampectomized Ss should perseverate side responses which were no longer reinforced. Hippocampal lesioned Ss were found to be distinctly inferior in acquiring the position reversal task relative to control Ss. Cohen, LaRoche, and Baharry (1971) required rats to learn a left-right discrimination in a uniformly colored cross maze. When tested for perseveration by changing the start box to the opposite side, hippocampal lesioned Ss were found to perseverate the original turning response in the reversal situation. In a second stage of the same experiment, one choice arm was painted black thus adding a

brightness cue. This procedure did not lead to a significant difference between hippocampal lesioned and operated control Ss. These investigators concluded that response perseveration after hippocampal damage appears to be a function of minimal external stimulus differentiation.

Resistance to extinction has been found to increase in hippocampal damaged animals, and has, therefore, often been used as a measure of response perseveration. Niki (1965) reported that hippocampectomized rats did not lower their bar pressing responses when a signal was introduced to indicate that no reinforcement would ensue during its presence. He interpreted the observation as a clear lack of the Pavlovian type of internal inhibition. Douglas and Pribram (1966) found no differences between hippocampectomized and normal monkeys on size and brightness discrimination tasks. However, they found the experimental Ss significantly more resistant to extinction than the controls, and described their behavior as an insensitivity to the absence of reward. Peretz (1965) trained hippocampally ablated and neocortical ablated control rats to open a small window for a food reward. When the latency of responses reached an asymptotic level, Ss were given 20 extinction trials. The extinction trial latencies were shorter for the experimental than for the control Ss.

In addition to resistance to extinction, experiments have indicated that animals with hippocampal lesions perseverate during changes in reinforcement schedules. Jarrard (1965) showed that rats with hippocampal lesions bar pressed

at consistently higher rates than control groups on a variable interval schedule. Hippocampal Ss were apparently less able to withhold responding when reinforcement was not available. Clark and Isaacson (1965) demonstrated significantly poorer performance in hippocampectomized than in normal rats when they were shifted from a continuous reinforcement schedule to a DRL - 20. The experimental Ss did not wait 20 sec. between bar press responses. However, if they were not pre-trained on a continuous schedule, hippocampectomized Ss could learn the DRL - 20 reinforcement schedule as quickly as normals (Schmaltz and Isaacson, 1966). Finally, Swanson and Isaacson (1967), in an attempt to show that hippocampal lesions disrupt an inhibitory process, and result in the observations recorded in extinction and reinforcement schedule studies, ran a discrimination study where a specific S^{Δ} signaled the absence of reward. They shaped hippocampally ablated, cortically ablated and normal control rats to bar press on a CRF schedule. After stable response rates had been established, the 30 min. training sessions were interrupted by five, two min. intervals during which S^{Δ} (a train of medium intensity clicks) was presented continuously and reinforcement was withdrawn. The hippocampal Ss were distinctly impaired in the capacity to withhold responses during S^{Δ}. In the first two studies, the lesion-induced differences with VI and DRL schedules may have been the result of an impaired ability to time or pace behavior. There are no specific cues to inform the animal when not to

respond. The last study, however, suggests that hippocampal damaged animals perseverate responses despite lack of reinforcement or cues indicating changes in reinforcement schedules.

Measuring acquisition rates during avoidance task performance has also been employed as an index of response perseveration. Performance on active avoidance tasks should be improved by hippocampal lesions since the perseveration of motor responding (such as shuttling in a shuttle box) leads to faster acquisition. Isaacson, Douglas and Moore (1961) trained rats to cross to the other side of a shuttle box when a buzzer was sounded. If a response was not made during the 5 sec. while the buzzer was on, Ss received a shock. The experimenters found that the hippocampal Ss learned this double active avoidance problem significantly faster than either normal or cortically ablated control animals. Similar results were reported by Niki (1962) on the acquisition of a one-way active avoidance task. He trained hippocampal lesioned and control rats to jump from an electrified grid into a safe goalbox. Each learning trial began with the sounding of a buzzer that continued until the animal jumped into the goal box. If, after 5 sec., the animal had not crossed into the safe box, an electric shock was delivered along with the buzzer until crossing occurred. The S was left in the goal box for 30 sec. and then was replaced to the grid side and a new trial was begun. Hippocampectomized

Ss learned and retained the avoidance task as well as controls. The two studies seem to indicate that hippocampal ablation does not interfere with the acquisition of either a one-way or a two-way active avoidance task.

Acquisition of passive avoidance tasks, on the other hand, should be hindered by lesions of hippocampus. In passive avoidance tasks the animal must learn to inhibit responding in order to perform well. Various studies have borne out this prediction. Kimura (1958) showed deficits in shock avoidance learning after hippocampal lesions. He trained 2 groups of rats (hippocampal lesioned and control) in a straight runway for food reward. After acquisition, the food cup was electrified and a shock was administered to the Ss mouth when reaching for the food. Hippocampal lesioned Ss showed a deficit in acquiring the passive avoidance task. Similar results were reported by Isaacson and Wickelgren (1962). They trained bilaterally ablated hippocampal and cortical animals to enter a small goal box for food. After 4 days of training, the animals were given a shock while eating in the goal box. The cortical damaged animals would not re-enter the goal box while the hippocampal lesioned Ss did. The effect of the shock on the hippocampectomized animals was transient and slight, resulting in impaired passive avoidance learning. Teitelbaum and Milner (1963) placed hippocampal and normal rats on a safe platform in the middle of an electrified grid. They found that Ss with dorsal hippocampal lesions could not inhibit their unconditioned locomotor activities and

would repeatedly leave the safe platform.

The above cited studies of avoidance learning suggest that, depending on the type of avoidance task involved, damage to the hippocampus may either enhance or interfere with avoidance conditioning. The perseveration of motor responding will lead to faster acquisition of an active avoidance task such as shuttling back and forth in a shuttle box. The same perseverative responding will interfere with the acquisition of a passive avoidance task which requires the animal to inhibit its responses.

Studies have demonstrated that hippocampal ablations did not affect discrimination learning when no inhibition was involved. Truax and Thompson (1969) trained hippocampal and normal rats on a white-grey door discrimination task under threat of foot shock. There were no significant acquisition differences between the two groups. Silviera and Kimble (1968) showed that hippocampal rats acquired both visual and spatial tasks as easily as did normals. However, when the acquisition of a discrimination task was dependent upon the S's ability to inhibit its responses, hippocampal damage lead to an acquisition deficit. Stein and Kimble (1966) trained hippocampal lesioned and control rats on a successive brightness discrimination. The experimental animals took significantly longer to learn the discrimination task than the control animals. Similar results were reported by Buerger (1969) for cats. Removal of the ventral portion of the hippocampus caused a post-

operative acquisition deficit on a successive visual pattern discrimination. Ss were reinforced with milk if they pressed a key when L was presented or if they did not press when T was presented. The hippocampal damaged Ss took almost three times as many days to learn this task as the controls. Kimble (1963) trained hippocampal lesioned, cortical lesioned and unoperated control rats in a T maze on a successive and a simultaneous discrimination task. In the simultaneous discrimination, one of the arms of the maze was always white, the other black. In the successive discrimination, both of the arms were either black or white on any given trial. The hippocampal damaged Ss took significantly longer to learn the successive discrimination task, while no differences appeared on the simultaneous task between the experimental and control groups.

The observations reported in the above studies are consistent with a perseverative deficit hypothesis of hippocampal functioning. In a simultaneous discrimination, all the relevant stimuli are present on each trial and the task is of a "go-go" type. On each trial, the animal must decide which of the stimuli to respond to. The solution of a successive discrimination task, on the other hand, appears to depend upon the strengthening of an approach response to a stimulus over many individual trials (Spence, 1960). The task is of a "go-no go" kind where the S is required to respond to one stimulus but withhold responding to another. If hippocampal damage results in

perseverative responding, then one would expect a deficit in hippocampal lesioned animals on the successive discrimination problem. Perseverative responding should interfere with a "go-no go" type task. The same perseverative responding should not interfere with the acquisition of a simultaneous discrimination task. The observed results support this hypothesis.

Some other studies using discrimination tasks suggest that in situations where inhibition of responding determines the quality of performance, perservative responding depends on situational factors. For example, Winocur and Mills (1969) allowed hippocampal lesioned and operated control Ss to explore and feed in the four alleys of a cross-shaped maze. Food was always available in all four alleys. Test trials were administered in which each S was placed in the centre of the maze (always facing the same direction) and allowed to run down the alley of its choice to obtain food. They recorded the alley chosen. In this test situation where several alternatives were available and any of the responses were equally likely to be reinforced, there was no significant difference between lesioned and control Ss with respect to alley preference. Neither group perseverated its responding to one particular alley. The investigators interpreted their results to mean that perseveration or reduced response inhibition is not an invariable consequence of hippocampal damage but depends on situational factors. Hippocampal animals did not perseverate to a

specific choice when others were available and equally reinforced.

Several investigators have shown that animals become less distractible after hippocampal ablation. Wickelgren and Isaacson (1963) trained rats in a straight runway task. Normal rats slowed their running speed when tactile (sandpaper) distracting stimuli were placed in the runway, while hippocampal Ss did not. Riddell, Rothblatt and Wilson (1969) taught hippocampal, neocortical control, and unoperated control rats to run a straight runway for food reward. Running speed was used as a measure of distractibility. They introduced visual (series of flashes 300/min.) and auditory (series of clicks) distracting stimuli. Hippocampal Ss were less distractible than the two control groups. Leaton (1965) established base rates for exploratory behavior in the T maze and then recorded exploratory activity after hippocampectomy in rats. He found that the hippocampal lesioned animals had significantly higher rates of locomotor activity than did cortical lesioned or sham operated controls. He also noted, however, that the hippocampal lesioned Ss did not show any preference for entering arms with novel stimuli as opposed to empty arms. It seems that hippocampal damage may increase general locomotion but not exploration. The hippocampal lesioned Ss were not distracted by novelty.

Cohen and Swenson (1970) allowed hippocampal and sham operated rats to explore a novel alley introduced into

one side of a straight runway. They hypothesized that in hippocampal Ss, previous experience with a novel alley on a particular side of the runway should result in more exploratory entries into other novel alleys introduced on the same side than on the opposite side of the runway. The hippocampal lesioned animals continued to run down the straight alley, rather than being distracted by the introduction of new alleys on either side. In another study, Cohen (1970) found similar distraction deficits in hippocampal ablated rats as compared to normals when the distracting stimuli were blind side alleys. Changes in side alley location failed to distract hippocampectomized Ss from running down a straight runway.

An obvious similarity among these experiments is the fact that all of them measured distractibility against a strong, well-established, ongoing response. Hendrickson, Kimble and Kimble (1969) investigated distractibility in hippocampal lesioned Ss in the absence of a strong ongoing response. Although hippocampal damaged Ss were less distracted from a drinking response by an external click than controls, they were just as easily distracted by the clicks when the water was absent. The hippocampal Ss exhibited normal orienting responses. The investigators concluded that hippocampally lesioned animals were found to be less distractible than controls only when either a motivationally relevant or a novel neutral stimulus had been previously attended to. While the hippocampus does

not seem to be critically involved in the actual production of the orienting response, it may play a critical role in shifting attention. Therefore, a normally functioning hippocampus may be essential in tasks where rapid shifts of attention are necessary.

In general, the above reported studies on distractibility in hippocampectomized animals indicate that lesions of the hippocampus produce Ss that are less distractible than normals. Hippocampal damaged Ss seem to pay less attention to the introduction of novel visual, tactile or auditory stimuli into their environment.

In summary, the changes in behavior found after damage to the hippocampus are almost always of a perseverative nature. Interpretations of the above findings have generally taken one of two positions.

One interpretation is an external cue model proposed by Douglas and Pribram (1966), and Douglas (1967). The hippocampus is postulated to exclude stimulus patterns from attention through a process of sensory gating. Damage to the hippocampus results in a breakdown of the gating mechanism and the animal is unable to stop responding to a previously attended to external stimulus.

The other interpretation, an internal inhibition model of perseverative responding, has been proposed by Kimble (1968). In Kimble's response (internal) cue model, the animal perseverates because of an inability to stop an ongoing motor response in spite of external stimulus

change. Both models receive ample empirical support, and the functional similarity between the internal inhibition (response deficit) and attentional deficit explanation is apparent. Both models make similar predictions but for different reasons. Douglas (1967) maintains that response perseveration is due to an attentional deficit of external stimuli, while Kimble (1968) attributes it to an internal response inhibition deficit.

The finding that perseverative responding may be task dependent led Winocur and Mills (1969) to propose an explanation similar to that of Douglas (1967). They found that perseverative observations depend on situational factors and are most prominent in tasks where drastic shifts occur in the experimental conditions. They found that on tasks where several equally reinforced responses were available, hippocampal damaged Ss did not perseverate to a specific choice. The response inhibition hypothesis could not explain these observations. They suggested instead that the perseverative behavior found on some tasks is secondary to a fundamental deficit involving a failure to integrate relevant sensory information. Thus, they maintained that lesions of the hippocampus result in a basic deficiency in processing information about changes in environmental events.

The present experiment was designed to further explore the relationship between hippocampal lesions and the Douglas and Kimble models of response perseveration.

Specifically, it was expected to reveal whether the perseveration observed in hippocampal lesioned animals was due to: a) an inability to inhibit an ongoing motor response, or b) an inability to stop responding to a previously attended to external stimulus, or c) a general information processing deficit.

Sham operated control and hippocampally lesioned experimental rats were trained to learn a discrimination task with two redundant relevant cues - brightness and response alternation. The discrimination task consisted of simultaneously presented black and white doors. The position of the doors was varied in a single alternation sequence (LRLR...). Equal number of Ss were trained to the black and the white doors as positive stimuli. The day after acquisition criterion was reached, all Ss were tested to determine which dimension (brightness or alternation) they used in solving the discrimination task. The test for alternation consisted of 16 trials in which S could make free choice responses to simultaneously presented grey doors. The number of left and right responses were counted and the number of alternations were recorded. The brightness test consisted of free choice responding to black and white doors presented in a double alternation sequence (LLRRLL...). The number of times the incorrect brightness door was chosen was recorded.

The redundant relevant cue task provides a method for evaluating which theory of perseveration offers the

more parsimonious explanation of the behavior of hippocampal lesioned rats. The discrimination task could be learned by the use of either an internal stimulus (i.e., recall of the previous position response) or an external stimulus - brightness, or both. Testing for the cues utilized during acquisition should show whether hippocampal Ss perseverate to external or internal cues.

Several specific hypotheses can be generated about the expected results based upon the Douglas (1967), Kimble (1968), and Winocur and Mills (1969) models of response perseveration in hippocampectomized animals. If hippocampal lesions produce a general information processing deficit as proposed by Winocur and Mills (1969), then the hippocampal lesioned Ss would be expected to take longer in acquiring the redundant relevant cue task and show a relative lack of cue utilization during the testing phase. If, on the other hand, hippocampal lesioned animals perseverate previously learned motor responses, as Kimble suggests, then, during the test phase, hippocampectomized rats should continue to alternate responses in the absence of external brightness cues and to perform more poorly on the double-alternation brightness test task than control Ss. Lastly, if hippocampal damaged animals perseverate previously attended to external cues, then based on Douglas' model, hippocampal Ss should depend more on the brightness cue and show a deficit in the ability to alternate in the absence of the brightness stimulus. Sham operated controls

would be expected to be able to utilize both internal alternation response cues and external brightness cues. This prediction is based on the findings of Bruner, Matter, Papanek (1955) which demonstrated that intact rats could easily utilize both brightness and response alternation cues during the learning of a redundant relevant cue task.

In the present study, small radio frequency lesions were made in the posterior hippocampus. This location was selected on the basis of previous research (Kimura, 1958 and Nadel, 1968) indicating that perseverative responding was most obvious following lesions in this area.

Chapter II

Method

Subjects

Twenty-four male albino rats from the breeding colonies of Woodlyn Farms, Guelph, Ontario were used. Each subject was 90 to 100 days old and weighed approximately 300 to 350 grams at the time of surgery. Half the Ss were randomly assigned to an experimental group, hippocampal operates (HP). The other half served as the control group, sham operates (SH).

Apparatus

A discrimination box as shown in Figure 1 (79.0 x 46.0 x 30.0 cm.) was used. The apparatus was divided into a decision chamber, 47.0 x 46.0 cm., and two goal chambers (37.0 x 23.0 cm.). Entry into the decision chamber was gained through a covered start box (18.0 x 13.0 x 8.0 cm.) at floor level midway on the wall opposite the discriminanda. A manually operated, clear plexiglass guillotine door could be lifted to expose S to the decision chamber. Access to reinforcement was through a doorway (13.0 x 11.0 cm.) to each of the goal chambers. Each doorway was 8.0 cm. from the other and 8.0 cm. from the nearest wall. Interchangeable stimulus doors could be attached behind each doorway. Except for the two

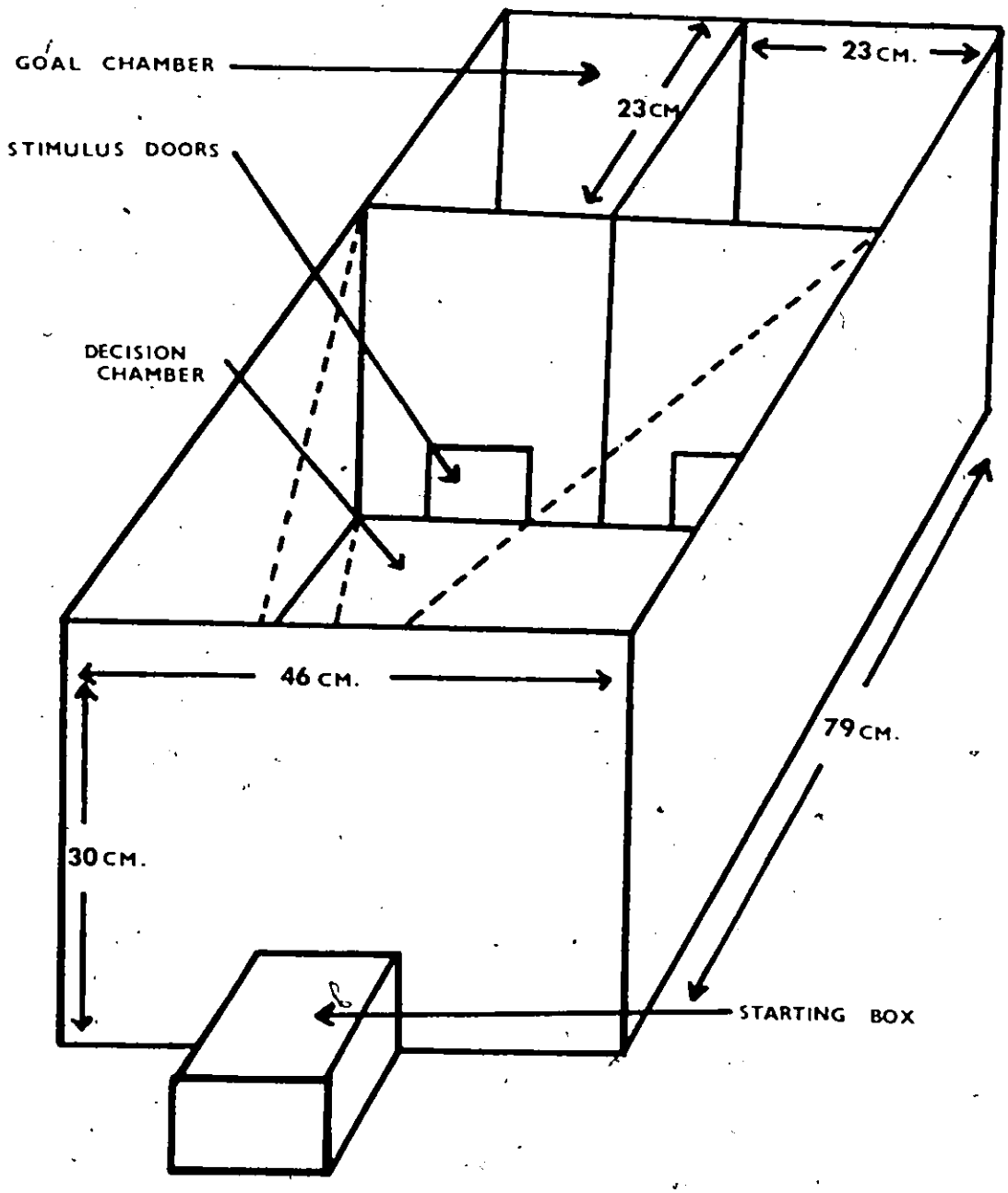

Fig. 1 Discrimination apparatus.

discrimination doors, all interiors were painted flat grey. The only source of illumination was provided by a 100 watt incandescent bulb situated over the entrance to the decision chamber. The stimulus objects were two doors, one white and one black.

Procedure

Surgery. After a one week handling period during which each S was handled for 5 min. per day, all animals were subjected to surgery. All operations were performed in one stage using aseptic surgical techniques. Each S was anesthetized by an intraperitoneal injection of 1.5 cc. of Nembutal solution (10 mg./ml.). The skull was exposed and the animal was secured in a Stoelting stereotaxic instrument. Bilateral openings were made in the skull for the insertion of the lesioning electrode, 2 mm. anterior to the inter-aural line and 5 1/4 mm. from the midline suture. A Formvar insulated stainless steel electrode (Clay-Adams insect pin size 00), with a 3 mm. long exposed strip on one side of the electrode tip was positioned into the brain such that the exposed portion faced the cortex, leaving the thalamus protected from damage by the insulated side. The electrode was entered through the predrilled holes 2 mm., anterior to the inter-aural lines, 5 1/4 mm. from the midline suture, and 4 mm., below the brain surface, perpendicular to it. Bilateral radio-frequency lesions were made by passing a 30 ma. current for 5 sec. through the electrode

at this site. An LM4 model Grass lesion maker was the power source. SHAM (SH) animals received exactly the same operation, except that no current was passed through the electrode. All animals were given a 10 day recovery period in their home cages before the beginning of pretraining.

Pretraining. After the 10 day recovery period, all Ss were placed on a 21-hour water deprivation schedule and pretraining was begun. The 3-hour water maintenance schedule was selected since it was considered great enough to motivate the animal but not too great to interfere with the acquisition of the redundant relevant cue task. This deprivation parameter was based on earlier RRC research in normal rats (Telegdy and Cohen (1971) . During the first 5 days of pretraining, Ss were handled 5 min. per day while allowed to drink a 10% sucrose solution. For the next 5 days, Ss were permitted to explore freely in the discrimination apparatus and allowed to drink in either goal chamber for 5 min. on each day. For the next 5 days, grey doors were placed in the doorways and Ss had to push them open to secure the sucrose water. During these last 5 days of pretraining each S received 16 spaced trials per day during which it was allowed to drink for 10 sec. in the goal box on each trial. NO attempt was made to break any position habits S may have formed during pretraining. However, the grey doors were randomly alternated during these trials to prevent extraneous (ex-olfactory) cues being associated with specific doors. It was felt that since perseveration is a

consistently found deficit in hippocampally damaged animals, its presence in the HP group would lend empirical support to the correct placement of the lesions. In order to measure perseveration following surgery, the number of left-right position responses during the last 16 pretraining trials were recorded. Each animal experienced approximately a 3 min. intertrial interval, since an S received one trial and then was replaced in its home cage while another S was given a trial. The number of animals run at a time were controlled so that an approximate 3 min. intertrial interval was maintained. This procedure was continued throughout the study.

Discrimination Training. The discrimination task consisted of a black and a white door presented simultaneously. Equal number of Ss (in both the experimental and control groups) were trained to the black and the white door as the positive stimulus. The position of the two doors was varied in a single alternation sequence (LRLRLRLR). In this and all subsequent phases, S was given 16 spaced, corrected discrimination trials per day. A trial consisted of a number of runs made until S chose the correct door. S was replaced in the start box when it had made an error. The stimulus doors were changed only between trials and not between runs on any one trial. An error was considered to have been made when S pushed or touched the incorrect door. (Since each door, when touched, "gave" about 0.25 cm. observing mistakes was not difficult.) A correct response

constituted running to the appropriate door or switching over to it if the incorrect door had been approached but not touched. A correct response was reinforced by a 10 sec. drink of the 10% sucrose solution. An S reached discrimination acquisition criterion when it made one or less errors within a block of 16 trials. The day after acquisition criterion was reached, the test phase was begun. The number of errors and trial blocks to acquisition criterion were recorded.

Testing. This phase was designed to test whether the stimulus dimension of brightness, or alternation or both were used in learning the original discrimination. Each S was presented with a block of 16 alternation test trials and a block of 16 brightness test trials. During test trials, both stimulus doors were unlocked and S could receive reinforcement by entering through either one. This procedure was used to prevent the test trials from becoming specific transfer discrimination trials for the animal.

The alternation test consisted of 16 trials in which S could make free choice responses to simultaneously presented grey doors. On these trials both doors were grey. The number of left and right door responses were counted and the number of alternations were recorded.

The brightness test consisted of free choice responding on a double alternation task. On these trials, one door was black the other white and the position was varied according to a double alternation sequence such that the

black door appeared twice on the left then twice on the right (LLRRLLRR...). The number of times the incorrect brightness door was chosen was recorded. A double alternation sequence was selected over a random sequence in order to maximize the possible number of errors made by an animal if it were using alternation as a cue. Hippocampal and control Ss were counterbalanced for the order in which the brightness and alternation test trials were presented. Between the brightness and alternation test trials, all Ss were given a block of 16 redundant relevant cue training trials in order to reestablish previous responding and control for any effect one set of test trials might have had on the other test.

Perfusion. After completing the test phase, all Ss were immediately sacrificed by ether and perfused through the heart with physiological saline (0.9%) and 10% formalin. Heads were removed and submerged in 10% formalin for 48 hours. The brains were then removed and allowed to further stand in 10% formalin for another 48 hours.

Histology. A frozen section technique for obtaining 50 micron unstained coronal sections as described by Hutchinson and Renfrew (1967), was employed. After visual location of the lesion, sections were obtained from the anterior to the posterior extent of the lesion, and every fifth section was temporarily mounted, examined microscopically, and permanently recorded on 35 mm. photograph transparencies. The anterior-posterior extent of the lesions in HP animals was determined

by the number of 50 micron sections in which the lesion could be seen. The lesions' vertical and distal extent was calculated by comparing the actual sections with the appropriate plates from DeGroot's atlas (1955). Only Ss with bilateral lesions that did not invade the thalamus were used as experimental HP animals. A visual examination of the sham (SH) animals was also made to check for lesions.

Chapter III

Results

Figure 1 represents the extent of the smallest and largest lesions sustained by the HP subjects. The examination of tissue sections revealed that all bilateral lesions invaded the hippocampal arch. In some cases, slight intrusions into the overlying cortex or lateral geniculate bodies were seen but the thalamic area remained intact in all cases. The lateral extent of the lesions was approximately 1.5 mm. All lesions extended vertically from 3 to 6 mm. below the brain surface and extended distally about 1 mm. from the electrode. Histological examination of the SH operated brains failed to reveal any lesions in any Ss.

Behavioral Results

Three basic types of behavioral measures were analyzed: 1) the number of trial blocks and errors required to reach discrimination acquisition criterion by the HP and SH groups, 2) the number of errors made by the two groups during the black-white test trials, and 3) the number of alternating responses made by each group during the last block of pretraining compared to the number of alternating responses made during the alternation test trials. The within cell S^2's for both the number of errors on the black-white test and the number of alternations on the alternation test appeared to be heterogeneous. Individual

HP 3

HP 11

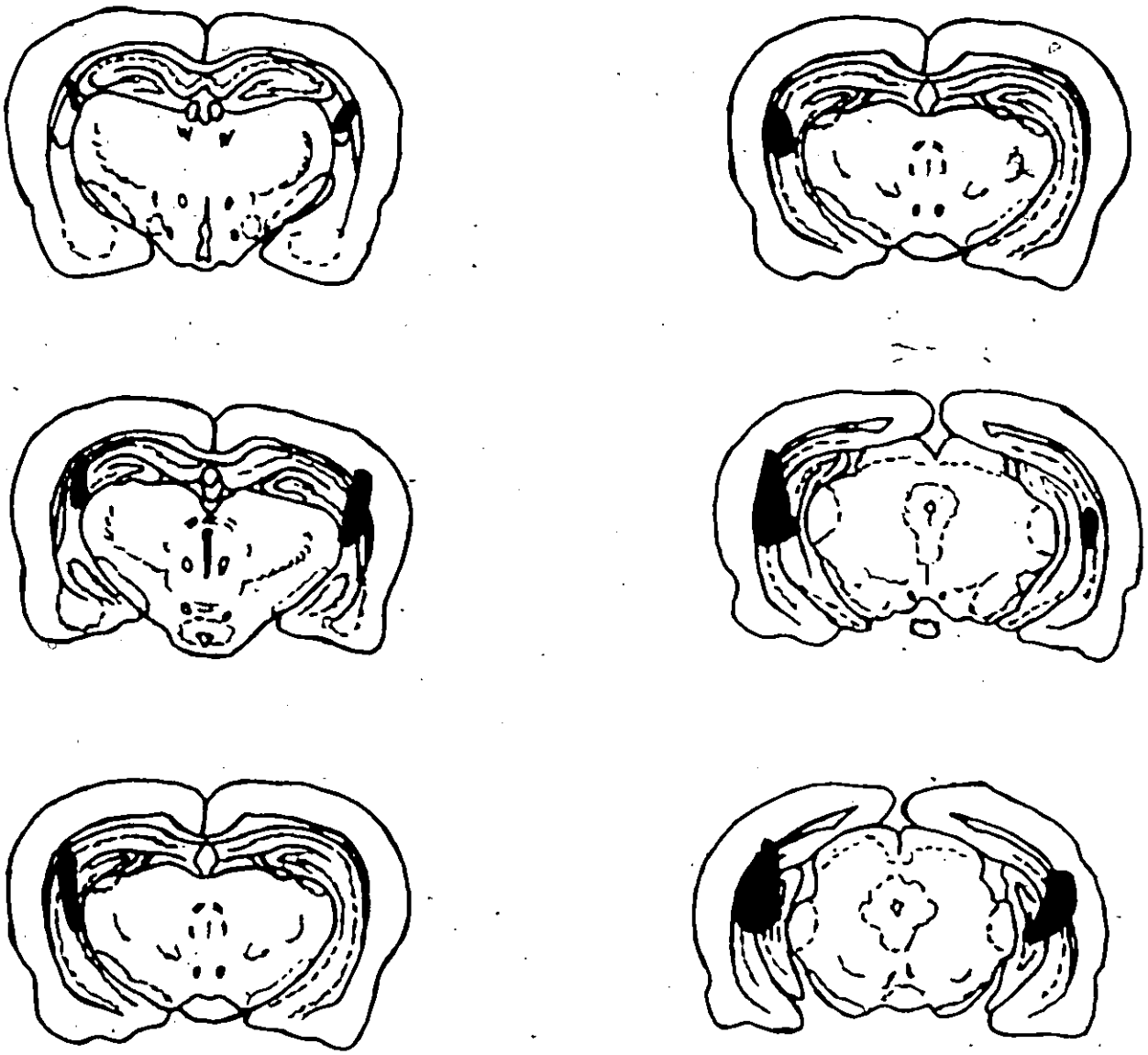

Figure 2. Example of the extent of the smallest and largest hippocampal lesions in the HP animals.

F_{max} tests were run to test the homogeniety of error variance. The observed F_{max} statistics exceeded the critical value in both cases (see Appendix A). The assumption of the homogeniety of variance was not supported and the raw scores were transformed. Since the data involved were numerically small frequency measures, the transformation formula took the form: $x' = \sqrt{x} + \sqrt{x+1}$ as suggested by Winer, (1962). Further F_{max} tests on the transformed data revealed homogeniety of variance (see Appendix A). Subsequent statistical analyses on the number of black-white test errors and the number of pre and post discrimination alternations were performed on the transformed scores.

Table 1 presents the mean number of trial blocks and errors made by the HP and SH groups to reach acquisition criterion. There was no significant difference between the two groups in either errors made or the number of trial blocks required to reach discrimination acquisition criterion ($t = 0.62$, $df = 22$, $p > .05$; $t = 0.35$, $df = 22$, $p > .05$). These results indicate that hippocampal damaged animals acquired the redundant relevant cue task as easily as the sham operated control animals.

In order to ascertain the presence of perseverative responding in the hippocampectomized animals following surgery, the number of random left-right position responses during the last block (16 trials) of pretraining was recorded. A summary of the data for both the raw scores and transformed scores are shown in Table 2a, (p. 35).

Table 1

Mean Number of Errors and Trial Blocks during Discrimination Acquisition for HP and SH Groups (Standard Deviations in Parentheses)

	HP	SH	t
Errors	31.90(17.90)	29.30(15.00)	0.62 NS
Trial Blocks	4.25(1.21)	4.08(1.18)	0.35 NS

NS - not significant, $p>.05$

Table 2a

Mean Number of Alternations on 16 Trials during Pretraining and the Alternation Test Phase (RS-Raw Scores, TS-Transformed Scores, SD-Standard Deviations for Transformed Scores)

Group	Pretraining			Test Phase		
	RS	TS	SD	RS	TS	SD
HP	1.16	2.06	1.35	4.25	3.89	1.76
SH	3.30	3.65	1.56	5.83	4.89	0.90

Table 2b

Analysis of Variance on Number of Alternations during Pretraining and the Alternation Test Trials (Transformed Scores)

Source of Variation	SS	df	MS	F
A (HP vs. SH)	20.8	1	20.8	9.45**
B (Order of test trial presentation)	1.2	1	1.2	0.55 NS
AB Interaction	2.6	1	2.6	1.18 NS
Subjects within groups	44.2	20	2.2	
C (Pretraining vs. testing)	27.6	1	27.6	11.04**
AC Interaction	1.0	1	1.0	0.40 NS
BC Interaction	0.3	1	0.3	0.12 NS
ABC Interaction	0.1	1	0.1	0.04 NS
C x subjects within groups	49.3	20	2.5	

** $p \leq 0.01$

NS - not significant, $p > 0.05$

Table 2c

Individual Comparisons of HP and SH Groups on Number of Pretraining and Test Phase Alternations

Pretraining vs. Test Phase	F
HP	9.04**
SH	4.20*
HP vs. SH	
During Pretraining	6.75*
During Test Phase	2.72 NS

** $p \leq 0.01$

* $p \leq 0.05$

NS - not significant, $p > 0.05$

The number of position alternating responses made by the HP and SH groups were statistically compared.

A 2 x 2 x 2 repeated measures analysis of variance (see Table 2b, p. 36) was carried out on the number of alternating responses made by the HP and SH Ss during the last 16 trials of pretraining and the alternation test trials. A summary of the number of pretraining and testing phase alternations is shown in Table 2a (p. 35). The HP group increased its mean number of alternations from 2.06 to 3.89 between the pretraining and testing. Similarly, the SH group increased from 3.65 to 4.89. During the 16 pretraining trials, the SH group made an average of 3.65 alternations compared to 2.06 by the HP group. On the 16 alternation test trials SH Ss made a mean of 4.89 alternations as opposed to 3.89 for the HP group. Significant main effects were found for the number of alternations made by HP and SH Ss ($F = 9.45$, $df = 1/20$, $p \leq .01$) and for the number of pretraining versus testing phase alternations ($F = 11.04$, $df = 1/20$, $p \leq .01$). No significant interaction effect was found.

Individual comparisons on the pretraining and testing alternation trials were carried out to test the hypothesis that the HP and SH groups were different in their number of alternations. (See Table 2c, p. 37.) The hippocampal lesioned group made significantly fewer alternating responses during the pretraining test trials than during the alternation test trials ($p \leq .01$). Similarly, the sham

operated control group made significantly fewer alternations during the pretraining trials than during the test trials ($p \leq .05$). It seems that all animals (both HP and SH) at least noticed the position dimension of the redundant cue task. Both groups made more alternating responses after the discrimination training phase than before.

When the performance of the HP and SH groups was compared on the number of alternations made during the pretraining trials, it was found that the hippocampal lesioned Ss made significantly fewer alternating responses than the shams ($p \leq .01$). These results suggest that the hippocampal damaged Ss were perseverating following surgery. During the alternation test trials, however, while the HP group still made fewer alternations than the SH, the difference did not reach statistical significance ($p \leq .05$). These findings indicate that the HP group acquired the alternating responses as well as the SH, and appeared to break their position responding habit during RRC training phase.

Table 3a (p. 41) presents the mean number of errors made by the HP and SH groups on the 16 black-white cue utilization test trials. An error was defined as a response to a brightness door other than the one responded to during discrimination training. The HP group made an average of 1.41 errors while the SH group made 0.50 errors on the 16 brightness test trials. From this small number

of errors it appears that both the HP and the SH Ss acquired the brightness dimension. Even the two HP animals (#7 and #11) that had lesions slightly invading the lateral geniculate bodies made 0 and 3 brightness errors respectively, indicating that the ability to make brightness discriminations was not impaired. A 2 x 2 analysis of variance (Table 3b, p. 41) revealed no significant differences between the HP and SH groups on either the number of errors made or the order of presentation of the test trials. No significant interaction effects were found, individual comparisons again revealed no significant difference between the HP and SH groups on the number of brightness errors (Table 3c, p. 43).

The type of black-white errors made by the two groups was also examined. An S could make brightness errors for two reasons: 1) because it was responding to a particular position, (this can be defined as a position error), or 2) because it was alternating its responses from trial to trial (this can be defined as an alternation error). Either of these two strategies of responding during the black-white test trials would lead to errors. Consequently, all black-white errors were typed as being of the alternation or position type. In the HP group, of the total of 15 black-white errors, 8 were position and 7 were alternation. In the SH group of the total of 5 errors, 2 were position and 3 were alternation type. There appeared to be no significant difference between the

Table 3a

Mean Number of Errors on 16 Black and White Cue Utilization Test Trials (RS-Raw Scores, TS-Transformed Scores, SD-Standard Deviations for Standard Scores)

	HP			SH		
	RS	TS	SD	RS	TS	SD
Number of Errors	1.41	2.41	1.19	0.50	1.58	0.88

Table 3b

Analysis of Variance on Number of Errors on 16 Black-White Test Trials (Transformed Scores)

Source of Variation	SS	df	MS	F
A (HP vs. SH)	4.6	1	4.6	3.50 NS
B (order of B/W test presentation)	0.4	1	0.4	0.30 NS
AB Interaction	0.8	1	0.8	0.60 NS
Within cell	26.5	20	1.3	

* $p \leq .05$

NS - $p > .05$

HP and SH groups on the nature of the black-white errors. (Fisher exact probabilities test).

In view of the fact that both groups made few alternations, it appeared that Ss (both HP and SH) responded to specific positions during the pretraining and alternation test trials. According to a Binomial test, an S had to alternate 12 or more times out of 15 to reach a .05 level of significance and 7 or more times for above chance alternation. None of the HP or SH Ss met either of these criteria. However, when position responding was examined, only one animal (a SH) showed no position preference, and only during the alternation test trials. All other animals responded 9 or more times to one position or the other during both the pretraining and test phase trials. Another way of analyzing the alternation data was to look at the type of position responses made by individual Ss. The following aspects of position responding were examined: 1) the degree to which the HP and SH Ss responded to any particular position during the pretraining and alternation tests and 2) how strongly this responding was maintained during the alternation test. To this end, the number of responses to a preferred side during both the pretraining and the alternation tests were compared. A preferred side during either phase was defined as the side to which more than one-half (9 or more) of the 16 possible responses were made. Table 4a (p. 43) shows a summary of the data. The HP group

Table 3c

Individual Comparisons of HP and SH Groups on Number of Black-White Test Errors (Transformed Scores)

HP	SH	F
2.14	1.58	3.20 NS

NS - not significant, $p>0.05$

Table 4a

Mean Number of Responses to Preferred Side during Pretraining and the Alternation Test Trials (Standard Deviations in Parentheses)

Group	Pretraining	Testing
HP	15.00 (1.52)	12.75 (2.41)
SH	13.50 (2.36)	11.25 (2.12)

decreased its mean number of responses to any preferred side from 15.0 to 12.75 between pretraining and the alternation tests. Similarly, the SH group decreased from 13.5 to 11.25. During both pretraining and the alternation test, the HP group made more preferred side responses than the SH group (15 compared to 13.5 and 12.75 compared to 11.25).

A 2 x 2 x 2 repeated measures analysis of variance (Winer 1962, Table 4b, p. 45) was carried out. A significant difference was found for pretraining versus the test phase ($f = 24.3$, $df = 1/20$, $p-.01$). No significant difference was found between the HP and SH groups on the strength of the preferred side responding. The order of test trial presentation and interaction effects were not significant.

Individual comparisons of the HP and SH groups on the number of responses to the preferred side during pretraining and the test phase revealed no significant differences. These results suggest that both the HP and SH groups showed strong position preferences during the pretraining and alternation test trials. The interpolated RRC learning significantly weakened positions responding as such, but hippocampal damage did not have any significant effect. However, the above data do not reveal whether the observed position preference during the pretraining trials was maintained for the same side.

To answer this question, the number of responses made to the preferred side during pretraining was

Table 4b

Analysis of Variance on Number of Responses to Preferred Side during Pretraining and the Alternation Test Phase

Source of Variation	SS	df	MS	F
A (HP vs. SH)	27.0	1	27.0	3.86 NS
B (Order of test trial presentation)	21.3	1	21.3	3.04 NS
AB Interaction	4.1	1	4.1	0.58 NS
Subjects within groups	140.8	20	7.0	
C (Pretraining vs. testing)	60.7	1	60.7	24.30 **
AC Interaction	0.0	1	0.0	0.00 NS
BC Interaction	1.4	1	1.4	0.56 NS
ABC Interaction	2.0	1	2.0	0.80 NS
C x subjects within groups	49.9	20	2.5	

** $p \leq 0.01$

* $p \leq 0.05$

NS - not significant, $p > 0.05$

Table 4c

Individual Comparisons of HP and SH Groups on Number of Responses to Preferred Side during Pretraining and Test Phase

Pretraining vs. Test Phase	F
HP	4.35*
SH	4.35*
HP vs. SH	
During Pretraining	1.96 NS
During Test Phase	1.96 NS

* $p \leq 0.05$

NS - not significant, $p > 0.05$

compared to the number of responses made to the same side during the alternation test phase. Table 5a (p. 48) shows the mean number of responses made by each group. Both the HP and SH groups decreased their number of responses between pretraining and the test phase from 15.0 to 12.8 and 13.5 to 7.9 respectively.

A 2 x 2 x 2 repeated measures analysis of variance (Table 5b, p. 49) revealed significant main effects for HP versus SH ($F = 13.1$, $df = 1/20$, $p \leq .01$), and for pretraining versus testing ($F = 26.7$, $df = 1/20$, $p \leq .01$). A significant surgery treatment X pretraining/testing interaction was found ($f = 4.8$, $df = 1/20$, $p \leq .05$). No other main or interaction effects were significant.

Individual comparisons (Table 5c, p. 50) were again carried out. A significant difference was found between the HP and SH groups during the alternation test trials only ($p \leq .01$). There was no difference between the two groups during pretraining ($p > .05$). When the performance of the two groups during pretraining was compared to the test phase, only the SH group showed a significant decrease in responding to the same side during testing as during pretraining ($p \leq .01$).

The above results indicate that while the interpolated RRC learning task weakened the positional responding of both groups, the HP group had a stronger original position preference than the SH group. During the

Table 5a

Mean Number of Responses to Preferred Side during Pretraining and the Same Side during the Alternation Test Phase (Standard Deviations in Parentheses)

Group	Pretraining	Test Phase
HP	15.00 (1.52)	12.75 (2.41)
SH	13.50 (2.36)	7.90 (3.89)

Table 5b

Analysis of Variance on Number of Responses to Preferred Side during Pretraining and the Same Side during the Alternation Test Phase

Source of Variation	SS	df	MS	F
A (HP vs. SH)	120.3	1	120.3	13.1 **
B (Order of test trial presentation)	3.0	1	3.0	0.3 NS
AB Interaction	0.8	1	0.8	0.1 NS
Subjects within groups	183.8	20	9.2	
C (Pretraining vs. testing)	184.1	1	184.1	26.7 **
AC Interaction	33.3	1	33.3	4.8 *
BC Interaction	3.0	1	3.0	0.3 NS
ABC Interaction	19.3	1	19.3	2.8 NS
C x subjects within groups	136.9	20	6.9	

** $p \leq 0.01$

* $p \leq 0.05$

NS - not significant, $p > 0.05$

Table 5c

Individual Comparisons of HP and SH Groups on Number of Responses to Preferred Side during Pretraining and the Same Side during the Alternation Test Phase

Pretraining vs. Test Phase		F
	HP	3.29 NS
	SH	20.36 **
HP vs. SH		
	During Pretraining	1.47 NS
	During Test Phase	15.21 **

** $p \leq 0.01$

* $p \leq 0.05$

NS - not significant, $p > 0.05$

alternation test trials, HP Ss showed a significantly stronger tendency than SH Ss to respond to the same side as the one preferred during pretraining.

To determine how many Ss preferred a particular position during pretraining and the test phase, a series of non-parametric tests (Siegel, 1956) were executed. Two criteria of position preference were employed: 1) above chance responding (>50%) and 2) 75% or more. Above chance responding was defined as 9 or more responses out of 16, while 75% or more responding was defined as 12 or more responses out of 16. The number of Ss in each group that preferred the same or different side during both pretraining and test trials is presented in Table 6 (p. 52). All 12 HP Ss preferred the same side >50% of the time during both pretraining and testing. Eight of these 12 preferred the same side more than 75% of the time. In the SH group, only 5 of the 12 Ss preferred the same side during both pretraining and testing more than 50% of the time. Three of these 5 preferred the same side >75%. Of the remaining 7 SH Ss, 6 preferred the opposite side more than 50% of the time, and one showed no preference. Three of the 6 preferring the opposite side did so more than 75% of the time. Fisher exact probability tests revealed that significantly more HP Ss preferred the same side during both pretraining and testing than SH under both the 50% and 75% conditions ($p \leq .05$).

These findings indicate that during the

Table 6

Number of Ss Preferring the Same Position during both Pretraining and the Alternation Test Phase

Group		Same	Different
HP	>50%	12	0
	≥75%	8	0
SH	>50%	5	6
	≥75%	3	3

Table 7

Number of Ss Preferring Any Position during both Pretraining and the Alternation Test Phase

Group		Pre	Post
HP	>50%	12	12
	≥75%	12	8
SH	>50%	12	11
	≥75%	10	6

alternation test trials, in the absence of the external brightness dimension, all HP Ss reverted to responding to the same position as the one they responded to during pretraining. In the SH group, however, less than half (5) of the 12 Ss reverted to the same position while the rest responded to the opposite position.

Table 7 (p. 52) shows the number of Ss in each group that preferred any side during both the pretraining and alternation test trials, more than 50% and more than 75% of the time. All 12 HP Ss showed either a left or right position preference during pretraining under both the 50% and 75% conditions. Similarly, all 12 SH Ss showed some position preference above 50% and 10 Ss above 75%. During the alternation test trials, all 12 HP Ss preferred a position more than 50% of the time, and eight of them more than 75% of the time. In the SH group, 11 preferred a position more than 50% of the time and 6 over 75% of the time. Fisher exact probability tests disclosed no significant differences between the two groups ($p>.05$). It seems that both HP and SH Ss exhibited position preferences during both pretraining and alternation test trials.

Chapter IV

Discussion and Conclusions

The hippocampal damaged group made significantly fewer alternating responses during the pretraining than the sham group. These results are similar to those found in previous studies employing reinforced free choice situations (Racine and Kimble, 1965). It should be noted, however, that both groups failed to alternate above chance and showed strong position preferences. Damage to the hippocampus did not interfere with the acquisition of the redundant relevant cue (RRC) task as measured by errors made or trials required to reach acquisition criterion. On the brightness cue utilization test trials, hippocampal damage did not result in any deficits in acquiring this dimension. Both groups (HP and SH) acquired the relevance of the black-white cues. During the alternation test trials HP animals did not differ from SH animals in their frequency of alternations, and none of the Ss, either HP or SH, could be considered to have acquired the relevance of the alternation dimension of the RRC task.

Both groups showed position response perseveration during the alternation test trials. However, only the HP animals reliably perseverated to the same position that they responded to during the initial pretraining

trials. Sham animals did not reliably continue to respond to the first preferred side during the alternation test trials.

The above findings did not support predictions based on any of the three proposed models of hippocampal function. All three theories would have predicted that the hippocampal lesioned Ss should have continued to make more position responses during RRC training than the sham animals. According to the Douglas (1967) model, the HP Ss should have found it more difficult to switch their attention from previously attended to stimuli, i.e., the left or right side, to the new brightness stimuli. According to the Kimble (1968) model, the position response, per se, should not have been as easily inhibited by HP Ss as SH controls. Winocur and Mills' (1969) model would have predicted poorer acquisition of the RRC task by HP rats because of their inability to integrate new information. All three models would, therefore, have predicted difficulty in the RRC acquisition by the HP group. The present study, however, found no RRC acquisition differences between the groups.

The three theories also could not explain the findings of the cue utilization test trials. The Douglas (1967) model would have predicted that during testing, the HP Ss should have shown a greater reliance on the brightness dimension than SH Ss. However, there was no significant difference between the two groups on the number of brightness test errors or the degree of brightness cue utilization. According

to the Kimble (1968) model, the HP Ss should have continued to alternate during the test trials after RRC training. The results did not support this hypothesis. Hippocampal damaged Ss did not differ from sham Ss in their alternating response frequency during the test trials. Finally, both groups utilized the brightness dimension but not the alternation dimension. There was no difference between the two groups on the amount of information gained from the task. Therefore, there appeared to be no general information processing deficit in the HP Ss.

From the foregoing discussion it would seem that the hippocampal lesioned Ss could 1) "gate out" sensory information, 2) could change their response patterns, and 3) could adequately handle newly introduced information. In these respects they were no different from the control Ss. However, there was a definite difference in the response pattern of the two groups. Although both the HP and SH groups showed response perseveration, their mode of perseveration was different. During the alternation test trials, HP Ss went back to the originally preferred side while SH Ss did not reliably do so. As long as the brightness cues were available, the HP Ss behaved like the control animals. However, when the brightness cues were removed (and replaced by neutral stimuli) the HP Ss ceased alternating and reverted to their pretraining position response. Response perseveration appeared to be a function of minimal external cue differentiation. The hippocampal lesioned

animals seemed to perseverate only when the external cues became vague or ambiguous.

Several investigators have reported similar findings. Jackson and Strong (1969) found that traditional maze-learning deficits following hippocampal lesions were related to an inability to make use of inconspicuous cues. Moreover, Ellen and Deloache (1968) and Leaton (1969) demonstrated improved maze performance following increased availability of stimuli in the external environment. Cohen, La Roche and Beharry (1971) found that response perseveration was not evident in situations where external brightness cues differentiated response choices. The above studies show that the response perseveration of HP Ss is more obvious under ambiguous cue conditions.

In a recent study Winocur and Breckenridge (1973) demonstrated that the often observed impairment of hippocampally damaged rats in learning complex mazes could be improved significantly by the addition of highly discriminable brightness stimuli. Hippocampal lesioned Ss made significantly more errors than controls in learning a fixed response sequence in a complex maze. Following the introduction of brightness cues, the HP rats could learn the sequence as well as a control group. Performance of the HP group, unlike that of the controls, deteriorated following removal of the brightness cues used in original learning. Careful examination of the results revealed that the HP group not only made more errors at each choice point of the

complex maze, but also responded in a qualitatively different way from the control group. They seemed to make most of their errors at two particular choice points (3 and 5). When the external stimuli were introduced, the HP Ss no longer had this selective difficulty and made equal errors at all choice points. During a re-test with the brightness cues removed, they again experienced difficulty at the same two choice points. It seems that in the absence of the brightness cues, the HP Ss reverted to errors at the same two choice points as during original learning. Winocur and Breckenridge interpreted their results to mean that the hippocampus is important in processing relevant stimulus cues and in the organization of appropriate response strategies.

The above observations are similar to those of the present study. HP Ss appeared to learn that 1) reinforcement could be received on a particular side when two grey doors were present, and 2) that reinforcement was associated with one color (Black or White). They did not seem to be able to combine the two specific pieces of information to form a new information pattern. In more parsimonious and descriptive terms, the interpolated RRC training did not break the original S-R habit of the HP Ss. It would appear that damage to the hippocampus resulted in a deficit in learning appropriate response strategies demanded by the test situation. An intact hippocampus seemed to be necessary to re-process or change previous information. These observa-

tions can be explained by an extension of the general information processing deficit hypothesis. Hippocampal damage appears to cause difficulty in processing specific types of sensory information rather than a general deficit. Jackson and Strong (1969) described this deficit as an inability to process inconspicuous cues. Response perseveration is most obvious in situations where the external cues are ambiguous.

Implications for Further Research

Since response perseveration due to hippocampal damage is only found in non differentiated stimulus conditions, it is difficult to emperically test Douglas' attentional model. In ambiguous cue situations, it would be almost impossible to establish to what specific cue the animal was continuing to attend. The Douglas model is only testable if the ambiguous cue situation itself can be assumed to be a discriminable cue. Under this assumption, the Douglas model is also capable of explaining the position perseveration of HP Ss during the post discrimination alternation test. It can be argued that during testing, the neutral grey doors served as a cue for the HP Ss to respond in the same way they had responded during pre discrimination. However, for this explanation to be tenable, the ambiguous cue situation had to serve as a discriminable cue. A way of testing this hypothesis would be to replicate the present experiment with one change. During the alternation cue utilization

test phase, instead of the two grey doors, doors of a different color should be used. If the HP Ss still revert to pre-discrimination position responding, one can argue that the ambiguous grey doors did not serve as discriminable stimuli.

The present study did not really test the limit of the capacity of HP Ss to acquire information. It only showed that the HP Ss learned as much about the two cues of the RRC task as the SH's. They both picked up brightness and neither picked up alternation. Previous research (Telegdy and Cohen, 1971) has shown that brightness is an extremely salient dimension. It is therefore possible that the brightness dimension overshadowed the alternation dimension during RRC acquisition. Because of its salience, both groups appeared to learn the RRC task by relying on the brightness dimension, and neither group seemed to utilize the alternation dimension. A more valid test of the general information deficit hypothesis would insure that the RRC dimensions used would be approximately equally salient. One way of doing this would be to select cues that were close in salience on the basis of previous research. In the present study, alternation was obviously the more difficult dimension. By giving animals several blocks of pretraining alternation trials, the salience of this dimension could be increased. The present experimental design could then be used to test the general information deficit hypothesis.

Lastly, several investigators (Snyder and Isaacson, 1965; Nadel, 1968; Jackson, 1968; Jarrard, 1973) have

demonstrated that the hippocampus is not equipotential. The position and size of hippocampal lesions have differential behavioral effects. The present experiment used small radio frequency lesions in the posterior hippocampus. It is possible that the observations of this study are specific only to this location and size of lesion. Further research should investigate the effects of lesions in different hippocampal areas on the retention of pre task position habits.

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APPENDIX A

F_{max} Test on Brightness Errors Before Transformation

SS largest	SS smallest	F_{max}
13.5	0.84	16.0 *

* $p \leq 0.05$

F_{max} Test on Number of Pretraining Alternations Before Transformation

SS largest	SS smallest	F_{max}
69.4	5.0	13.8*

* $p \leq 0.05$

F_{max} Test on Number of Test Phase Alternations Before Transformation

SS largest	SS smallest	F_{max}
75.5	4.9	15.0*

* $p \leq 0.05$

APPENDIX A (Continued)

F_{max} Test on Brightness Errors After Transformation

SS largest	SS smallest	F_{max}
3.6	1.8	2.0 NS

NS - not significant, $p>0.05$

F_{max} Test on Number of Pretraining Alternations After Transformation

SS largest	SS smallest	F_{max}
26.7	19.7	1.3 NS

NS - not significant, $p>0.05$

F_{max} Test on Number of Test Phase Alternations After Transformation

SS largest	SS smallest	F_{max}
34.0	21.0	1.6 NS

NS - not significant, $p>0.05$

APPENDIX B

Number of Errors and Trial Blocks Required by Individual Ss to Reach Acquisition Criterion

HP No.	Trial Blocks	Errors	SH No.	Trial Block	Errors
1	6	63	1	6	48
2	3	15	2	3	18
3	3	15	3	3	4
4	5	34	4	5	35
5	4	33	5	5	46
6	4	68	6	4	12
7	5	33	7	4	21
8	3	18	8	3	11
9	4	30	9	3	33
10	6	36	10	3	37
11	4	4	11	5	51
12	4	34	12	5	35

APPENDIX C

Number of Pretraining and Test Phase Alternations for Individual Ss

HP No.	Pre Acquisition	Post Acquisition
1	0	0
2	2	5
3	0	5
4	2	5
5	2	2
6	0	8
7	0	2
8	0	2
9	0	0
10	2	10
11	6	2
12	0	9

APPENDIX C (Continued)

Number of Pretraining and Test Phase Alternations for Individual Ss

SH No.	Pre Acquisition	Post Acquisition
1	0	10
2	2	7
3	4	2
4	2	5
5	8	9
6	4	4
7	2	4
8	4	5
9	4	5
10	2	7
11	0	5
12	10	7

APPENDIX D

Number of Responses to Each Side During Pretraining and Alternation Test Trials by Individual Ss

HP No.	Pre Acquisition L	Pre Acquisition R	Post Acquisition L	Post Acquisition R
1	0	16	0	16
2	15	1	10	6
3	16	0	15	1
4	3	13	3	13
5	2	14	3	13
6	0	16	1	15
7	16	0	14	2
8	16	0	12	4
9	0	16	0	16
10	1	15	6	10
11	5	11	7	9
12	0	16	6	10

APPENDIX D (Continued)

Number of Responses to Each Side

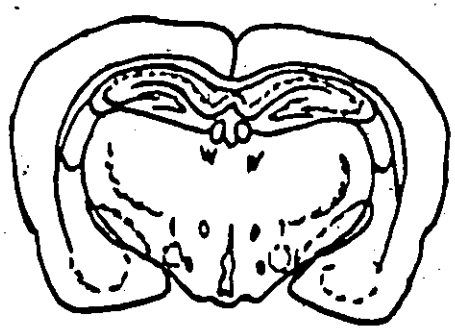
During Pretraining and Alternation

Test Trials by Individual Ss

SH No.	Pre Acquisition L	Pre Acquisition R	Post Acquisition L	Post Acquisition R
1	0	16	10	6
2	15	1	7	9
3	12	4	10	6
4	1	15	3	13
5	7	9	10	6
6	14	2	15	1
7	1	15	14	2
8	2	14	12	4
9	12	4	9	7
10	1	15	4	12
11	16	0	3	13
12	7	9	8	8

APPENDIX E

Extent of Lesions for Animals in HP Group



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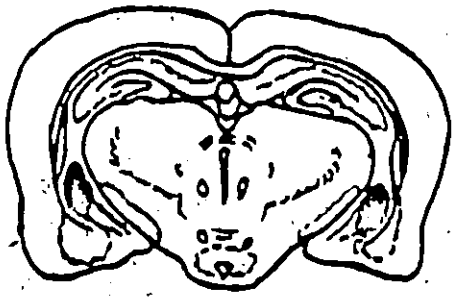

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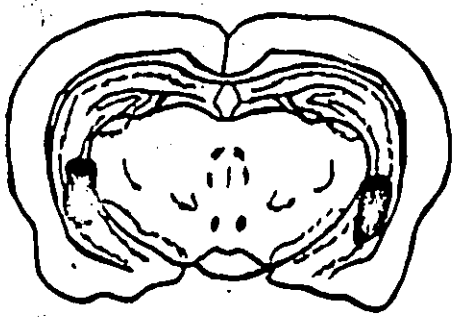

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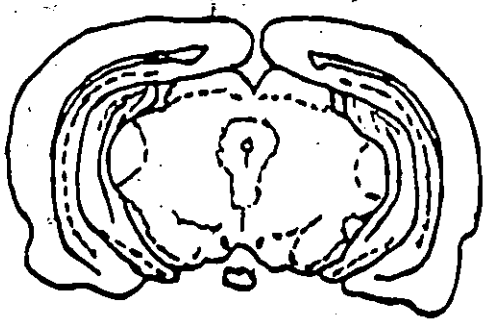

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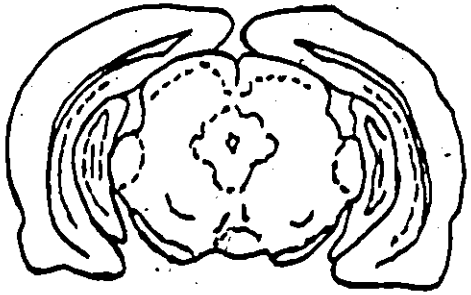

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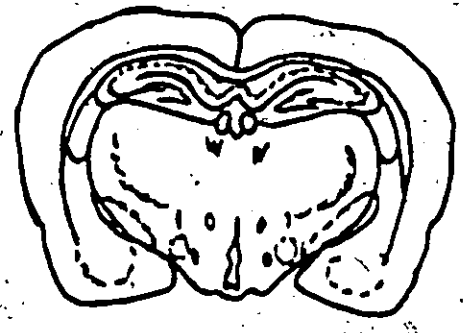

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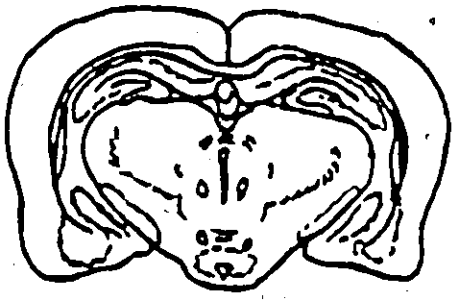

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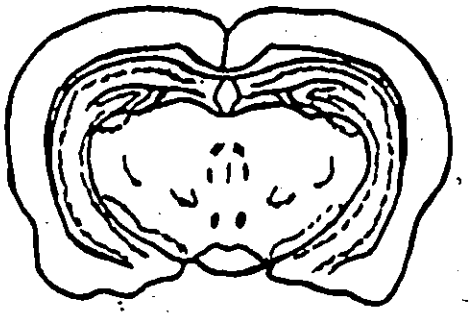

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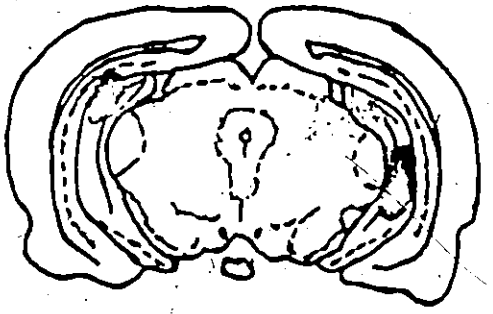

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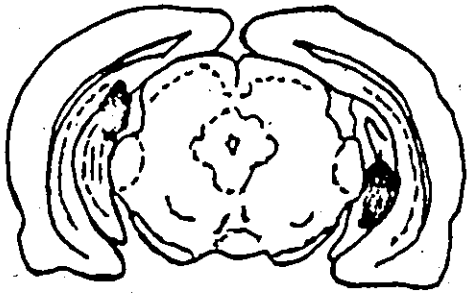

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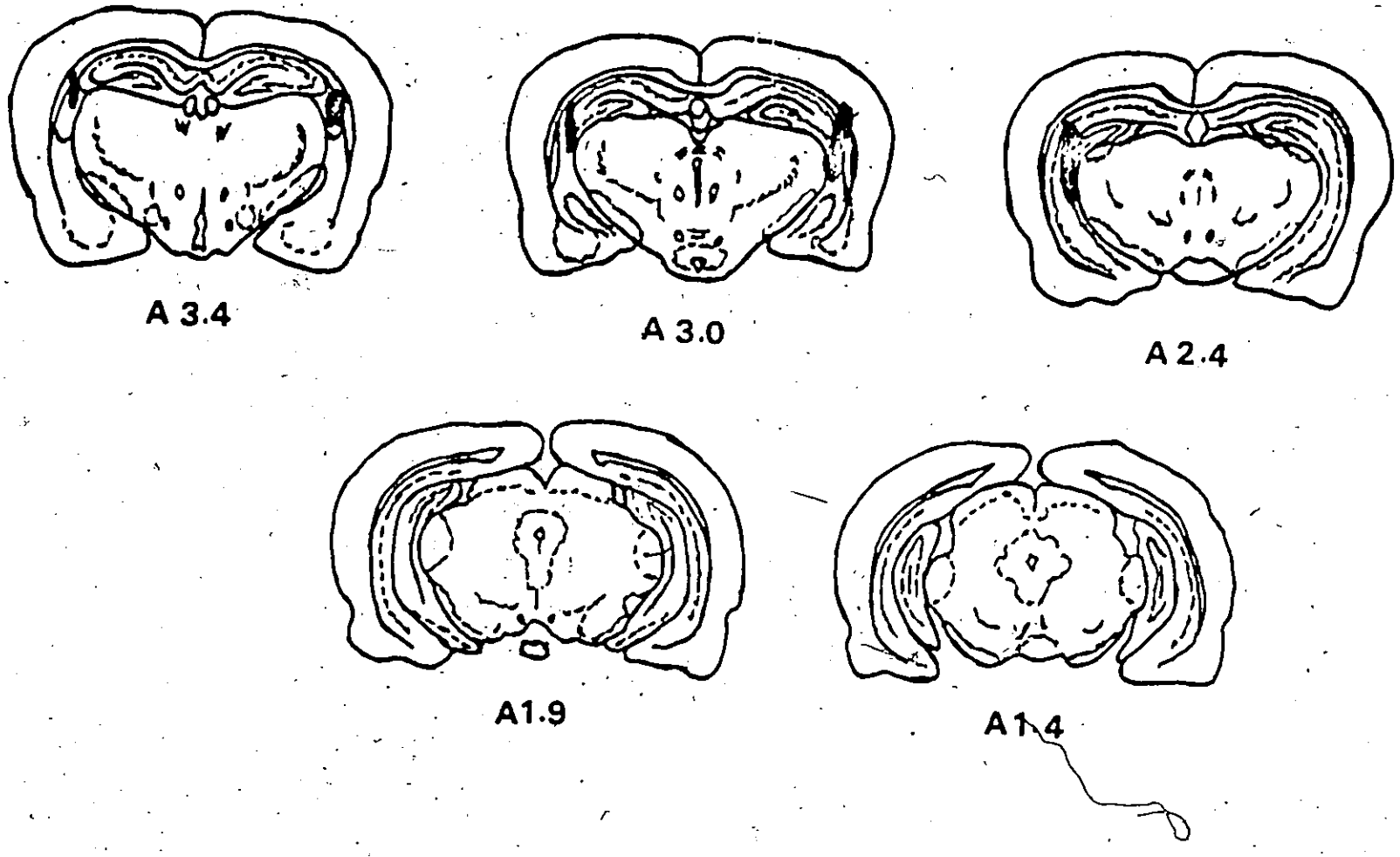

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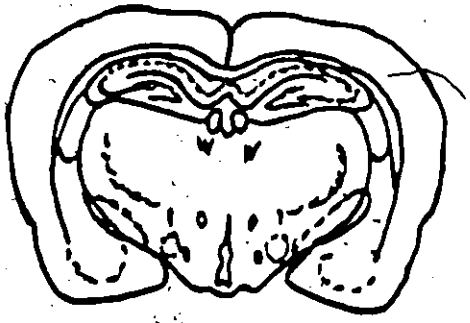

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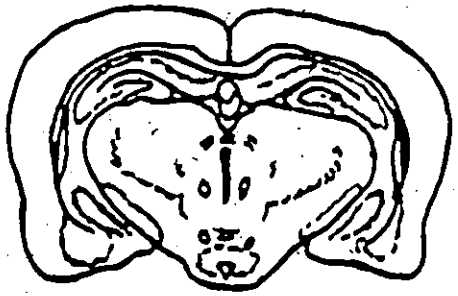

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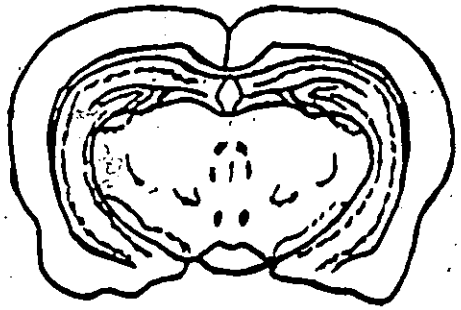

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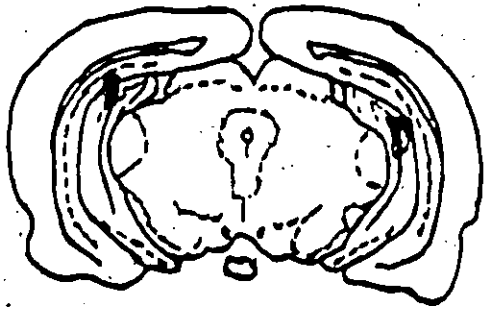

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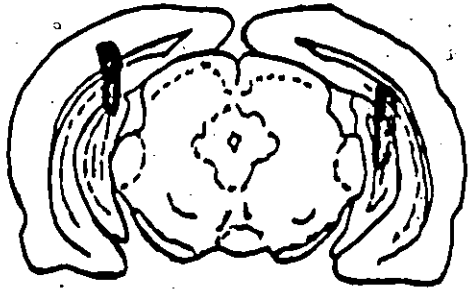

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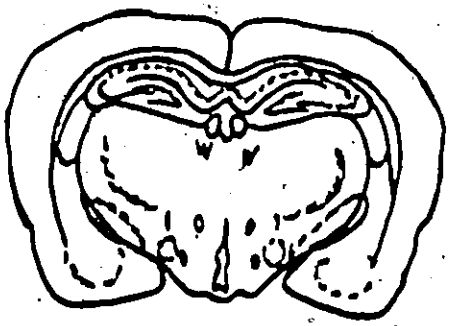

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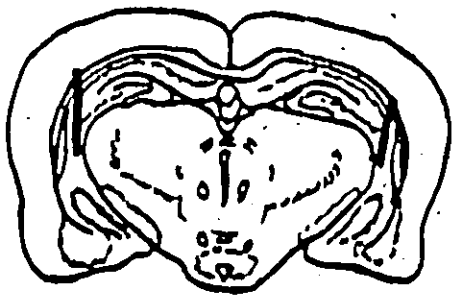

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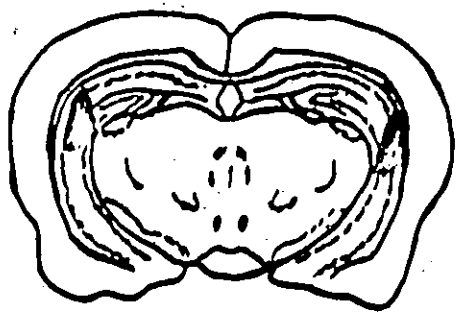

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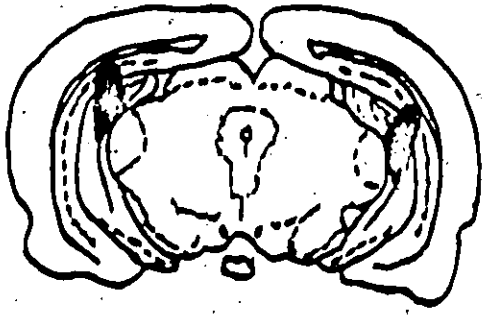

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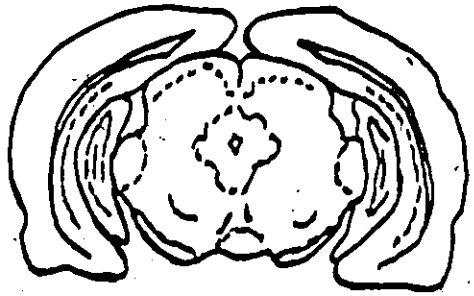

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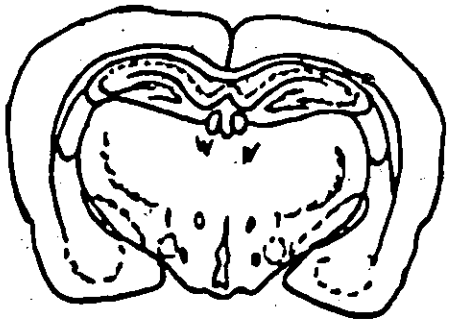

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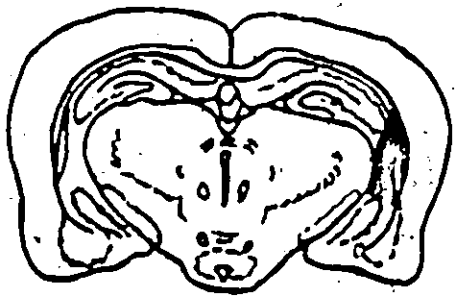

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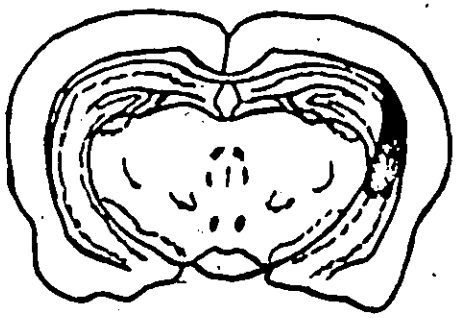

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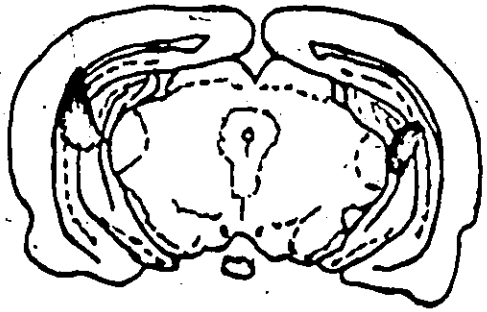

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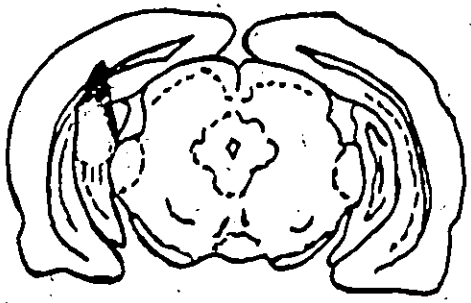

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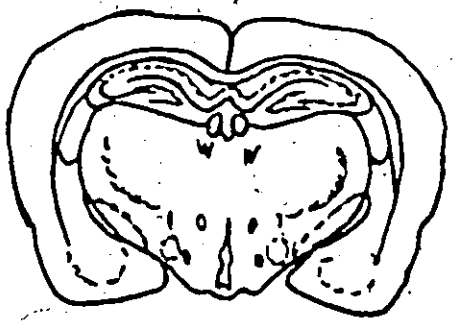

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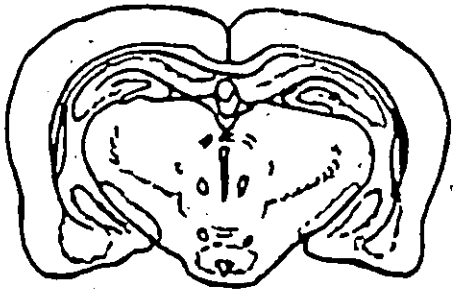

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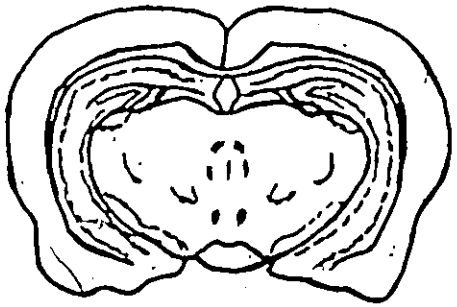

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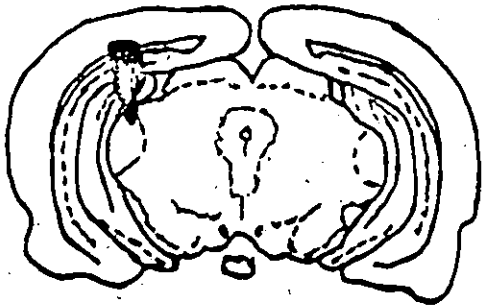

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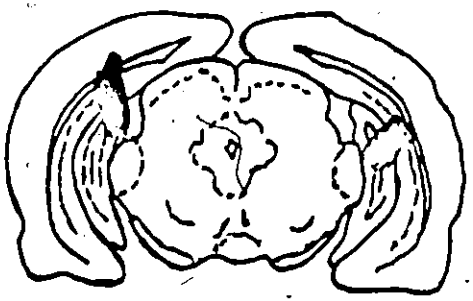

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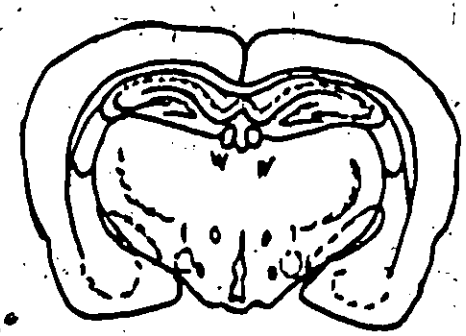

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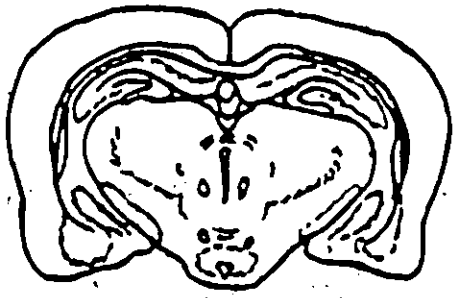

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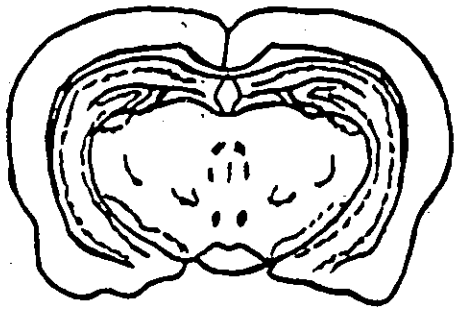

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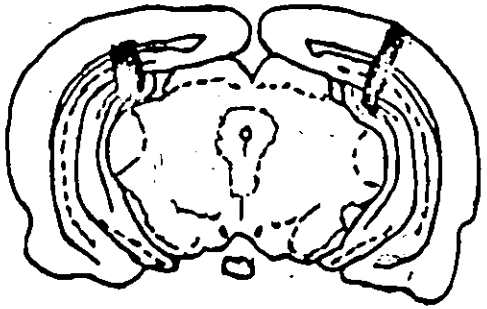

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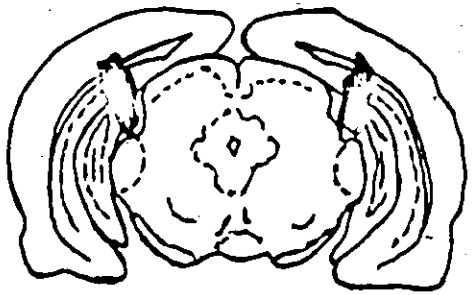

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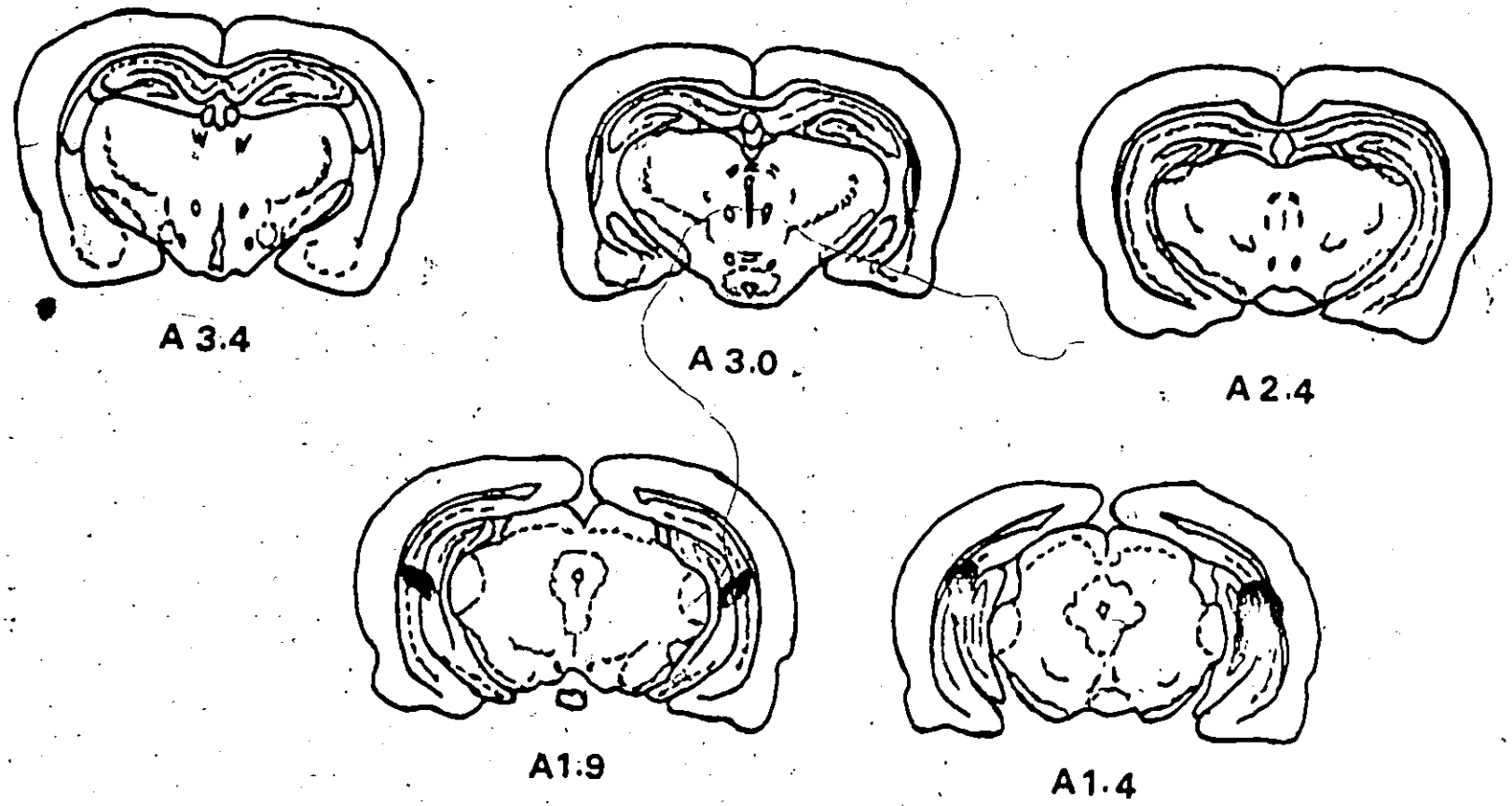

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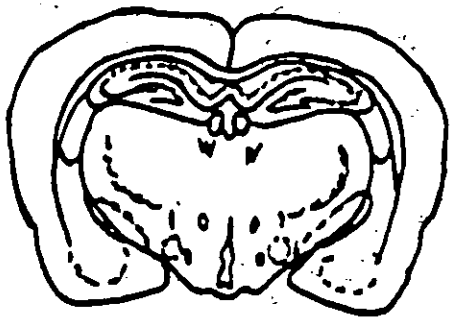

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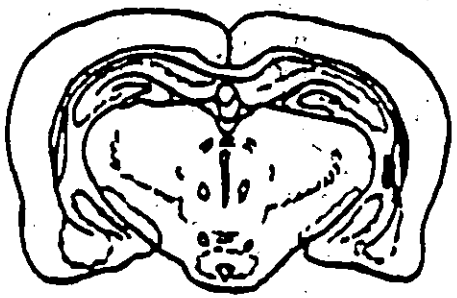

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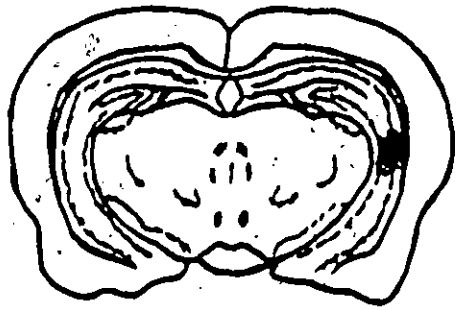

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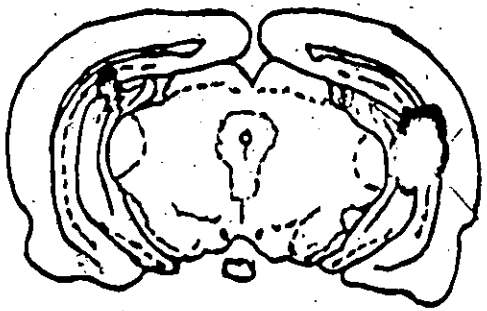

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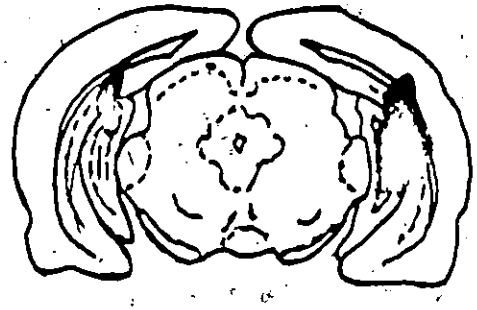

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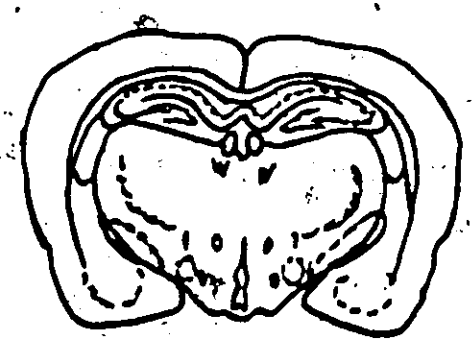

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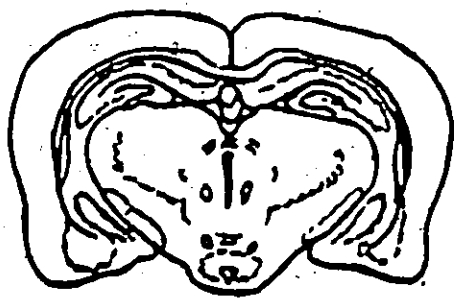

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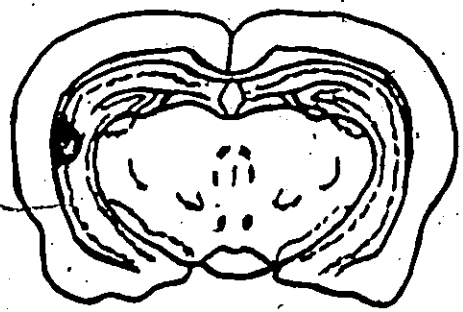

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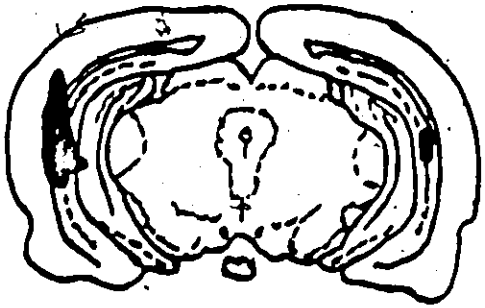

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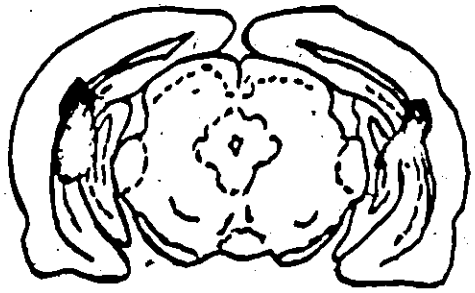

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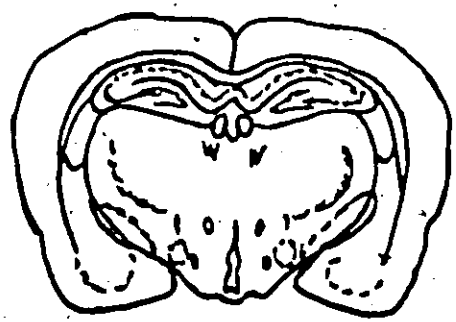

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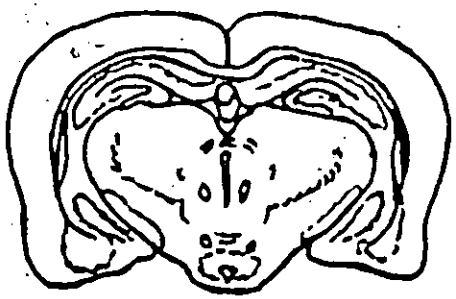

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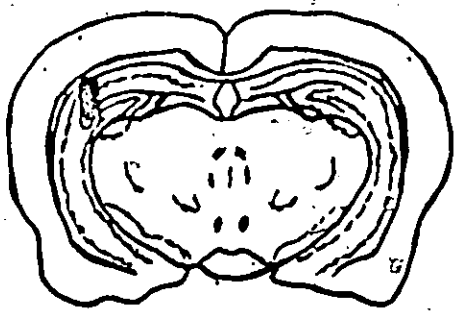

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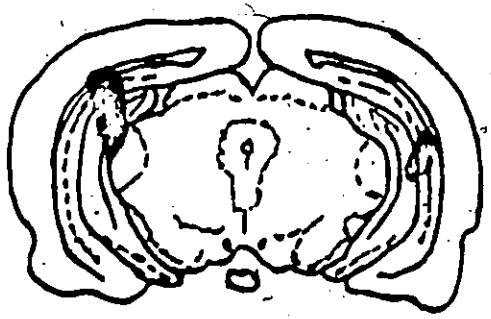

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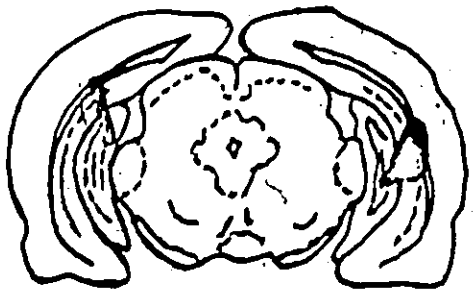

A1.4

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EDUCATION:

Primary
Our Lady of Mount Royal School
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1959-1963

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1963-1965

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B.A.
1965-1968

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Windsor, Ontario
M.A,
1968-1970

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1968-69

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1969-70

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1968-1969
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Cedar Springs
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Teaching Assistant
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1969-1970
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1970-1971

Teaching Assistant
Experimental Psychology
1971-1972
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Sessional Instructor
Introductory Statistics
Summer School, 1972
University of Windsor

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Windsor Separate School Board
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AWARDS:

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PUBLICATIONS:

Telegdy, G. A., and Cohen, J. S. Cue utilization and drive level in albino rats. Journal of Comparative and Physiological Psychology, 1971, 75, 248-253.

Rourke, B. P., and Telegdy, G. A. Lateralizing significance of WISC verbal-performance discrepancies for older children with learning disabilities. Perceptual and Motor Skills, 1971, 33, 875-883.

Cohen, J. S., and Telegdy, G. A. Effect of drive level on habit strength in a discrimination task. Psychonomic Science, 1970, 19, 27-29.

READINGS:

Rourke, B. B., and Telegdy, G. A. The relationship between WISC Verbal-Performance discrepancies and motor skills in children with learning disabilities. Canadian Psychological Association, Winnipeg, May, 1970.

Cohen, J. S., Telegdy, G. A., Hurley, N., and Maitre, S. The effects of pretraining shock experience and

observation of other animals in pain upon exploratory behavior of the rat. Canadian Psychological Association, Montreal, June, 1972.

Konopasky, R., Telegdy, G. A. The strength of an imitative response versus a response to an environmental cue in a two dimension discrimination task. Canadian Psychological Association, Montreal, June, 1972.