The effect of cue distinctiveness on successive discrimination performance in hippocampal lesioned rats

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Twenty rats received bilateral lesions at three levels of the hippocampus, 20 received bilateral lesions of the amygdaloid complex, and 20 served as unoperated controls. Sets of lesion groups were trained on one of four discrimination tasks differing in stimulus distinctiveness. It was found that hippocampal lesioned rats were deficient on those tasks low in cue distinctiveness but similar to controls on those tasks high in cue distinctiveness. A control experiment showed that these findings could not be explained in terms of a failure of hippocampal lesioned rats to habituate to an irrelevant tactile stimulus present in those discrimination tasks in which hippocampal lesioned rats were deficient.

Rats with hippocampal lesions are said to persevere because of an inability to suppress or stop the initiation or execution of prepotent responses. Thus, deficits in the learning of a new task may be the result of perseveration on an old task. Since successive discrimination impairments in hippocampal lesioned rats can be interpreted as a result of perseveration on the response against which discrimination learning is measured (Douglas, 1967; Isaacson, Schmaltz, & Douglas, 1966), the aim of the present experiment was to determine whether perseveration was an inevitable consequence of hippocampectomy in rats, or whether it varied as a function of cue distinctiveness. Since it has been shown that rats with hippocampal lesions are less distracted by irrelevant stimuli during a trained runway response (Raphelson, Isaacson, & Douglas, 1965; Riddell, Rothblatt, & Wilson, 1969; Wickelgren & Isaacson, 1963), it might be expected that hippocampal lesioned rats would not notice the relevant stimuli in a runway go, no-go successive discrimination task.

EXPERIMENT 1

Stimuli were used which were thought to vary in distinctiveness because of the inherent dominance of certain sensory modalities in the rat and because of the inherent sensitivity of the rat to certain stimulus dimensions. Tactile stimuli (roughness and temperature) were used as highly distinctive stimulus dimensions, while visual stimuli (brightness and orientation) were used as relatively indistinct dimensions. Further, it could be suggested that brightness was relatively higher in distinctiveness than the orientation dimension.

According to the present hypothesis, it might be expected that hippocampal lesioned rats would show

an increasing successive discrimination deficit as cue distinctiveness decreased.

Method

Subjects

Sixty male albino rats served as subjects. Twenty animals received bilateral lesions at three levels of the hippocampus (dorsal, intermediate, and ventral), 20 rats served as lesioned controls and received bilateral lesions of the amygdaloid complex, and 20 served as unoperated controls. The rats were 3-4 months of age at the time of surgery and were individually housed throughout the experiment.

Apparatus

The apparatus was a modified version of those used by Hull (1950), Raben (1949), and Verplanck (1942). It is consisted of a runway 85 cm long, 15 cm wide, and 25 cm high, constructed of pine planks and painted matt gray. Swing doors were located at the entrance and exit of the goalbox and startbox, respectively. These were operated by lever-pulley systems which enables the experimenter to operate the doors from behind a black curtain. A mirror was situated approximately 180 cm above the runway to enable continuous observation of a rat in the runway.

A ground-glass screen was situated on the end wall of the runway, within the goalbox. The visual stimuli were projected onto this from a slide projector situated behind the runway. The floor of the runway consisted of a sliding tray which served to present the tactile stimuli. The food well was secured just below the ground-glass screen.

The two stimuli from the roughness dimension were rough (R) and smooth (S) stimuli, produced by floors of coarse and fine sandpaper, respectively. The stimuli from the temperature dimension were cold (C) and hot (Ht) stimuli, approximately 5° and 50°C, respectively. C was produced by a metal plate which had a "zig-zag" of copper piping soldered to it, through which ice-cooled water was pumped at regular intervals. Ht was produced by a metal plate heated with electrical heating elements.

The two stimuli from the brightness dimension were a black (B) circle with a white surround and a white (W) circle with a black surround. The area covered by the circle equaled the area covered by the surround.

The two stimuli from the orientation dimension were vertical (V) black and white stripes and horizontal (H) black and white stripes. Each stripe was 3 cm wide, giving a visual angle of 2°28' from the entrance of the startbox into the runway.

The startbox door initiated a Stoelting electric clock (permitting

measurements of 1/100 sec), which was stopped by the interruption of a light beam across the entrance of the goalbox.

Procedure

Surgery took place under sodium pentobarbitone anesthesia. Lesion coordinates were obtained from De Groot (1959), and RF lesions were produced by a Grass LM 3 lesion maker.

Following 3 weeks of recuperation, the rats were placed on a deprivation schedule until their body weights had reduced to 85% of their free-feeding weights. They were maintained at this level throughout the experiment.

Adaptation. For 4 successive days, each rat spent 8 min per day exploring the apparatus.

Pretraining. For the next 4 days, each rat was trained on the runway running response: 10 trials on each of the first 2 days and 16 trials on each of the second 2 days. On every trial, the rat was rewarded with $\frac{1}{4}$ peanut, and the runway response time was recorded.

Discrimination training. The present experiment was designed as the first part of a much broader experiment which required relevant visual stimuli to be combined with irrelevant tactile stimuli, and vice versa. Four rats from each lesion group were required to learn the HV discrimination, two rats having the RS stimuli and two the HtC stimuli irrelevant. Seven rats from each lesion group were required to learn the BW discrimination, three having the RS stimuli and four the HtC stimuli irrelevant. Five rats from each lesion group were required to learn the RS discrimination, two having the HV stimuli and three the BW stimuli irrelevant. Four rats from each lesion group were required to learn the HC discrimination with the BW stimuli irrelevant.

If the stimuli were relevant, then one of the pair of stimuli was consistently reinforced while the other was never reinforced. If the stimuli were irrelevant, then there was no consistent relationship between reinforcement and the stimuli. For each of the stimulus pairs, H, W, Ht, and R were always associated with reinforcement, while V, B, C, and S were never associated with reinforcement.

Each rat had 16 trials per day. The reinforced stimulus occurred on 8 of the trials; half of these were paired with one irrelevant stimulus and half with the other. With these restrictions, the stimuli were presented randomly.

Two learning criteria were used. Learning was complete when the median running time to the unreinforced stimulus was twice as long as the median running time to the reinforced stimulus on (1) any given day, (2) on 2 consecutive days.

After completion of behavioral testing, the rats were sacrificed with an overdose of sodium pentobarbitone. Their brains were removed and placed in 10% Formalin for 2 weeks and then sectioned at 60- μ intervals through the lesions. Every fourth section was kept for examination, and of those, the ones showing the greatest amount of damage were kept for photographing.

Results

Figure 1 shows sections taken through the maximal extent of lesions that are representative of the sort of damage done to the hippocampus and amygdaloid complex.

Figure 2 shows the means of the mean runway response time for hippocampal (H) lesioned, amygdaloid (A) lesioned, and normal (N) rats for each of the 4 days of pretraining.

Kruskal-Wallis analyses yielded significant lesion effects on Day 1 ($p < .02$), Day 2 ($p < .02$), Day 3 ($p < .01$), and Day 4 ($p < .001$).

During pretraining, it was observed that some response times were relatively long because rats tended to explore the runway. This was particularly the case for normal and amygdaloid damaged rats. Indeed, if median running times were used to reduce the

Figure 1. Representative damage to the hippocampus and amygdaloid complex.

effects of these extreme running times, then the difference between lesion groups was markedly reduced. Kruskal-Wallis analysis now showed significant lesion effects only on Day 1 ($p < .01$) and Day 4 ($p < .01$).

A consideration of the data from discrimination training revealed that there was little difference between days taken to reach Criterion 1 and Criterion 2. In view of this, only the data from Criterion 1 will be

Figure 2. Mean runway response times for each of the 4 days of training.

reported. Three of the four animals trained on the HV discrimination failed to reach Criterion 1 within 68 days and were therefore assigned a score of 68. Figure 3 shows the group mean days to criterion for each discrimination problem.

Kruskal-Wallis analyses yielded significant lesion effects for the HV problem ($p < .008$) and the BW problem ($.01 < p < .02$) but not for either of the tactile problems.

Discussion

The faster runway responses of hippocampal lesioned rats relative to controls has previously been found by Wickelgren and Isaacson (1963) but not by Swanson and Isaacson (1967). A tentative explanation for this is reduced exploration by hippocampal lesioned rats. Indeed, it has been previously reported that hippocampal lesioned rats do not explore to the same extent as controls during runway responses (Cohen, 1970; Raphelson et al., 1965; Wickelgren & Isaacson, 1963). This is to a degree supported by the failure of hippocampal lesioned rats to produce extreme running times, commonly associated with exploration, during the early days of pretraining.

A similar interpretation can be used for the results from discrimination training: hippocampal lesioned rats fail to notice stimuli during a prepotent running response, particularly when they are low in distinctiveness. Thus, hippocampal lesioned rats were almost incapable of learning the HV problem, were poor at learning the BW problem, and were no different from controls at learning the tactile problems. It would seem, then, that perseveration is not an inevitable consequence of hippocampectomy. If the deficit in solving the more difficult problems can be regarded as perseveration on the pretrained runway response, then perseveration seems to be dependent on the distinctiveness of the relevant cues.

EXPERIMENT 2

While it has been frequently shown that hippocampal lesioned animals are less than normally distracted by irrelevant stimuli during the performance of a response, Douglas and Pribram (1969) have shown that hippocampal lesioned monkeys are just as distractible as normals when the distractor is similar to the cues "guiding" or associated with the response. What is significant about this study is that the hippocampal lesioned animals failed to habituate to the distractor. If such distractors may be viewed as highly conspicuous stimuli by virtue of their similarity to the guiding stimulus, then it is possible that in Experiment 1, the hippocampal lesioned rats were distracted by and failed to habituate to the irrelevant, but highly distinctive, tactile stimuli, and were therefore deficient at noticing the relevant visual stimuli.

In the light of this, it was decided to determine whether the irrelevant tactile stimuli had, in fact, caused the performance deficit in hippocampal lesioned rats. This was done by merely testing a set of lesion groups on the brightness discrimination with the irrelevant tactile stimuli absent from the task.

Method

Subjects

Twenty male albino rats served as subjects. Eight rats received bilateral lesions at three levels of the hippocampus, six received bilateral lesions of the amygdaloid complex, and six rats served as unoperated controls. The rats were 4-5 months of age at the time of surgery and were individually housed throughout the experiment.

Apparatus

The apparatus was the same as that used in Experiment 1.

Procedure

The procedure was identical to that used in Experiment 1, except that rats were trained only on the BW discrimination without any irrelevant tactile stimuli.

Figure 3. Mean days to criterion for each discrimination problem.

Figure 4. Mean runway response times for each of the 4 days of training.

Results

The sections shown in Figure 1 of Experiment 1 are representative of the lesions produced in the present experiment.

Figure 4 shows the group means of the runway response times for each of the 4 days of pretraining. Kruskal-Wallis analyses yielded significant lesion effects on Day 1 ($p < .01$) and Day 2 ($p < .05$) but not on Days 3 and 4. These results are fairly similar to the pretraining results of Experiment 1.

Since Experiment 1 and 2 were conducted at different points in time, using animals from different colonies, it was felt that a comparison between Experiment 1 rats and Experiment 2 rats was not legitimate. However, if the hippocampal lesioned rats of Experiment 2 showed a deficit on the BW discrimination, then the possible effect of the irrelevant tactile stimuli in Experiment 1 could be disregarded.

Table 1
Group Means and Standard Deviations of Days to Criteria 1 and 2

Group	Criterion 1		Criterion 2	
	Mean	SD	Mean	SD
H	19.50	7.63	26.25	3.73
N	10.50	2.08	12.50	2.67
A	8.00	3.20	10.83	3.50

It was found that there was a discrepancy between days taken to Criteria 1 and 2. Table 1 shows the group means and standard deviations of days to Criterion 1 and Criterion 2. Kruskal-Wallis analyses showed that there was a significant lesion effect for days taken to reach Criterion 1 ($p < .01$) and Criterion 2 ($p < .01$).

Discussion

It is clear that the results of Experiment 1 compare favorably with the results of Experiment 2 with respect to both pretraining and discrimination training. It seems reasonable to assume, then, that the findings of Experiment 1 cannot be explained in terms of a failure by hippocampal lesioned rats to habituate to the highly distinctive irrelevant tactile stimuli. Rather, it would seem that the relevant visual stimuli were too low in distinctiveness to attract the attention of hippocampal lesioned rats as compared to control rats.

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(Received for publication January 18, 1978;
revision accepted July 5, 1978.)