Assessment of the generality of enhanced learning following unilateral lesions of posterior neocortex in rats*

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Sixty albino rats with unilateral lesions of striate cortex, unilateral orbital enucleations, or sham operations were trained on black-white and horizontal-vertical discriminations, with order of problem presentation counterbalanced. Mastery of the initially acquired discrimination greatly enhanced acquisition of the second; however, the previously reported enhancement of acquisition associated with unilateral striate ablation proved to be of limited generality: it occurred only during initial learning of the horizontal-vertical problem.

Unilateral lesions of striate cortex give rise to enhanced rates of acquiring a pattern discrimination in albino rats (Dunsmore, Creel, & Sheridan, 1965; Creel & Sheridan, 1966; Boles & Sheridan, 1969). This phenomenon might have a good deal of generality: pigeons with unilateral tectal lesions exhibit an enhancement of visual discrimination learning (Bingelli, Tschirgi, & Wenzel, 1963); similarly, even though not testing for behavioral enhancement, Krech, Rosenzweig, & Bennett (1960) found that unilateral lesions of somatic cortex in the rat were followed by increased cholinesterase levels in homologous contralateral cortex. These findings suggest that there is an across-the-midline interference that is eliminated by the introduction of unilateral ablations. On the other hand, the findings may be only superficially similar with different functional bases. A good deal of research needs to be done toward determining the exact conditions under which such enhancement occurs before functional identity can be determined.

In the experiment reported here, some limiting conditions of the enhancement phenomenon were established. In all previous experiments a single type of problem (discrimination of horizontal vs vertical stripes) was employed, whereas in the present experiment both horizontal vs vertical and black vs white discriminations were used. Further, each S was required to master both types of discrimination. This was an attempt to delimit behavioral conditions associated with the enhancement effect by making it possible to distinguish between lesion-enhancement effects on general (learning set-like) factors and the specific discrimination learning that is characteristic of a particular problem. The importance of distinguishing between general and specific components of discrimination learning has been underlined by Levinson & Sheridan (1967), who found that a large portion of discrimination learning is general across pattern and black-white problems. Prior learning of a black-white discrimination greatly facilitated acquisition of a horizontal-vertical discrimination, and vice versa. The nature of this general learning is not known, although it might consist of learning to orient to the E-defined relevant cues, to pause at the choice point, to extinguish interfering emotional responses, or to eliminate "spatial hypotheses," etc. In any case, the two aspects of learning might well be differently affected by lesions. Thus, the experiment reported here assessed the influence on the unilateral lesion-enhancement effect of two classes of variation in problem type. These included a variation in the relevant cue dimension (black-white vs horizontal-vertical) and a variation in "general" vs "specific" learning (in the sense that the problem learned second is acquired at a time when general learning has already taken place and consists, therefore, of relatively pure "specific" learning). Since animals were trained in simple avoidance prior to actual discrimination training, it was also possible to determine if the unilateral lesion-enhancement effect might be related to modifications in simple avoidance learning.

SUBJECTS

Ss were 60 male Sprague-Dawley albino rats obtained from Simonsen Laboratories, Gilroy, California. They were approximately 60 days of age at the time of surgery.

APPARATUS

The apparatus, a modified Thompson-Bryant box (Thompson & Bryant, 1955), utilized shock motivation and consisted of a startbox, runway, choice point with two alternative cue doors, and a goalbox. Motivational shock in the startbox and choice areas was a pulsed (½ sec on, ½ sec off) current of about 250 mW, supplied by a Lehigh Valley Electronics sine-wave shocker, Model 1311. A door between the startbox and runway closed a microswitch mounted on the side of the box. When the door was lifted out, the switch was tripped and a tone came on for 10 sec before shock was presented in the startbox. Thirty seconds after the start of the trial, the shock came on and continued to pulse in the runway until the trial was terminated by the animal's running into the goalbox. In front of each goalbox entryway, there was a grid extending approximately 4 in. into the runway. This grid was continuously electrified in front of the incorrect cue door, and that door was locked. Any contact with the grid in front of the incorrect door was counted as an error. Detection of such contact was facilitated by a neon lamp which brightened when current flowed through the erring animal via the grid.

PROCEDURE

Surgery

Equal numbers of Ss were assigned randomly to receive a unilateral striate ablation, a sham operation, or a unilateral orbital enucleation; each S was anesthetized preoperatively with sodium nembutal (1 cc/kg). Striate ablations were accomplished by subpial aspiration; sham operations were identical to the striate ablations, short of cutting the dura mater.

Table 1
Mean Trials to Criterion

	Trials to Criterion			
	Black-White		Pattern	
Surgical Condition	First	Second	First	Second
Striate*	55.4	25.0	38.5	24.6
Controls** (Sham and Enucleate)	47.6	29.1	60.1	21.4

*Each mean has an N of 10; **each mean has an N of 20.*

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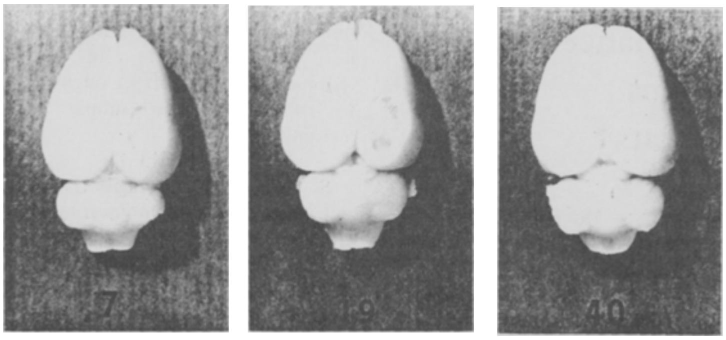

Fig. 1. Dorsal view of brains of three typical striate-lesioned Ss.

Orbital enucleations were done by grasping the eye of the anesthetized rat with a forceps and cutting the orb away with scissors. Laterality of enucleations and ablations was determined randomly, with the constraint that half of the operations be performed on the right side and half on the left. Fourteen days of postoperative recovery time passed before training was started.

Avoidance Training

Ss were trained to run from the startbox to the goalbox upon delivery of a 500-Hz warning tone. Ten seconds were allowed in the startbox and an additional 20 sec in the runway before shock was delivered. Both goalbox doors were completely open during this phase. Criterion for termination of the avoidance training phase was the running of three successive trials without receiving shock. Upon reaching criterion, Ss were shaped to push over gray doors which, first partially then in gradual steps, completely obstructed the goalbox entryways. Warning signal and shock delivery in this phase were on the same schedule as in the avoidance training phase. Door shaping ended when S had successfully pushed over a fully placed door during five successive shockless (and thus errorless) trials.

Discrimination Training

Order of problem and correct cue presentation were counterbalanced across Ss. In the nonenucleated animals, the eye contralateral to the operated hemisphere was covered by an opaque contact occluder which covered the eye to its base; too, stimulus doors containing either the black and white or the horizontal and vertical cues replaced the grey shaping doors, and discrimination training was begun. Twenty-five trials per day were given, with a ~1-min intertrial interval, until 18 correct responses were made in 20 consecutive trials.

Histology

Upon completion of training, operated Ss were perfused in mammalian Ringer's solution followed by 10% formalin. Photographs were made of the dorsal aspects of the brains. Several typical lesions are shown in Fig. 1. In general, lesions were highly uniform. Further, brains were embedded in combined celloidin and paraffin, and sections from 7 to 10 microns in thickness were made, with several sections taken from the dorsal-lateral geniculate nuclei (lgn). Sections were stained in combined luxol fast blue and cresyl violet. Degeneration of the lgn was found to be extensive, although not always complete, in Ss with posterior lesions. Figure 2 shows the degenerated and the undegenerated lgn for one typical ablated S.

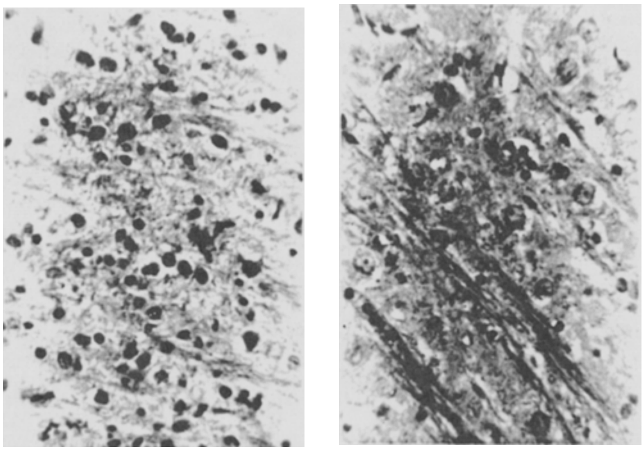

Fig. 2. Sample photographs of degenerated (left side of figure) and undegenerated (right side of figure) dorsal-lateral geniculate nuclei from an animal with a unilateral striate lesion.

With histological materials at hand, behavioral data were reanalyzed to determine if there were behavioral variations associated with variations in extent of lesion. It was clear by inspection that there was no association.

RESULTS

Avoidance Training

Comparison of acquisition rates under the various lesion conditions indicated that enhancement did not occur in simple avoidance learning. Mean trials to three consecutive avoidances were 8.25, 6.30, and 3.95, respectively, for striatally lesioned, sham-lesioned, and enucleated animals; analysis of variance revealed that these means did not differ reliably [$F(2,57) = 1.71$, $p > .05$]. It seems likely, then, that the enhancement effect has its focus in factors associated with discrimination learning. Analysis of discrimination learning data made it possible to specify the focus still further.

Discrimination Training

Since, as in a previous study (Boles & Sheridan, 1969), there was no significant difference between sham-operated and enucleated Ss [$t(38) = 0.13$], the two groups were combined to serve as controls for purposes of analysis. Table 1 presents mean number of trials to criterion for the animals of each of the eight conditions resulting from the combination of two problem types, two problem orders, and two lesion conditions.

Order of problem presentation ($F = 51.5$, $df = 1/112$, $p < .001$), as well as the interaction of all three factors ($F = 5.5$, $df = 1/112$, $p < .025$), yielded a significant F ratio. The reliability of the third-order interaction was due to the striate lesion's strongly influencing the rate of learning of a pattern as a first discrimination, but having no effect on any of the other conditions. The pattern discrimination, when presented first, was learned in significantly fewer trials by striatally lesioned Ss than by controls [$t(28) = 2.27$, $p < .05$, two-tailed].

DISCUSSION

These results confirm the earlier enhancement findings reported above, but indicate sharp limitations in their generality. The unilateral striate-enhancement effect occurs neither with a simple avoidance task nor with a simple black-white discrimination, suggesting that whatever underlies the improvement in acquisition must have to do with the complex analysis involved in pattern discrimination. It is, therefore, paradoxical that facilitation did not occur when the pattern discrimination was learned after the black-white discrimination, for this should be the purest case of specific pattern-discrimination learning. Two hypotheses could account for this finding. First, it might be that "general" learning (as we have described it earlier) somehow interacts with the mechanism of pattern analysis in producing the enhancement effect. If, for example, the lesion improved the saliency of pattern cues, the S might find it easier to abandon incorrect hypotheses, such as position hypotheses, that normally slow pattern acquisition. When pattern training followed black-white training, position hypotheses would already have been eliminated, so lesion-induced saliency of cues might be of little or no value. The second hypothesis stems from the finding that no marked tendency toward enhancement with striate ablation occurred during second-problem acquisition. The second problem is learned so quickly that it might well be difficult to improve on those performances. It would not be unreasonable to suppose that similar considerations apply to the black-white problem, since black-white discriminations are commonly more easily acquired than are pattern discriminations. However, black-white was acquired no more quickly than was the horizontal-vertical task in the present experiment.

The finding of powerful interproblem facilitation between the two types of problems confirms the earlier finding of Levinson & Sheridan (1967), that these discrimination tasks include, besides the aspects specific to the problem type, a general component that is found in both the black-white and the pattern problem. It would be interesting to know to what extent these two problem components react differently to various independent variables. In the present study, any enhancing effects of unilateral striate ablations would appear to be restricted to the specific component of the pattern problem, since the effects are restricted to the latter problem type. Nevertheless, the finding that enhancement failed to occur when the pattern problem was second, coupled with the assumption that second-problem learning is primarily specific-component learning, suggests that both general and specific components somehow interact in the production of such enhancement effects.

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The effect of a stranger's presence on the exploratory behavior of rats*

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A two-group randomized design was used to evaluate the exploration of a five-path elevated maze by 40 male rats in the presence of Ss' caretaker and in the presence of a stranger. Ss explored the maze more in the presence of the caretaker than in the presence of the stranger ($p < .01$). Further analysis indicated that Ss avoided the paths of the maze adjacent to the stranger ($p < .01$), but did not approach the paths adjacent to the caretaker ($p > .01$). The data suggest that the caretaker effect in rats is a function of the presence of a stranger, rather than the presence of S's caretaker, during exploration.

McCall, Lester, & Dolan (1969) reported that rats exploring a modified Hebb-Williams maze spent a greater proportion of the exploration time on the side of the maze adjacent to their caretaker than the side adjacent to a stranger. This effect was attributed to some undetermined characteristic of the caretaker. Further investigation by McCall, Lester, & Corter (1969) indicated that this "preference" for the area of the maze adjacent to the caretaker was mediated by olfactory but not visual cues.

In the McCall et al investigations, both the caretaker and the stranger were present during all exploration trials. Under those conditions it was impossible to determine whether it was the stranger's or the caretaker's presence that was influencing the rat's exploratory behavior. The present experiment was designed to determine if the caretaker effect described in the McCall et al investigations was caused by a tendency of the rats to approach the caretaker, avoid the stranger, or both.

SUBJECTS

The Ss were 40 male 70-day-old rats obtained from Holtzman. Upon receipt, Ss were housed four per cage and placed in an isolated room on ad lib food and water under a 12-h-on/12-h-off lighting schedule. The Ss were handled briefly by the caretaker when approximately 102 days old, but were not exposed to the experimental apparatus prior to testing at 120 days of age.

APPARATUS

The exploration apparatus consisted of a five-path elevated maze similar to that used by Lachman (1965). The five paths, each 1.5-m long and 6.6-cm wide were attached to five adjacent sides of an equilateral dodecagon 38.1 cm in diam.

Because rats tend to explore partially enclosed paths more than completely open paths (Lester, 1969), each path was converted into a tunnel approximately 7.6 cm wide and 22.8 cm high by enclosing the path with 1.2-cm mesh hardware cloth. A piece of wood, 30.4 cm high x 6.6 cm wide, was attached vertically to the end of each path, and guillotine doors were mounted 45.7 cm from the distal ends of the paths to prevent Ss from returning to the start area once a path had been explored.

The entire maze was elevated 91.41 cm above the floor and centered in an empty 5.48 x 2.89 m room located approximately 45 m from the animal colony. A lab stool was placed 76.20 cm from each side of the 12-sided start platform on an imaginary line passing through the center of the platform and running perpendicular to the center path. The room was illuminated by a 60-w red light bulb suspended 96.5 cm over the center of the elevated maze.

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