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VISUAL DISCRIMINATION PERFORMANCE FOLLOWING PARTIAL ABLATIONS OF THE TEMPORAL LOBE: I. VENTRAL VS. LATERAL[1]

MORTIMER MISHKIN AND KARL H. PRIBRAM

Laboratory of Physiology, Yale University and Department of Neurophysiology, Institute of Living, Hartford, Conn.

Recent investigation has demonstrated that extensive bilateral ablation of the temporal lobes of monkeys produces marked impairment in their performance on visual tasks (1, 8, 13). Similar impairment, independent of visual field defects, has not resulted from lesions in other areas (1, 4, 5, 6, 9). The aim of the present study was to extend this analysis of the lesion variable by comparing the effects of partial ablations within the temporal lobe, and to begin an analysis of test and training variables by comparing postoperative measures of initial learning and of retention on a variety of visual problems.

PROCEDURE

Subjects

Eight mature baboons (animals VTH-1 and VTH-4, *Papio papio*; the others, *Papio porcarius*), whose weights ranged from 9 to 12 kg., were divided into three operate groups and subdivided into two training groups.

Surgical Procedures

The present experiment is one of a series (10, 12) in which surgical removals were made with reference to neuronographic charts. On the basis of neuronographic relationships (11) temporal cortex may be divided into three regions: *polar*, related to the anterior and limen insula and to the posterior orbital cortex of the frontal lobe; *lateral*, related to the posterior insula; and *ventral*, related to the anterior (nonstriate) cortex of the occipital lobe. The hippocampus, while not included in any of these divisions, is related afferently to at least two, its anterior extremity to the polar and the major portion to the ventral. This study compares the effects of (*a*) total temporal ablation, or "lobectomy," with those following ablations restricted to (*b*) the lateral and (*c*) the ventral division, the latter including the hippocampus. The effects of restricted polar ablations are not dealt with in this study, since lesions which have included only this portion of the temporal lobe have not produced impairment in visual discrimination performance (10).

Animals were anesthetized with sodium amytal (0.6 cc. per kg. body weight) injected intraperitoneally. The temporal bone was removed and the dura incised over the lateral surface of the temporal lobe. For lobectomies the zygoma was removed as well, in order to expose the pole, and for lobectomies and ventral-hippocampal removals anastogmotic veins were coagulated and severed to permit exposure of the ventral surface. Extirpations were made by subpial resection with a small-gauge sucker. Symmetrical bilateral operations were performed in two stages—the left hemisphere first and then the right—with two to three weeks intervening between each stage.

Lateral temporal resections were performed on LT-1 and -2. An attempt was made to extirpate the superior and middle temporal convolutions, sparing the pole but resecting as much of the banks of the superior temporal sulcus as possible. *Ventral temporal-hippocampal* resections were performed on animals VTH-1, -2, -3, and -4; the attempt was to extirpate the inferior temporal, fusiform, and posterior hippocampal gyri and the hippocampal formation. For the *lobectomies*, performed on T-1 and -2, the two partial ablations (lateral temporal and ventral temporal-hippocampal) were combined, and, in addition, the polar region, including the amygdala, was removed.

Tests

The following tests were used: visual spatial delayed response with opaque screen interposed during delay, and five visual discrimination problems, the paired discriminanda consisting of: (*a*) a plus sign and an outline square, each with an area of 3 sq. in., painted flat black on yellow backgrounds; (*b*) a cut-out circle and a cut-out square, both of wood ½ in. high and 4 sq. in. in top surface area, painted flat black and mounted on yellow backgrounds; (*c*) four horizontal stripes and a diamond, each covering an area of 3 sq. in., painted flat black on white backgrounds; (*d*) red (RT-1) and green (GT-1) Color-Aid papers (Color-Aid Company, New York, N.Y.); and (*e*) light gray (Gray 3) and dark gray (Gray 6) Color-Aid papers.

Three-inch by 4-in. plaques, serving as background for the black patterns, entirely covered by the papers, and used unpainted in delayed response, constituted the interchangeable lids of two choice-cups. The cups were spaced 12 in. apart on a sliding tray and could be concealed from the animal by an opaque screen.

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A one-way-vision screen separated the animal from the *E*.

By the direct method of baiting, animals were trained on delayed response at 0-, 5- and 10-sec. delays in succession; for the retention tests, however, delays below 10 sec. were eliminated. In visual-discrimination training, the first of each pair of discriminanda was made the positive stimulus for all animals. Left and right cups were baited in a predetermined, balanced order. The noncorrection technique was employed and no punishment, other than withholding the peanut reward, was given for errors. Fifty trials a day were presented on a given test until the criterion of 90 correct in 100 consecutive trials was achieved. Postoperatively, if the criterion was not attained in 1000 trials, training on that test was discontinued.

Investigation was made also of extent of visual field, acuity, and responses to familiar objects using the methods described by Chow (4). Briefly, visual fields were determined by observing head-turning and reaching responses to a peanut moved gradually into the left or right, upper or lower, quadrants while the animal was oriented directly ahead; a second test consisted of placing several peanuts in a horizontal row and noting whether the animal consistently neglected those on either side. Visual acuity was evaluated by training the animal to pull in a peanut tied to the far end of a short length of string, and then testing for the same response using threads of successively smaller diameter. One method used for testing reactions to familiar stimuli consisted of presenting pieces of food scattered among several small wood and metal objects; unoperated animals placed in this situation select food, exclusively, after the first or second trial. Additional observations were made using trainer's gloves and net, objects which ordinarily evoke violent avoidance reactions because of methods of handling the animals prior to training.

Training Schedule

Training-Group A. The first animal in each operate group, T-1, LT-1, and VTH-1, received the delayed-response and visual-discrimination problems both preoperatively and after the two-stage bilateral removals.

Training-Group B. The five other animals were trained preoperatively only on delayed response and on the plus-square discrimination; after unilateral operations they were retested on these two problems; following the second-stage removals they were trained on all the tests. Two exceptions were made in this schedule: T-2 received interoperative training on all problems, and VTH-4 was not tested on delayed response either pre- or interoperatively. The procedure of training Group B on the last four discriminations after operation only (T-2 after unilateral and the others after bilateral lesions) permitted a comparison of their initial postoperative learning with the preoperative learning of animals in Group A.

At each stage of the experiment the problems were presented in the order in which they are described in the preceding section. Training following operation was begun two days after the unilateral and two weeks after the contralateral lesions.

The informal tests (extent of visual fields, etc.) involving no special training were presented to all animals in one daily session both before operation and after the unilateral removal. Within the first two weeks following the contralateral operation these tests were again presented in one session and then readministered at semimonthly intervals.

Anatomical Procedures

After the behavioral observations were completed, the animals were sacrificed and their brains embedded in celloidin. Coronal sections were cut at 25 mu with every twentieth section stained in aniline thionin. Reconstructions of the lesions were made from every fourth stained section. The amygdaloid complex, hippocampus, and thalamus were examined microscopically for evidence of damage or degeneration.

Serial reconstructions and cross sections indicating extent and depth of lesions are shown in Figure 1. Deviations from the intended removals may be noted. Thus, in T-1 the posterior portion of the lobe is spared on the right; in LT-2 the posterior half of the middle convolution is minimally involved bilaterally; and in the VTH group the lesions are limited in general to the middle portion of the lobe and remnants of the hippocampus (see Table 1) are spared in each. Lesions which are more extensive than intended appear in the cases of LT-2, where the anterior fusiform gyrus is damaged on the right; VTH-3 and -4, where the middle temporal convolution is invaded bilaterally; and VTH-1, where there is unilateral damage to the pole and amygdaloid complex. It should be noted, however, that these are minor deviations relative to the gross and consistent differences among the three types of lesions.

Table 1 gives the locus and extent of retrograde thalamic degeneration. The anterior half of the lateral geniculate bodies shows some involvement in all T and VTH operates, but in the majority of cases the gliosis is restricted to the ventrolateral tip of the nucleus. This finding supports the suggestion of Bucy and Klüver (2) that degeneration in the ventrolateral horn is due to interruption of a small portion of radiation fibers adjacent to the ventral cortex. More extensive gliosis, involving the posterior half of the geniculate as well, is present in the left hemisphere of T-1 and in the right hemisphere of VTH-3.

The medial geniculate bodies of the T and LT operates are only minimally involved, correlating with the incomplete destruction of the posterior supratemporal plane in these animals.

Clear signs of degeneration are present in restricted loci of the pulvinar. Thus, all animals have gliosis and loss of cells in the posteroventral portion of *n. pulvinaris lateralis*; the T and VTH operates, in the ventral half of *n. pulvinaris inferior*; and the T and LT operates, in the posteroventral portion of *n. pulvinaris medialis*. The latter finding is consistent with results obtained by Chow (3). The first two findings, however, suggest that the cortical projection fields of the posteroventral part of *n. pulvinaris lateralis* and of the ventral part of *n. pulvinaris inferior*,

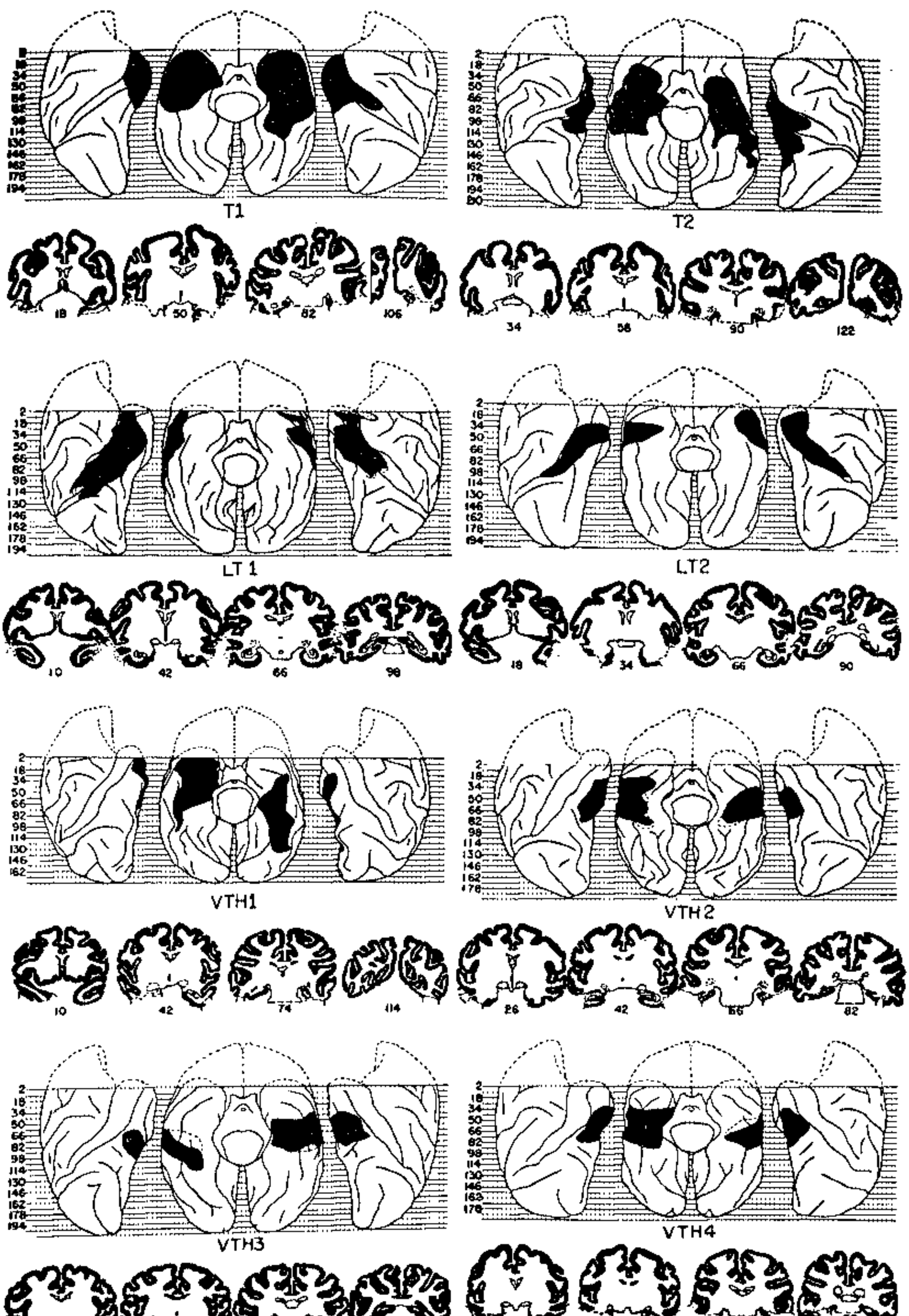

FIG. I. Reconstructions of lesions. The ventral view is bounded on each side by the lateral view of the corresponding hemisphere. Four representative cross sections numbered according to serial position are shown below the reconstructions for each animal. In the reconstructions, black indicates lesion; in the sections, black indicates intact cortex.

TABLE 1

Extent of Damage to Amygdaloid Complex and Hippocampus and Extent of Retrograde Degeneration in Geniculate Bodies and Pulvinar

AC, amygdaloid complex; H, hippocampus; LG, lateral geniculate bodies; MG, medial geniculate bodies; PL, *n. pulvinaris lateralis*; PI, *n. pulvinaris inferior*; PM, *n. pulvinaris medialis*; a, anterior; p, posterior; pv, posteroventral; v, ventral. Extent of damage and of degeneration is indicated as follows: C, almost complete; L, large; S, small; ?, small doubtful; —, none.

ANIMAL	HEMI-SPHERE	AC	H	LG a	MG p	PL pv	PI v	PM pv
T-1	rt.	C	C	S	—	S	S	L
	lt.	C	C	L	?	L	C	L
T-2	rt.	C	C	?	?	L	S	L
	lt.	C	C	?	S	L	C	L
LT-1	rt.	—	—	—	?	S	—	L
	lt.	—	—	—	S	?	—	L
LT-2	rt.	—	—	—	—	L	—	L
	lt.	—	—	—	S	S	—	L
VTH-1	rt.	L	C	?	—	S	S	—
	lt.	—	C	—	—	L	L	—
VTH-2	rt.	—	L	?	—	S	S	—
	lt.	—	L	S	—	S	L	—
VTH-3	rt.	—	L	L	—	L	L	—
	lt.	—	L	S	—	S	S	—
VTH-4	rt.	—	C	S	—	S	S	—
	lt.	—	L	?	—	S	S	—

which in Chow's analysis overlap in the lateral temporo-occipital area, probably extend to the ventral temporal cortex, as well.

RESULTS

Informal Tests

For several days following bilateral removals both T-1 and T-2 were unusually responsive to visual stimuli. Repeated manual and oral examination was elicited even by trainers' gloves and net, stimuli which were clearly aversive previously. This hyperreactivity, appearing also in their responses to the test plaques and thereby temporarily interfering with their performance on delayed response, abated a few days after training was begun. However, repeated indiscriminate selection of food and nonfood objects persisted for nearly three months in both animals. The only other operates that showed alterations on informal testing were VTH-3 and -4, their postoperative responses on the visual field tests indicating a left homonymous defect (found also in T-1 interoperatively) and a central defect, respectively. Animal VTH-4 showed, in addition, a transient failure on the food–nonfood discrimination. No animal with lateral or ventral-hippocampal lesions was altered in its reactions to aversive stimuli.

Delayed Response

Results on the delayed-response problem are shown in Table 2. Animal VTH-4 failed to

TABLE 2

Visual Spatial Delayed Response

Scores are trials and errors preceding 90 correct choices in 100 consecutive trials at delays of 0, 5, and 10 sec. with opaque screen interposed during the delay. For the retention tests delays below 10 sec. are eliminated. A dash indicates that the animal was not tested at that stage of the experiment. A score of 1000 trials denotes failure to acquire the habit within the limits of training.

ANIMAL	DELAY SECS.	PRE-OPERATIVE		INTER-OPERATIVE		POST-OPERATIVE	
		TRIALS	ERRORS	TRIALS	ERRORS	TRIALS	ERRORS
T-1	0	0	0				
	5	60	24	—	—		
	10	0	0			90	42
T-2	0	30	14				
	5	280	94				
	10	390	152	90	17	120	42
LT-1	0	130	24				
	5	10	5	—	—		
	10	0	0			0	0
LT-2	0	20	5				
	5	120	42				
	10	0	0	0	0	0	0
VTH-1	0	100	67				
	5	0	0	—	—		
	10	0	0			0	0
VTH-2	0	0	0				
	5	60	22				
	10	0	0	20	6	0	0
VTH-3	0	0	0				
	5	80	34				
	10	480	112	20	4	0	0
VTH-4	0					30	13
	5	—	—	—	—	1000	303
	10						

meet the criterion within the limits of *initial* postoperative training at the 5-sec. interval. All other animals, trained preoperatively and retested at the 10-sec. delay, showed either complete retention or rapid relearning after both unilateral and bilateral removals.

Visual Discriminations

Results with respect to lesions. In contrast to this generally high level of performance on delayed response, two of the three bilateral operate groups had marked and consistent impairment on the visual discrimination problems. Scores for the plus-square discrimination, on which all animals were trained prior to operation, are presented in Table 3. The five operates retested after unilateral ablation and the two LT operates retested after bilateral ablation relearned in less than 200 trials, or in half the number they scored preoperatively. The six T and VTH bilateral operates, however, failed to meet the criterion within the limit of 1000 trials, approximately three times the median number required before operation.

TABLE 3

Visual Discrimination 1: Plus–Square

Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. A dash indicates that the animal was not tested at that stage of the experiment. A score of 1000 trials denotes failure to acquire the habit within the limits of training.

ANIMAL	PRE-OPERATIVE		INTER-OPERATIVE		POST-OPERATIVE	
	TRIALS	ERRORS	TRIALS	ERRORS	TRIALS	ERRORS
T-1	940	427	—	—	1000	491
T-2	330	126	0	0	1000	502
LT-1	390	118	—	—	190	28
LT-2	300	106	110	49	150	45
VTH-1	320	134	—	—	1000	443
VTH-2	370	145	90	21	1000	308
VTH-3	280	131	0	0	1000	478
VTH-4	440	166	110	51	1000	514

Similar results were obtained on the last four discriminations, as shown in Table 4. Within Group B, animals T-2 and VTH-2, -3, and -4 failed within the limits of postoperative testing to learn any problem but the red-green discrimination, for which they required 400 to 990 trials. The extent of these deficits is indicated by a comparison with Group A's preoperative range of 0 to 100 trials for the same tests. (That Group A's preoperative scores are not biased in the direction of rapid learning is indicated by the fact that Group A's T-1, which obtained the poorest scores on the last four tests, also amassed on the plus-square discrimination more than twice the number of trials required by any other animal.) The only evidence of impairment in the performance of T-2 interoperatively and LT-2 postoperatively, on the other hand, appeared in their initial acquisition scores of 180 and 450 trials, respectively, for the circle-square, and 270 and 400 trials, respectively, for the stripes-diamond discriminations. Both animals attained the criterion immediately on the two remaining problems.

The postoperative scores obtained by the animals in Group A provide some evidence for a greater effect from lobectomy than from ventral-hippocampal removal. Animal T-1

TABLE 4

Visual Discriminations 2 to 5

Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. T-2's interoperative learning scores are placed in parentheses in the preoperative column. A dash indicates that the animal was not tested at that stage of the experiment. A score of 1000 trials denotes failure to acquire the habit within the limits of training. Pre = preoperative; Post = postoperative; T = trials; E = errors.

ANIMAL	CIRCLE-SQUARE				STRIPES-DIAMOND				RED-GREEN				LIGHT GRAY-DARK GRAY			
	Pre		Post		Pre		Post		Pre		Post		Pre		Post	
	T	E	T	E	T	E	T	E	T	E	T	E	T	E	T	E
T-1	100	42	760	365	40	17	1000	410	0	0	750	305	20	13	1000	459
T-2	(180)	(76)	1000	465	(270)	(96)	1000	466	(10)	(5)	540	142	(10)	(1)	1000	506
LT-1	40	13	20	4	20	15	0	0	0	0	0	0	20	13	0	0
LT-2	—	—	450	187	—	—	400	168	—	—	0	0	—	—	0	0
VTH-1	10	5	1000	366	0	0	400	91	0	0	10	7	0	0	0	0
VTH-2	—	—	1000	463	—	—	1000	447	—	—	400	140	—	—	1000	407
VTH-3	—	—	1000	491	—	—	1000	491	—	—	990	456	—	—	1000	417
VTH-4	—	—	1000	500	—	—	1000	424	—	—	790	322	—	—	1000	417

relearned two discriminations only (circle-square and red-green), and these with marked deficits, whereas VTH-1 relearned three problems, two of them (red-green and light gray–dark gray) immediately. Both operates, however, were markedly inferior to LT-1, which showed complete retention on all four tests.

The results for the eight animals are consistent in demonstrating severe impairment in discrimination performance following both bilateral lobectomy and bilateral ventral-hippocampal ablation, but only slight deficit following either unilateral lobectomy or bilateral lateral surface resection.

Results with respect to training groups. Comparison of the scores of Groups A and B indicates that the procedure of training animals initially after operation yielded deficits more frequently than did testing for retention. Thus, LT-2 showed impairment in the initial learning of two of the problems on which LT-1 had complete retention. Similarly, VTH-2, -3, and -4 were markedly deficient in their original acquisition on all discriminations, whereas VTH-1 relearned two tests immediately. It is unlikely that factors other than variation in training are accountable for these differences within operate groups since animals with the same lesions obtained identical scores when conditions of training were held constant (postoperative retention on the plus-square discrimination). Comparisons between initial learning and retention following bilateral lobectomy are not possible since both T-1 and T-2 received prior training on all tasks. However, T-2's interoperative scores, indicating slight deficit in original learning but none in retention, corroborate the results obtained for the lateral and ventral-hippocampal operates.

Results with respect to the test series. In addition to demonstrating selective effects of the lesions and of the training procedures, the results suggest that the occurrence and extent of deficit are functions also of a third variable, viz., test "difficulty." Difficulty is here defined in terms of the preoperative learning rates of the three animals in Training-Group A, their trial-and-error scores decreasing consistently in the order: plus-square, circle-square, stripes-diamond, light gray–dark gray, and red-green. Postoperatively, all six T and VTH operates failed to learn the most difficult discrimination (plus-square), whereas none failed the least difficult (red-green). Moreover, the three animals (T-2 interoperatively, LT-2 and VTH-1 postoperatively) that showed partial impairment on the last four tests scored deficits consistently on the more difficult problems (circle-square and stripes-diamond), and no deficits on the less difficult (light gray–dark gray and red-green).

DISCUSSION

The behavioral alterations observed in T-1 and T-2 following bilateral temporal lobectomy confirm results obtained in the monkey by Klüver and Bucy (8) and Blum, Chow, and Pribram (1). The effects include, consistently, approach to previously aversive stimuli, indiscriminate selection of food and inedible objects, and impaired performance on visual discrimination tasks. The absence in animal T-2 of demonstrable defects either in acuity or in visual fields, and, more directly, the finding of only minimal degeneration in this animal's lateral geniculate bodies support an earlier conclusion (1) that the behavioral effects of temporal lobectomy cannot be ascribed to geniculo-striate damage.

The analysis of the effects of subtotal temporal lobe lesions shows that, whereas responses to aversive stimuli were unaltered following any of the partial resections, marked and sustained discrimination impairment independent of field defects was produced by the bilateral ventral-hippocampal ablation. In contrast, little or no discrimination deficit was obtained after any form of unilateral damage or after bilateral resection of the lateral surface.

An account of the discrimination impairment in terms of the interrelationships among the lesion, test, and training variables may be summarized as follows: With respect to retention and relearning, bilateral lobectomy produced deficits on all discriminations, bilateral ventral temporal-hippocampal ablation on difficult tasks only, and bilateral lateral surface resection and unilateral lobectomy, none. With respect to initial postoperative learning, bilateral ventral-hippocampal ablation produced deficits on all discriminations, bilateral lateral surface resections and unilateral lobectomy, on difficult tasks only.

Whereas these results indicate correlations between deficit and (*a*) lesions, (*b*) training procedures, and (*c*) test difficulty, the last relationship can only be tentative, since the test order of decreasing "difficulty" corresponds closely to the sequence in which the tests were administered. Thus, the trend toward more rapid learning on successive discriminations may have been a function of cumulative transfer effects and, postoperatively, of time elapsed since operation, rather than of a decrease in difficulty per se.

The failure of the animals with lobectomy and ventral-hippocampal lesions to react differentially to paired patterns, colors, or shades of gray appeared without concomitant impairment on delayed response. Previous results on delayed-response performance following temporal lobe ablations have been inconclusive. Blum *et al.* (1) reported complete failure to relearn the problem in one lobectomized macaque, whereas Jacobsen and Elder (7) reported perfect retention in an animal with a comparable lesion. Similarly, Chow (4) found a retention deficit in one monkey with a lateral surface extirpation but not in another. In the present experiment one baboon in eight showed impairment, and this animal, tested for initial learning, had only the partial ventral-hippocampal removal. The combined results suggest that temporal lobe lesions interfere only occasionally with performance on delayed response, and that these deficits, unlike discrimination deficits, are not consistently related either to the locus or extent of lesion or to the schedule of training.

SUMMARY

1. Two baboons with temporal lobectomy, two with lateral surface ablations, and four with ventral surface-hippocampal ablations were split into two training groups matched on the basis of lesion. One group was tested for postoperative retention, the other primarily for initial postoperative learning, on a series of visual discriminations. All animals received, in addition, the delayed-response test, visual field and acuity tests, and tests of reactions to familiar objects.

2. Following the behavioral observations the animals were sacrificed, the lesions verified, and the thalami examined for retrograde degeneration. The degeneration findings suggested an extension of the known projection field of the pulvinar.

3. Analysis of the behavioral results showed that ventral-hippocampal ablation, as well as lobectomy, in contrast to lateral resection (or any form of unilateral lesion) produced marked impairment in visual discrimination performance. Deficits occurred more frequently in initial learning than in retention and appeared to be related to test difficulty, confounded with order. With the exception of the lobectomized animals' increase in approach responses to inedible and previously aversive objects, no consistent postoperative effects were obtained with any of the other tests.

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