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VISUAL DISCRIMINATION PERFORMANCE FOLLOWING PARTIAL ABLATIONS OF THE TEMPORAL LOBE: II. VENTRAL SURFACE VS. HIPPOCAMPUS[1]

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This study is the second in a series dealing with the effects of partial ablations of the temporal lobes on visual discrimination performance. Results of the initial experiment (5) demonstrated that marked impairment on visual discriminations may be produced by lesions limited to the ventral portions, including the hippocampal formation and the cortex on the ventral surface, as compared with lesions of the lateral portions of the lobe. The present investigation was designed to delimit further the locus and extent of damage necessary to produce gross decrement in performance. To this end, comparisons were made of the effects of separate ablations of ventral temporal cortex and of the hippocampal formation.

An additional aim of the experiment was to determine whether or not the occurrence and degree of deficit vary directly as a function of test difficulty. Evidence suggesting such a relationship was presented in the earlier study; however, the results were not conclusive since the postoperative deficits appeared to be related also to the particular sequence in which the tests were administered. In the present experiment, therefore, the sequence of presentation was controlled, in order to permit an evaluation of the effects of test difficulty per se.

METHOD

Subjects

Eight immature male monkeys (*Macaca mulatta*), ranging in weight from 3 to 7 kg., were divided into three operate groups and subdivided into two training groups.

Surgical Procedures

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 those animals that were to receive ablations of the anterior portions of the lobe, the zygoma was removed in order to expose the pole; for all other operates anastomotic veins were coagulated and severed at their entrance into the lateral sinus to permit exposure of the ventral surface. Cortex was removed by subpial aspiration with a small-gauge sucker. Symmetrical bilateral operations were performed in two stages, left hemisphere first, with two to three weeks separating the unilateral removals.

Ventral surface lesions. An attempt was made to resect the inferior temporal, fusiform, and posterior hippocampal gyri in animals VT-1,-2, and-3.

Hippocampectomies. Resection of the hippocampal formation was attempted through an incision in the inferior convolution in animals H-1 and H-2, and via the amygdaloid complex in animal HA.

Control lesions. Resections that controlled for the incidental damage associated with the hippocampectomy procedures were performed on animals HC and HAC. In HC, the control for H-1 and H-2, a scalpel incision was made in the inferior convolution and extended into the temporal horn of the lateral ventricle; but the hippocampal formation itself, visible in the floor of the ventricle, was not resected. In HAC, the control for HA, the periamygdaloid cortex and amygdala were resected, but the hippocampal formation, visible posteriorly, was left intact. In order to control also for extent of lesion in the H and VT operates, the resection in HAC was extended to include the lateral polar cortex and the superior temporal convolution including the supratemporal plane.

Tests

Tests included the direct method of delayed response with a sliding panel interposed during delay, and five visual discriminations, the paired discriminanda consisting of: (*a*) an inverted and an erect equilateral triangle, each with an area of 2 sq. in. and painted flat black on yellow backgrounds; (*b*) a cut-out circle and a cut-out square, both of wood ½ in. in height 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

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Company, New York, N. Y.); and (*e*) light gray (Gray 3) and dark gray (Gray 6) Color-Aid papers.

Preoperatively, animals were trained on delayed response at 0-, 5-, and 10-sec. delays presented in succession; postoperatively, only the 10-sec. interval was used.

On the first discrimination, the inverted triangle was the rewarded stimulus for all animals. On the last four discriminations, however, the first stimulus of each pair was made positive for four of the animals (VT-2, H-1, H-2, HC) and negative for the other four. This procedure was adopted to determine whether or not the rapid preoperative learning of these tasks in the previous study (5), in which the rewarded stimuli were the same for all animals, could have been due to an initial preference for the positive discriminanda.

The experiments were conducted in an air-conditioned, soundproof room. The testing cage faced a sliding panel which, when raised, disclosed two rectangular cups spaced 12 in. apart. Each cup was covered by a 3-in. by 4-in. plaque—unpainted for delayed response, painted as background for the black patterns, and entirely covered by the papers—which the animals learned to displace to obtain the concealed reward. A one-way-vision screen separated the animal from *E*. Daily testing sessions consisted of 30 trials a day with left and right cups baited in a predetermined balanced order. The noncorrection technique was employed, and no punishment, other than withholding the peanut reward, was given for errors.

In addition to the delayed response and visual discrimination tasks, other procedures were used for evaluating changes in extent of visual field, visual acuity, and reactions to food vs. nonfood and aversive vs. indifferent stimuli. These informal tests, involving no special training, have been described by Chow (3) and were outlined in the previous paper of this series.

Training Schedule

Preoperatively, all animals were trained to a criterion of 90 correct in 100 consecutive trials on delayed response, inverted-erect triangle, circle-square, stripes-diamond, red-green, and light gray-dark gray, in succession. Two weeks postoperatively, this order of presentation was maintained the *same* for four animals—VT-2, VT-3, H-2, and HA—and *reversed* for four—VT-1, H-1, HC, and HAC. The two training groups will be designated group S and group R, respectively.

Determinations of extent of visual field, visual acuity, and reactions to incedible and aversive objects were made in one daily session before operation. These tests were then repeated once after the unilateral removals, once within the first two weeks following the contralateral removals, and at semimonthly intervals thereafter.

Anatomical Procedures

Upon completion of the [illegible] animals were [illegible] [illegible] and the [illegible] Every [illegible] section was [illegible] through [illegible] stained section was used to reconstruct the lesions. The thalami, as well as the structures surrounding the ablation, were examined microscopically for evidence of damage or degeneration.

Reconstructions of the lesions and representative cross sections are presented in *Figure* 1. The operative results on two animals, HC and H-2, show considerable deviation from the intended removals. In both cases, in addition to deep incisions through the inferior convolution, large portions of ventral cortex are ablated bilaterally; and in HC, the lateral cortex of the left hemisphere is extensively damaged, apparently as a result of postoperative dural adhesions. The resections performed on the six other animals, however, conform in general to the experimental plan. Relatively minor deviations may be noted: slight damage to the posterior portion of the hippocampal formation in the left hemisphere of VT-1 (see Table 1); bilateral sparing of the posterior portion of the hippocampal gyrus in VT-2; invasion of ventral occipital cortex bilaterally in VT-2 and in the right hemisphere of VT-3; ablation of the right hippocampal gyrus but sparing of the posterior portion of the left hippocampal formation in HA; and incomplete destruction of the amygdaloid complex in HAC.

Retrograde thalamic degeneration findings are given in Table 1. Whereas the extensive bilateral involvement of the lateral geniculate bodies in H-2 is due in part to direct damage, gliosis and fading of cells in the ventrolateral horn, found also in VT-3 and HC, appear to be the result of damage to the ventral portion of the optic radiations. Degeneration in the medial geniculate bodies is present only in HAC, the one operate with a lesion of the supratemporal plane. In contrast to these isolated instances of geniculate involvement, pulvinar degeneration is found in all animals. The six operates with ventral surface damage or with incisions through the inferior convolution VT-1, -2, -3; H-1, -2; and HC, have degeneration in the posteroventral portion of *n. pulvinaris lateralis*; and the majority of these animals have degeneration also in the ventral portion of *n. pulvinaris inferior*. In the two remaining operates, HA and HAC, the posterior tip of *n. pulvinaris medialis* is involved, probably as a result of lateral polar resections (2). These findings of retrograde degeneration agree in detail with those reported for baboons (5).

RESULTS

Informal Tests

Transient visual field defects opposite the side of lesion were found in HC and H-2 following the unilateral operation, and again in H-2 after the contralateral operation. Animal H-2's transient partial anopsia may account for the [illegible] examination of food and nonfood that it exhibited for [illegible] food discrimination [illegible]

The two animals with ablations of the [illegible]

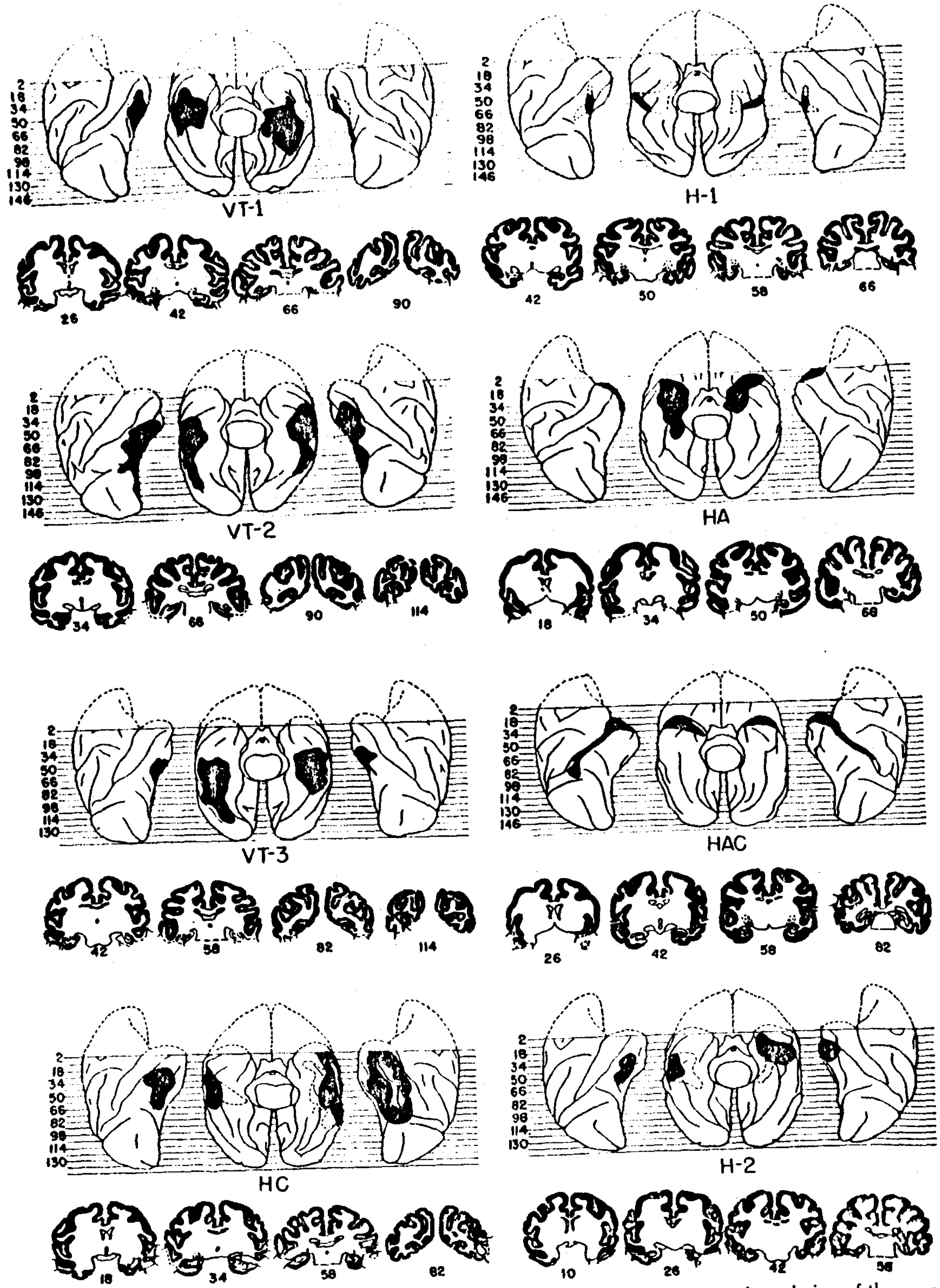

FIG. 1. Reconstructions of lesions. The ventral view is bounded on each side by the lateral view of the corresponding hemisphere. Four representative cross sections numbered according to serial position are shown below the reconstructions for each animal. In the reconstructions black indicates lesion; dashed lines in the vicinity of lesion indicate deep damage. 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

ANIMAL	HEMI-SPHERE	AC	HF	LG a	MG p	PL pv	PI v	PM pv
VT-1	rt.	—	—	—	—	S	—	—
	lt.	—	L	—	—	?	—	—
VT-2	rt.	—	—	—	—	S	?	—
	lt.	—	—	—	—	S	—	—
VT-3	rt.	—	—	S	—	S	L	—
	lt.	—	—	S	—	S	S	—
H-1	rt.	?	C	—	—	S	?	—
	lt.	—	C	—	—	?	S	—
HA	rt.	C	C	—	—	—	—	S
	lt.	C	S	—	—	—	—	S
HAC	rt.	L	—	—	S	—	—	S
	lt.	L	—	—	S	—	—	?
HC	rt.	—	?	S	—	L	?	—
	lt.	—	—	L	—	S	S	—
H-2	rt.	—	C	C	—	L	L	—
	lt.	?	C	L	—	L	S	—

Note: *AC*, amygdaloid complex; *HF*, hippocampal formation; *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.

TABLE 2

Visual Spatial Delayed Response

ANIMAL	GROUP	PREOPERATIVE		POSTOPERATIVE	
		Trials	Errors	Trials	Errors
VT-1	R	290	69	20	5
VT-2	S	130	32	0	0
VT-3	S	740	240	330	68
H-1	R	350	85	50	11
HA	S	170	40	140	47
HAC	R	200	57	50	24
HC	R	210	60	0	0
H-2	S	200	57	50	24

Note: Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. Preoperative trials and errors at 0-, 5-, and 10-sec. delays are combined into one total score, whereas postoperative trials and errors are for the 10-sec. delay.

and amygdaloid complex showed gross alterations in their responses to previously aversive stimuli. Trainer's gloves and net not only failed to evoke avoidance reactions, but frequently elicited manual and oral examination instead. The behavior of animal HAC, in which the destruction of the amygdaloid complex was incomplete, reverted to normal within the first few postoperative weeks; in animal HA, however, these behavioral alterations persisted until it was sacrificed five months after operation.

Delayed Response

Results for delayed response are given in Table 2. Retention tests were conducted at only the 10-sec. interval; nevertheless, all eight operates attained criterion in less than the total number of trials and errors they required preoperatively. Whereas there was no consistent relationship between rate of relearning and locus of lesion, the animals (group R) that received delayed response as the last postoperative test generally had greater saving than those (group S) that received delayed response first.

Visual Discriminations

Lesions. Results for the three pattern discriminations are shown in Table 3 and those for the red-green and light gray–dark gray discriminations are given in Table 4. The scores obtained by HC and H-2 cannot be used for the evaluation of the effects of selective damage since both animals had unintentionally extensive ablations (see *Anatomical Procedures*). Rated in terms of degree of impairment (measured as the absolute difference between postoperative and preoperative scores), these two operates rank first and third, respectively, in the series of eight. Both failed to relearn or were retarded by 600 trials in relearning each of the three pattern discriminations. In addition, operate H-2 showed a 400 to 500 trial deficit on the differential reactions to red and green and to light gray and dark gray.

Comparisons among the six remaining animals indicate that the three with ventral surface ablations (VT-1, -2, and -3) showed greater impairment than the three with lesions elsewhere in the temporal lobes (H-1, HA, and HAC). Thus, within training group R, animal VT-1 failed both the inverted-erect triangle and circle-square discriminations and was retarded by more than 600 trials in relearning the stripes-diamond discrimination. Operates H-1 and HAC, on the other hand, relearned these tasks with deficits no greater than 150 trials, and in the case of the inverted-erect triangle discrimination, with savings in terms of errors. Similarly, in training group S, VT-2 failed in 1,000 trials and VT-3 required

TABLE 3

Visual Discriminations: Patterns

ANIMAL	GROUP	INVERTED TRIANGLE–ERECT TRIANGLE				CIRCLE–SQUARE				STRIPES–DIAMOND			
		Pre		Post		Pre		Post		Pre		Post	
		T	E	T	E	T	E	T	E	T	E	T	E
VT-1	R	240	(89)	1000	(399)	150	(79)	1000	(398)	80	(26)	740	(53)
VT-2	S	200	(100)	1000	(502)	60	(20)	370	(106)	10	(9)	0	(0)
VT-3	S	200	(104)	890	(368)	200	(97)	370	(112)	0	(0)	10	(5)
H-1	R	210	(98)	220	(49)	50	(16)	200	(42)	10	(6)	140	(44)
HA	S	350	(146)	240	(54)	180	(74)	40	(4)	0	(0)	0	(0)
HAC	R	160	(76)	170	(40)	150	(69)	220	(87)	80	(35)	110	(54)
HC	R	270	(122)	1000	(253)	80	(21)	680	(228)	0	(0)	540	(219)
H-2	S	560	(259)	1000	(492)	100	(44)	1000	(456)	20	(12)	1000	(475)

Note: Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. A score of 1000 trials denotes failure to attain the criterion within the limits of training. *Pre* = preoperative; *Post* = postoperative; *T* = trials; *E* = errors (in parentheses).

TABLE 4

Visual Discriminations: Hue and Shades of Gray

ANIMAL	GROUP	RED-GREEN				LIGHT GRAY–DARK GRAY			
		Pre		Post		Pre		Post	
		T	E	T	E	T	E	T	E
VT-1	R	0	(0)	0	(0)	30	(27)	10	(4)
VT-2	S	0	(0)	0	(0)	0	(0)	0	(0)
VT-3	S	0	(0)	0	(0)	10	(4)	0	(0)
H-1	R	0	(0)	0	(0)	0	(0)	0	(0)
HA	S	0	(0)	0	(0)	0	(0)	0	(0)
HAC	R	0	(0)	0	(0)	10	(5)	0	(0)
HC	R	0	(0)	0	(0)	20	(14)	0	(0)
H-2	S	0	(0)	530	(258)	0	(0)	400	(171)

Note: Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. *Pre* = preoperative; *Post* = postoperative; *T* = trials; *E* = errors (in parentheses).

almost 900 trials to relearn the inverted-erect triangle discrimination; both were retarded by 200 to 300 trials in relearning the differential reactions to circle and square; in contrast, HA attained criterion on these tasks with savings of more than 100 trials over its preoperative scores.

Sequence of presentation. Analysis of the effects of differences in postoperative training procedures shows that reversing the preoperative order of presentation resulted consistently in greater impairment on tasks intermediate in the sequence (circle-square, stripes-diamond) than did maintaining the preoperative order. Thus, among the ventral-temporal operates, the animal in group R (VT-1) failed completely to relearn the pattern discrimination that both group S animals (VT-2, VT-3) relearned with deficits; and it was severely retarded in relearning the pattern discrimination that both group S animals retained. Similarly, among the three operates without ventral-temporal ablations, both animals in group R (H-1, HAC) were slightly retarded in relearning pattern discriminations that the animal in group S (HA) relearned with considerable saving.

Tests. The preceding comparisons between lesion groups and between training groups are based on the data for the three pattern discriminations only. Scores for the red-green[2] and light gray–dark gray discriminations do not differentiate among the groups since all but one operate showed complete retention on both. The occurrence and degree of deficit were thus observed to vary with the particular task employed, irrespective of the effects of operations or training schedules.

If the five discriminations are ranked in terms of the range of trials required by the eight animals to attain criterion on each task preoperatively, the following order is obtained: inverted-erect triangle (160–560), circle-square (50–200), stripes-diamond (0–80), light gray–dark gray (0–30), and red-green (0). Although the reward value of the last

[2] On the day in which an animal attained criterion on the red-green discrimination, it received two transfer tests presented for ten trials each: (*a*) pale red–bright green and (*b*) bright red–pale green. The four Color-Aid papers used were RT2, GHUE, RHUE, and GT2, respectively. Despite reversals of brightness values, errorless transfer was shown by all animals.

four stimulus pairs was reversed for half the animals, the arrangement in terms of preoperative learning rates is the same for all, and is used tentatively to define an order of test difficulty. Postoperatively, this arrangement of the tests is maintained, with the greatest number of failures appearing on the inverted-erect triangle discrimination, numerous instances of less severe deficit on the circle-square and stripes-diamond discriminations, and only a single instance of impairment on light gray–dark gray and on red-green. The observed relationship between deficit and test difficulty is remarkably consistent for all animals, whether trained, postoperatively, from the most through the least difficult tasks (group S) or in the reverse order (group R).

DISCUSSION

The severe discrimination impairments observed in the two operates with deep and unintentionally extensive ventral temporal lesions serve to confirm, and extend to other monkeys, results previously reported for baboons. Analysis of the effects of more restricted ablations indicates that damage to ventral cortex alone (three animals) also produced marked deficits on the discriminations. Removal of the hippocampus, on the other hand, either through a minimal incision in the inferior convolution, or through the amygdaloid complex (one animal each), resulted in little or no impairment. Finally, only slight deficit followed combined resection of the polar region and the superior lateral surface (one animal). The results demonstrate that the integrity of the cortex on the ventral surface, as compared with that of other regions in the temporal lobe, is of especial importance for visual discrimination performance.

The degree of impairment produced by the operations varied markedly with the particular task employed. The pattern discrimination that required the longest preoperative learning time yielded the largest number of severe postoperative deficits; the hue discrimination, which required the shortest preoperative learning time, disclosed but a single deficit. These results, obtained with sequence of presentation controlled, confirm the earlier finding of a direct relationship between extent of deficit, as measured in absolute terms, and degree of task difficulty. Order of presentation and test difficulty did interact, however; tasks intermediate in the sequence were relearned more rapidly by animals trained first on the most difficult tasks than by animals trained first on the least difficult tasks.

Deficit on the discriminations was not consistently associated either with retardation in relearning delayed response or with defects in visual fields or acuity. It is further significant that the two operates with amygdala lesions, while relatively unimpaired in their discrimination performance, showed marked changes in their reactions to aversive stimuli. Alterations in avoidance behavior have been observed previously following damage to the amygdala (6, 7); such changes did not appear following lesions restricted to the ventral surface.

It appears from these results that ablation of the ventral cortex of the temporal lobe interferes selectively with performance on visual discriminations, and that damage to this area is primarily responsible for the discrimination impairment shown by animals with temporal lobectomy (1, 4, 5).

SUMMARY

1. Eight macaques were trained preoperatively on a series of visual discriminations of varying difficulty. In addition, they were tested on visual-spatial delayed response and on tasks designed to evaluate extent of visual fields, visual acuity, and reactions to aversive visual stimuli.

2. Following the initial training, ventral temporal cortex was ablated bilaterally in three animals, the hippocampal formation was removed bilaterally in three others, and two animals received operations that served to control for cerebral damage incidental to the hippocampectomy procedures. All animals were then retested on all problems, with the visual discriminations presented in two different sequences.

3. Post-mortem examination of the brains indicated that one hippocampal and one control lesion invaded extensively the area removed in the ventral temporal operates; the six other lesions were accurately placed. Thalamic degeneration findings were con-

sistent with those previously reported for baboons.

4. Ventral temporal resections produced markedly greater impairment on the visual discriminations than did the hippocampal or control operations. The number of post-operative failures and the amount of retardation varied directly with the difficulty of the discriminations, irrespective of the order in which they were presented. Deficit on the visual discriminations was not correlated with impairment on any other task.

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