IMPAIRMENTS IN SELECTIVE ATTENTION TO VISUAL STIMULI IN MONKEYS WITH INFEROTEMPORAL AND LATERAL STRIATE LESIONS

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Bilateral removal of inferotemporal (IT) cortex in monkeys produces a severe impairment in discrimination learning limited to the visual modality (see Mishkin[12] for a review of these findings). While the visual deficits produced by IT lesions cannot be readily attributed to sensory losses[7,16] the nature of the disorder remains unclear. Chow and Orbach[5] attempted to determine whether IT ablation is associated with losses in selective attention by use of a discrimination task in which visual stimuli are briefly exposed, but found no impairment in IT monkeys in this situation. Subsequently, it was shown that the failure to obtain visual losses in IT monkeys under these conditions could be attributed to preoperative overtraining[6,13]. The present experiment reinvestigated the question of selective attention losses in IT monkeys by methods which avoid the problem of preoperative overtraining. In this experiment, monkeys with IT ablation, along with their controls — monkeys with lateral striate (LS) ablation and unoperated monkeys — were first trained to discriminate between two visual stimuli. Irrelevant features were then added to the stimuli in a series of tests in which the animals were required to relearn the discrimination problem. If the IT animals were to be retarded in relearning the discrimination, this might imply a loss in the ability to selectively attend to or abstract the relevant visual features.

METHODS

Subjects. Twelve rhesus monkeys (*Macaca mulatta*), ranging in weight from 5.3 to 11.4 kg served as subjects; 4 had bilateral ablation of IT cortex; 4 had bilateral ablation of LS cortex, and the remaining 4 were unoperated controls. Each group contained an equal number of males and females. The animals were housed in individual cages where they had free access to water and were fed Purina Monkey Chow (45 cal/kg body wt/day) supplemented occasionally with fresh fruit. All the monkeys had previously served as subjects in pattern equivalence[1] and size transposition[2] experiments.

Surgery and histology. Surgery had been conducted approximately 10 months prior to the present experiment. Details of the surgical procedures are described

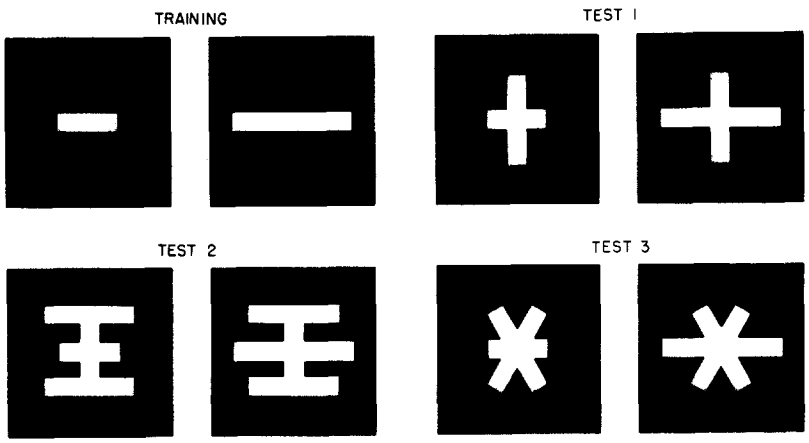


Fig. 1. Stimuli used in discrimination training and in the 3 tests. The left-hand member of each pair was positive. While the plaques were gray, they are illustrated here in black to make the stimuli clearer.

elsewhere[1]. Briefly, IT and LS cortex were removed by subpial aspiration with a narrow-gauge sucker through openings rongeured in the temporal and occipital bone.

Following the completion of testing, the operated monkeys were anesthetized with sodium pentobarbital and then perfused with 0.9% saline followed by 10% formalin. Their brains were then removed and prepared for embedding in celloidin. Coronal sections 40 μ in thickness were cut, and every tenth section was stained with thionin.

Apparatus and stimuli. The animals were trained and tested in a standard, 2-choice Wisconsin General Test Apparatus (WGTA), similar to one in which they had previously been tested[1].

In discrimination training the stimuli consisted of a 1.5-in. bar (positive) and a 3-in. bar (negative), each 0.5-in. in width (see Fig. 1). In subsequent tests, bars 2.25-in. in length and 0.5-in. in width were added to plaques containing the training stimuli, as shown in Fig. 1. The stimuli were constructed of white paper pasted on gray poster-board plaques, 4-in. sq. Several copies of each stimulus were used and were changed from day to day.

Procedure. The animals were first trained to discriminate between the 1.5-in. bar and the 3-in. bar, both of which were presented on each trial. Displacement of the plaque with the 1.5-in. bar was rewarded with half a peanut, while no reward was given for displacement of the plaque with the 3-in. bar. Thirty trials were administered daily, using non-correction technique, and the spatial position of the stimuli was determined by a Gellerman series[8]. Training was terminated upon attainment of 90 correct responses in 100 consecutive trials. On the day following the completion of training, *S*s were presented with the first pair of test stimuli and trained to discriminate between the test stimulus containing the 1.5-in. and the one containing the 3-in. bar, according to the same procedures used in discrimination training. Following reattainment of the criterion, the second pair of test stimuli and finally

the third pair of test stimuli were presented in the same manner as in training and in test 1.

RESULTS

The mean number of trials required by each of the groups to attain the discrimination learning criterion and to reattain the criterion in each of the subsequent tests is shown in Table I. The IT monkeys were significantly retarded in learning the original

TABLE I

MEAN TRIALS TO CRITERION OF N, LS AND IT GROUPS IN DISCRIMINATION TRAINING AND IN TESTS

Group	*Training*		*Test 1*		*Test 2*		*Test 3*	
N		293.3		90.8		150.5		53.8
	N.S.		0.025*		0.01*		0.05*	
LS		379.2		807.5		1246.5		440.0
			0.025*		0.05*		N.S.	0.025*
IT		1049.8		403.5		262.3		807.3

* $>$ P, by Dunnett multiple-comparison t-tests; $df = 9$ in all tests.

discrimination problem. Although the LS animals as a group required more trials to learn the discrimination than did the normal animals, three of the four LS animals' scores fell within the normal range, and the LS group was not reliably impaired. Nor did the LS group differ reliably from the IT group in learning. In the first test all the unoperated animals required less trials to relearn the discrimination than they did in training. This was also the case for the IT monkeys; however, compared to the normal animals, these animals still were significantly retarded in meeting the criterion. The LS animals were also reliably impaired in relearning, compared with the normal animals, although they did not reliably differ from the IT animals. Moreover, unlike any of the other *S*s, the LS *S*s all required *more* trials to relearn in test 1 than they required in training. In the second test the IT monkeys as a group needed less trials to relearn the discrimination than they did in the first test, and they were not significantly impaired. The LS group, on the other hand, performed on the average worse than they did in the previous test, and their impairment in relearning was highly significant. Moreover, the LS group required significantly more trials to meet the criterion than did the IT group in test 2 ($P < 0.01$, Dunnett multiple-comparison t-test). In the last test the IT group performed worse than they did in the 2 previous tests, and they were significantly retarded in relearning compared to the unoperated group, but not relative to the LS group. Although the LS monkeys performed better than they had in the two previous tests, they still required significantly more trials than did the normal animals.

Although both operated groups were retarded in relearning tests, they showed no apparent impairment in transferring to successive tests. Indeed, as seen in Table II, both operated groups tended to perform somewhat better on the first session of each

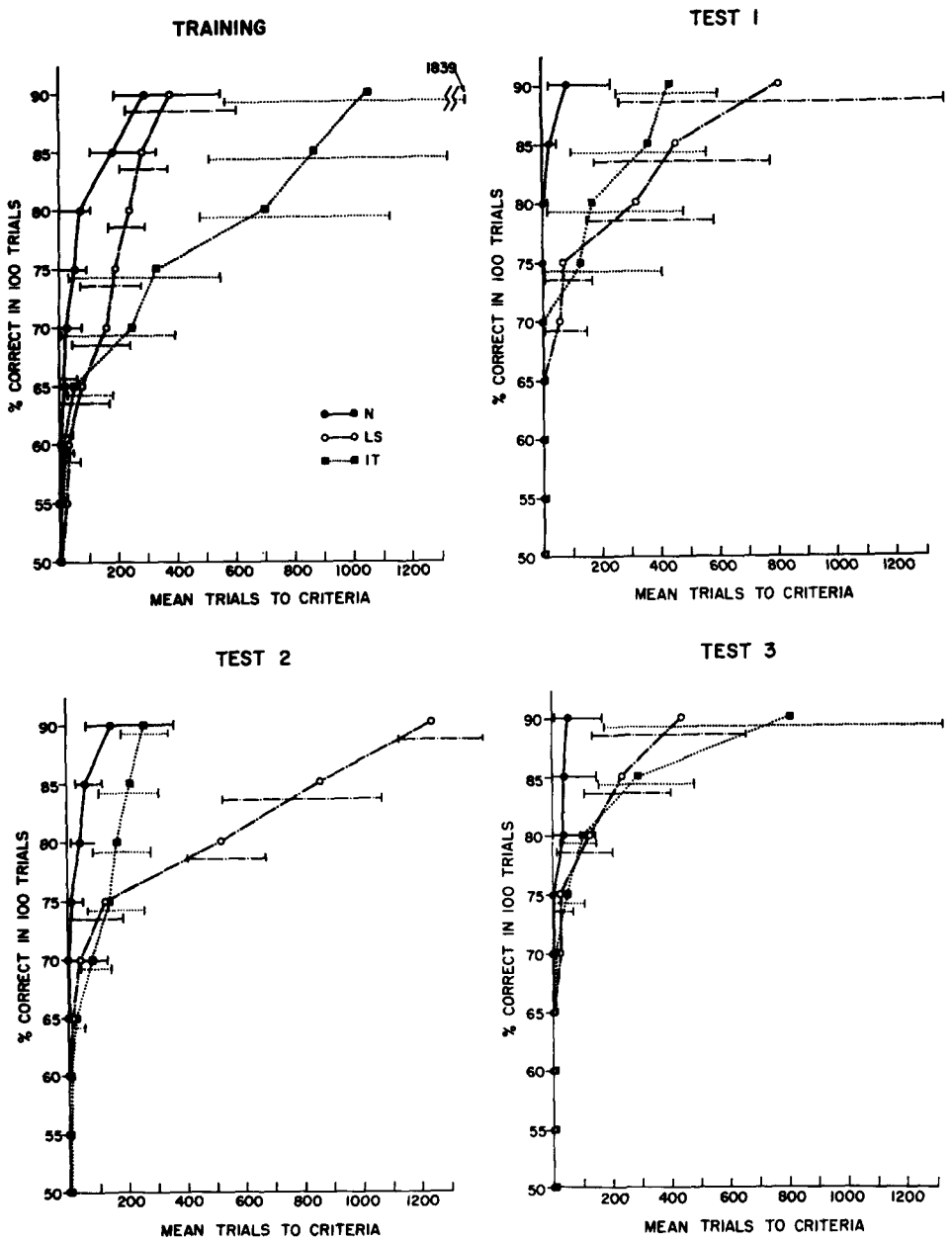


Fig. 2. Mean number of trials required by the LS, IT and unoperated groups in training and in the 3 tests to attain successive criteria in 100 consecutive trials. The scores plotted are cumulative, and the vertical lines represent the range of individual subjects' scores for each group.

test than did the unoperated group. Furthermore, an analysis of *S*s' learning curves in each of the tests reveals that both the LS and IT groups showed little impairment in reattaining 70–75% correct performance; their retardation in relearning was most obvious only after they had reattained this level of performance (see Fig. 2).

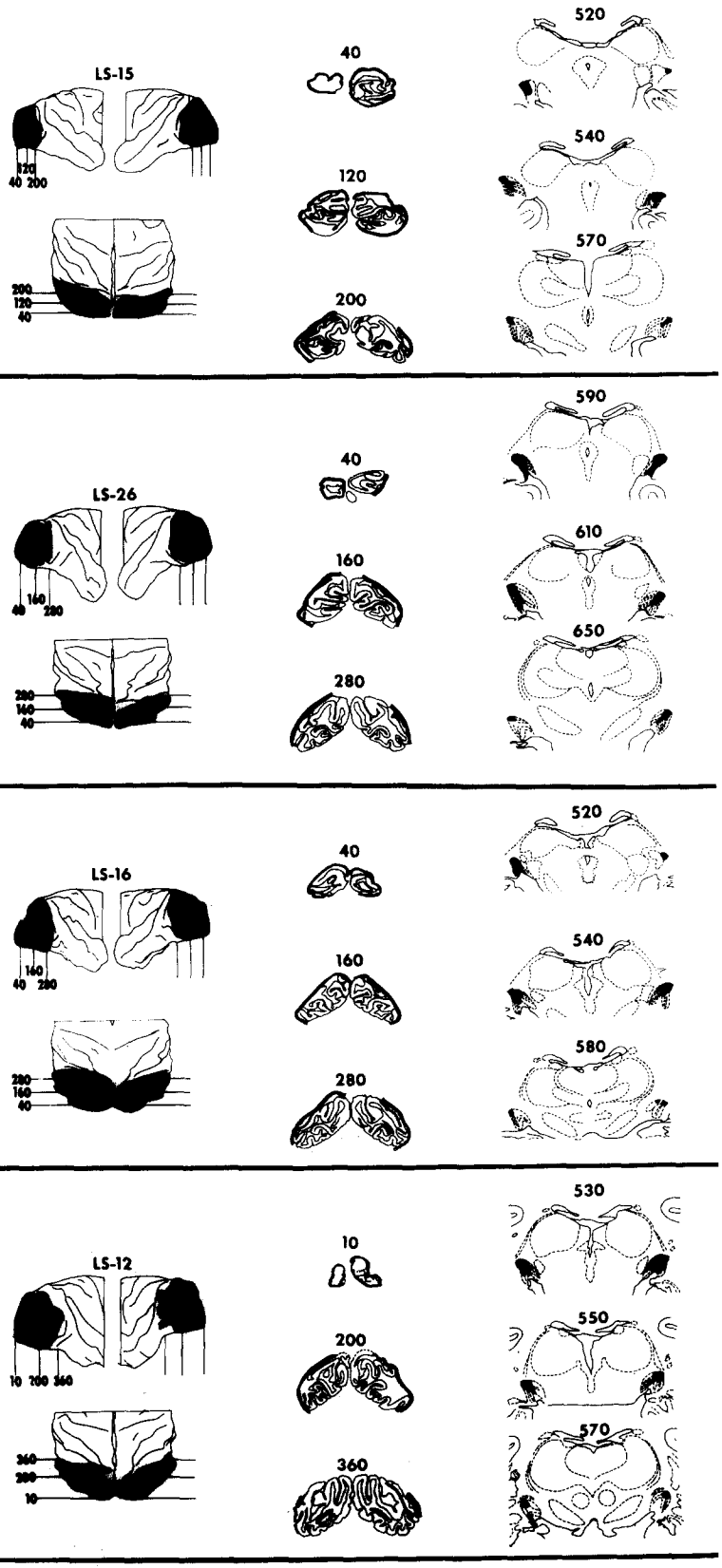

LS-15
120
40 200
200
120
40
40
120
200
520
540
570
LS-26
40 160 280
280
160
40
40
160
280
590
610
650
LS-16
40 160 280
280
160
40
40
160
280
520
540
580
LS-12
10 200 360
360
200
10
10
200
360
530
550
570

TABLE II

MEAN PER CENT CORRECT RESPONSES OF N, LS AND IT GROUPS ON FIRST SESSION OF TESTS

Group	*Test 1*	*Test 2*	*Test 3*
N	62.7	61.0	62.7
LS	67.7	75.0	64.3
IT	73.3	63.3	61.7

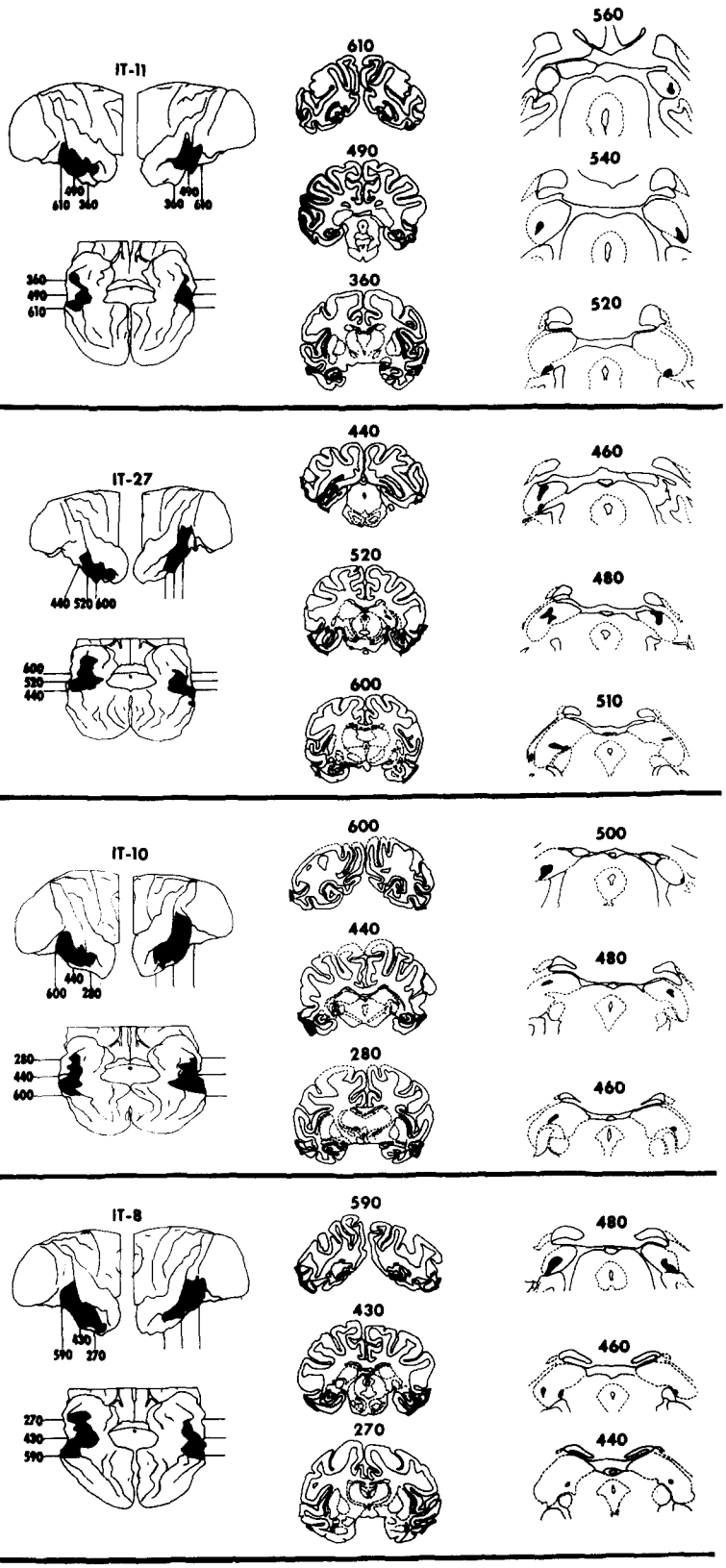
Figs. 3 and 4 show reconstruction of the LS and IT lesions, together with cross sections through the lesions and through thalamic nuclei in which retrograde degeneration was found. The IT lesions extended posteriorly into the ventral prestriate region unilaterally in 3 brains (IT-10, IT-11, and IT-27) and bilaterally in the fourth (IT-8), which also involved slight unilateral damage to striate cortex. The IT lesions produced irregular and variable regions of retrograde degeneration in the caudal, lateral and medial divisions of *n. pulvinaris*. In addition, the lateral geniculate nucleus showed slight degenerative changes bilaterally in 1 case (IT-8) and unilaterally in 2 others (IT-10 and IT-27). The LS lesions were complete in 2 cases (LS-12 and LS-16); in the other 2 brains (LS-15 and LS-26) small portions of anterior striate cortex were spared. In 2 cases (LS-12 and LS-16) the lesion extended into prestriate cortex. The lateral geniculate nuclei of the LS animals showed severe retrograde degeneration confined to the intermediate wedge-shaped portion which projects to the LS region[14], except for the right lateral geniculate of LS-12, which also showed degeneration in its lateral division.

There was no correlation between the degree of behavioral impairment in the 3 tests and extent of striate cortex damage or prestriate damage. Likewise, there was no relationship between the extent of the IT lesions and the severity of test deficits.

DISCUSSION

The tests employed in this experiment required the subjects to reattain mastery of a discrimination when irrelevant features were added to the discriminanda. Thus, considering the task requirements, the IT animals' retardation in relearning would appear to reflect an impairment in selectively attending to the relevant features of the stimuli. Alternatively, the IT monkeys' relearning loss might have been due to a deficiency in transfer independent of the particular stimulus features employed. Thus, for the IT monkeys (as well as for the LS monkeys) each successive test may have constituted a new learning task, more difficult perceptually than the initial learning task. Analyses of the IT monkeys' relearning curves supports the former rather than

Fig. 3. Reconstructions of the LS lesions along with cross sections through the lesions and through thalamic regions containing retrograde degeneration.


IT-11
610 360
490
360 610
360
490
610
610
490
360
560
540
520
IT-27
440 520 600
600
520
440
440
520
600
460
480
510
IT-10
600 280
440
280
440
600
600
440
280
500
480
460
IT-8
590 270
430
270
430
590
590
430
270
480
460
440

the latter interpretation. The IT animals performed at least as well as did the unoperated animals on initial test sessions, and they had little or no difficulty in reattaining criteria of 70 or 75% correct performance on tests in which they were impaired. These findings suggest that the IT monkeys were not deficient in transferring to successive tests. Moreover, the IT monkeys' retardation in relearning was revealed most clearly in their performance at criteria above 70%. This selective deficit in achieving high levels of performance supports the view that the IT monkeys were deficient in consistently maintaining a high degree of selective attention to the relevant stimulus features. According to this interpretation, an animal which is impaired in consistently attending to the relevant stimulus features (for example, one which attended only on 40% of the trials) might, like the IT animals, have little difficulty in attaining 70% correct performance (since it would perform correctly on one-half of the remaining trials by chance). But such an animal would have considerable difficulty in attaining higher criteria of performance. Moreover, this interpretation is consistent with the conclusion based upon pattern equivalence findings that IT lesions impair selective attention to spatial stimuli[1]. One other aspect of the IT monkeys' performance deserves mention. The finding that these animals were impaired in relearning after adding bars through the discriminanda, but not after adding bars around them, suggests that the proximity of the irrelevant features to the discriminanda was an important factor determining their performance.

To what extent the visual *learning* impairment of IT monkeys could be attributed to an attentional loss is not readily apparent from these data. With regard to this problem, it may be significant that the IT ablations performed in this experiment extended posteriorly in the region which appears to be selectively related to perceptual or attentional disturbances[9,10]. Thus it is possible that the deficits in test performance shown by the IT monkeys were due to invasion of the ventral prestriate area.

The LS monkeys' test impairment was the most unexpected outcome of this experiment; these animals, which were originally intended as operated controls, showed test impairments that were even more severe than those of the IT animals. Several prior experiments have shown that monkeys with LS removal are only minimally impaired in visual learning tasks[3,4,7,16]. This was also the case in the present experiment: the LS monkeys, unlike the IT monkeys, were not reliably impaired in initial learning. While the LS animals' test deficits cannot readily be attributed to learning factors, it might seem reasonable to attribute them to acuity losses, which are associated with LS lesions[7]. For, the irrelevant features interrupted the borders of the discriminanda in tests. However, it is doubtful that this factor could fully account for the LS monkeys' test deficits. Thus, the LS animals showed their most severe impairment in test 2, in which bars were added around the discriminanda, whereas they were least impaired in test 3, in which the discriminanda were most obscured by the bars. On the other hand, it is conceivable that acuity losses could

Fig. 4. Reconstructions of the IT lesions along with cross sections through the lesions and through thalamic regions containing retrograde degeneration.

have made it difficult for the LS monkeys to distinguish the discriminanda from the horizontal masking bars. Alternatively, it is possible that the LS monkeys' test impairment was at least in part due to losses in selective attention. This conclusion is supported by analyses of the LS animals' relearning curves which, like those of the IT animals, indicate abnormal difficulty in achieving consistently high levels of performance. Moreover, the LS monkeys' deficit in pattern–string tests[16] may be related to the test impairment described here. In the pattern-string tests, the monkey is required to retrieve food by pulling a string to which the food is attached and not an unbaited string, which crosses the baited string one or more times. It is possible that the LS monkeys' deficit in performing this task is due to a loss in abstracting the relevant cue (*i.e.*, the baited string). While the possibility of an attentional loss following striate lesions was unanticipated, it parallels reports that patients with occipital damage show a disturbance in identifying forms that are masked[11,15]. Thus, these findings, together with the present ones, suggest that striate cortex may contribute to integrative functions underlying perception, as well as to sensory functions.

SUMMARY

Monkeys with inferotemporal (IT) lesions, monkeys with lateral striate (LS) lesions and unoperated monkeys were first trained to discriminate between two bars differing in length and then tested for relearning after irrelevant features were added to the stimuli in successive tests. The IT monkeys were impaired in initial acquisition of the discrimination and in two relearning tests. Unexpectedly, the LS monkeys, which were unimpaired in acquisition, were severely impaired in relearning. Analyses of relearning performance supports the conclusion that LS lesions, as well as IT lesions, impair selective attention.

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REFERENCES

1 BUTTER, C. M., The effect of discrimination training on pattern equivalence in monkeys with inferotemporal and lateral striate lesions, *Neuropsychology*, 6 (1968) 27–40.
2 BUTTER, C. M., AND DOEHRMAN, S. R., Size discrimination and transposition in monkeys with striate and temporal lesions, *Cortex*, 4 (1968) 35–46.
3 BUTTER, C. M., AND GEKOSKI, W. L., Alterations in pattern equivalence following inferotemporal and lateral striate lesions in rhesus monkeys, *J. comp. physiol. Psychol.*, 61 (1966) 309–312.
4 BUTTER, C. M., MISHKIN, M., AND ROSVOLD, H. E., Stimulus generalization in monkeys with inferotemporal and lateral occipital lesions. In D. J. MOSTOFSKY (Ed.), *Stimulus Generalization*, Stanford University Press, Stanford, Calif., 1965, pp. 119–133.

5 CHOW, K. L., AND ORBACH, J., Performance of visual discrimination presented tachistoscopically with temporal neocortical ablations, *J. comp. physiol. Psychol.*, 50 (1957) 636–640.
6 CHOW, K. L., AND SURVIS, J., Retention of overlearned visual habit after cortical ablation in monkeys, *Arch. Neurol. Psychiat. (Chic.)*, 79 (1958) 640–646.
7 COWEY, A., AND WEISKRANTZ, L., A comparison of the effects of inferotemporal and striate cortex lesions on the visual behaviour of rhesus monkeys, *Quart. J. exp. Psychol.*, 19 (1967) 246–253.
8 GELLERMAN, L. W., Chance order of alternating stimuli in visual discrimination experiments, *J. genet. Psychol.*, 42 (1933) 207–208.
9 GROSS, C. G., AND COWEY, A., *Behavioral and Electrophysiological Experiments on Inferotemporal Cortex*, Paper presented at APA meeting, Sept. 1967.
10 IWAI, E., AND MISHKIN, M., *Two Inferotemporal Foci for Visual Functions*, Paper presented at APA meeting, Sept. 1967.
11 LURIA, A. R., *Higher Cortical Functions in Man*, Basic Books, New York, 1966, pp. 138–139.
12 MISHKIN, M., Visual mechanisms beyond striate cortex. In R. W. RUSSELL (Ed.), *Frontiers in Physiological Psychology*, Academic Press, New York, 1966, pp. 93–116.
13 ORBACH, J., AND FANTZ, R. L., Differential effects of temporal neocortical resections on overtrained and nonovertrained visual habits in monkeys, *J. comp. physiol. Psychol.*, 51 (1958) 126–129.
14 POLYAK, S., *The Vertebrate Visual System*, University of Chicago Press, Chicago, 1957, pp. 420–433.
15 TEUBER, H.-L., AND WEINSTEIN, S., Ability to discover hidden figures after cerebral lesions, *Arch. Neurol. Psychiat. (Chic.)*, 76 (1956) 369–379.
16 WILSON, W. A., AND MISHKIN, M., Comparison of the effects of inferotemporal and lateral occipital lesions on visually guided behavior in monkeys, *J. comp. physiol. Psychol.*, 52 (1959) 10–17.