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Physiology & Behavior, Vol. 18, pp. 403–407. Pergamon Press and Brain Research Publ., 1977. Printed in the U.S.A.

The Visual Discrimination Performance of Monkeys with Foveal Prestriate and Inferotemporal Lesions[1]

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(Received 28 October 1975)

CHRISTENSEN, C. A. AND K. H. PRIBRAM. *The visual discrimination performance of monkeys with foveal prestriate and inferotemporal lesions.* PHYSIOL. BEHAV. 18(3) 403–407, 1977. — The performance of monkeys with inferotemporal and foveal prestriate lesions was compared with that of intact animals in patterned string testing and postoperative retention and acquisition of visual discrimination problems. While both operated groups were impaired in postoperative retention testing, only monkeys with inferotemporal lesions maintained a deficit in the acquisition of a new discrimination. Monkeys with foveal prestriate lesions showed impairments in patterned string performance which were correlated with the extent of degeneration of the lateral geniculate nucleus. Although the discrimination deficit observed in these monkeys cannot be attributed to geniculostriate damage, the patterned string data suggest that alterations in sensory function may contribute to the impairments observed after ablation of foveal prestriate cortex. Data from this study also suggest that the greater foveal prestriate deficits observed by other investigators are due to encroachment upon the posterior portion of inferotemporal cortex.

Visual discrimination learning   Inferotemporal cortex   Foveal prestriate cortex

ALTHOUGH the circumstriate cortex of the primate brain has been the focus of numerous experiments, that experimentation has produced no unanimity concerning its role in the processing of visual information. Thus data collected in this laboratory have shown that radical resections of prestriate cortex fail to seriously impair visual discrimination behavior [16]. Animals with massive lesions of the circumstriate belt showed retention deficits, but relearning was rapid. This suggested that the integrity of this tissue is not essential to the functioning of the adjacent inferotemporal cortex, an area definitely involved in the performance of visual discrimination [6].

The absence of persisting deficits in visual discrimination behavior after prestriate ablations has usually been attributed to the sparing of tissue [13,14]. Yet this view cannot explain the surprisingly large deficits reported by Cowey and Gross [4] following the removal of only a portion of the circumstriate belt, which they called the foveal prestriate cortex. Less prestriate tissue was removed in their animals than those reported by Pribram *et al.* [16] and Mishkin [14]; indeed nearly all the foveal prestriate cortex appears to have been ablated in Pribram's animals.

The discrepancy between the data from the various laboratories has stimulated a reexamination of monkeys with prestriate lesions. The results of a comparison of the visual discrimination performance of monkeys with foveal prestriate and inferotemporal lesions and their normal controls are therefore presented here.

METHOD

Animals

Fifteen young adult Rhesus monkeys *(Macaca mulatta)* weighing between 4 and 6 kg were the subjects in this experiment. Group N (N = 5) were unoperated control animals. Group IT (N = 4) sustained bilateral inferotemporal cortex ablations intended to correspond to area TE of Von Bonin and Bailey [1]. The posterior extent of the lesion was restricted to several mm anterior to the ascending limb of the inferior occipital sulcus. Lesions of group FPS (N = 6) were intended to completely ablate foveal prestriate cortex by including both banks of the

[1]We would like to thank Dr. Leslie Ungerleider and Angela DiBerardino for invaluable assistance. This research was supported by NIMH Research Grant No. MH 12970 and NIMH Research Career Award to Dr. Pribram.

ventral one half of the lunate sulcus, the posterior bank of the ascending limb of the superior temporal sulcus, both anterior and posterior banks of the inferior occipital sulcus and the gyri between these areas [5,19]. Throughout the experiment the monkeys were housed in individual cages and maintained on a diet of Purina Monkey Chow supplemented with fresh fruit and vitamins.

Apparatus

All training and testing was carried out in a quiet cubicle using a computer controlled automated test apparatus (DADTA) devised by Pribram and described in detail elsewhere [15]. Discriminanda were presented on a vertical display by Industrial Electronics Engineers, Inc. rear projection readout units with the position of stimuli randomized over sixteen panels in a four × four array. The interior of the cubicle was illuminated from above and outside noises were masked by the hum of a ventilating fan.

Procedures

Preoperative training. Animals were shaped to press any one of twelve lighted panels in the panel array in order to receive a food reward. The shaping stimulus was the numeral 1. Shaping consisted of progressively diminishing the number of lighted panels until the animal responded well with only two of the stimuli lighted. At that time pretraining was discontinued. Preoperative training consisted of a simultaneous two-choice visual discrimination between the numerals 3 and 8 presented randomly over 16 positions at an intertrial interval of 5 sec. Fifty trials were presented daily five days per week until a criterion of 90% correct on two consecutive days was achieved. After a two week rest each animal was tested for retention and prepared for surgery.

Surgery. Preparation for aseptic surgery consisted of immobilization with Ketamine (12 mg/kg IM) followed by intravenous sodium pentobarbital anesthesia administered as needed. Fluids and supplemental anesthetics were administered during surgery via an intravenous catheter.

Both inferotemporal and foveal prestriate lesions were performed bilaterally in a one-stage procedure by subpial aspiration using a 19 gauge Pribram sucker through openings rongeured in the skull. Bleeding was controlled by means of cottonoid strips and a minimal use of electrocautery. After the dura was sutured, the wound was closed in anatomical layers.

Postoperative testing. Following a two week postoperative recovery period all operated animals were re-exposed to the pretraining paradigm until they consistently responded to the shaping stimulus in all 16 positions. Most animals were able to begin postoperative retention testing after a single day's experience with the pretraining stimuli. After completion of retention testing, all animals were trained further in the postoperative acquisition of a discrimination of the numerals 9 and 6.

Finally patterned string tests were presented [8]. The stimuli used consisted of patterns formed from two white strings, 1/16 in. in dia., arranged on a matte black plywood board (24 × 18 in.); the board was placed in front of and level with the monkey's cage (18 × 26 × 20 in.) floor. The two strings were attached at their near ends 5 in. apart and 3 in. from the monkey's cage. The far ends of the strings were tied to 1/4 in. white plastic recepticals that served to hold raisin rewards. Each of the 8 patterned string arrangements was 18 in. in length, the width varying for different patterns. The far ends of the strings were either 5 in. or 1-1/2 in. apart, depending on the pattern. Once a pattern had been formed, the experimenter rolled the horizontal testing board toward the monkey, who could then reach through the vertical bars (1-3/4 in. apart) of his cage to reach the string.

All monkeys were pretrained to reach through the bars and pull strings from their attached ends to obtain raisin rewards located at their far ends. Following pretraining, the monkeys were tested for 32 trials per day for 15 days. Each day's test consisted of 4 presentations of 8 patterns, such that each pattern randomly occurred once every 8 trials. Asymmetrical patterns were tested as 2 sets of mirror images presented twice each. The reward position was assigned to insure an equal occurrence of rewards on the right and left of each pattern. A noncorrection procedure was used. The configuration of the 8 patterns is shown in Figure 2. They were selected from those used by Harlow [8] and Wilson and Mishkin [18].

Histology. Following completion of behavioral testing the animals were perfused intracardially under deep barbiturate anesthesia with saline followed by 10% Formalin and the brains were blocked stereotaxically in the coronal plane. They were hardened in Formalin and 30% sucrose-Formalin and, after they were embedded in gelatin-albumin and frozen, 50 μ coronal sections were made. Sections were mounted and stained with cresyl violet for microscopic analysis of the lesions. Cortical lesions were reconstructed from enlarged tracings using serial sections one mm apart. Reconstruction of the actual lesions, representative coronal sections and thalamic degeneration for each operated group are shown in Fig. 1.

RESULTS

Table 1 shows the number of trials accumulated by all monkeys in attaining criterion during pre- and postoperative testing. The Kruskal-Wallis one-way analysis of variance by ranks [17] on retention savings scores (3 vs 8)

$$\frac{\text{preoperative trials} - \text{postoperative trials}}{\text{preoperative trials} + \text{postoperative trials}}$$

indicated that significant group differences were contained within the data ($H = 9.4$, $p<0.01$). Individual Mann-Whitney U tests of these savings scores showed that both inferotemporal ($U = 0$, $p<0.008$) and foveal prestriate animals ($U = 0$, $p<0.002$) were significantly impaired in postoperative retention of the 3–8 discrimination when compared with normal controls and did not differ significantly from each other ($U = 9.5$, NS). There was no overlap in either errors or trials accumulated by normal and operated animals on this test.

However, the two operated groups showed almost no overlap in postoperative acquisition of the 9–6 discrimination; foveal prestriate animals took far fewer trials to learn this problem. Comparison of the scores of operated and unoperated animals indicated that only inferotemporal monkeys showed a deficit in the second learning task ($U = 3.5$, $p<0.07$). The difference between the two operated groups was also significant ($U = 1$, $p<0.01$). The scores of foveal prestriate and normal monkeys could not be distinguished statistically ($U = 17$, NS).

Both operated groups accumulated more total errors in patterned string testing than did normal monkeys (foveal

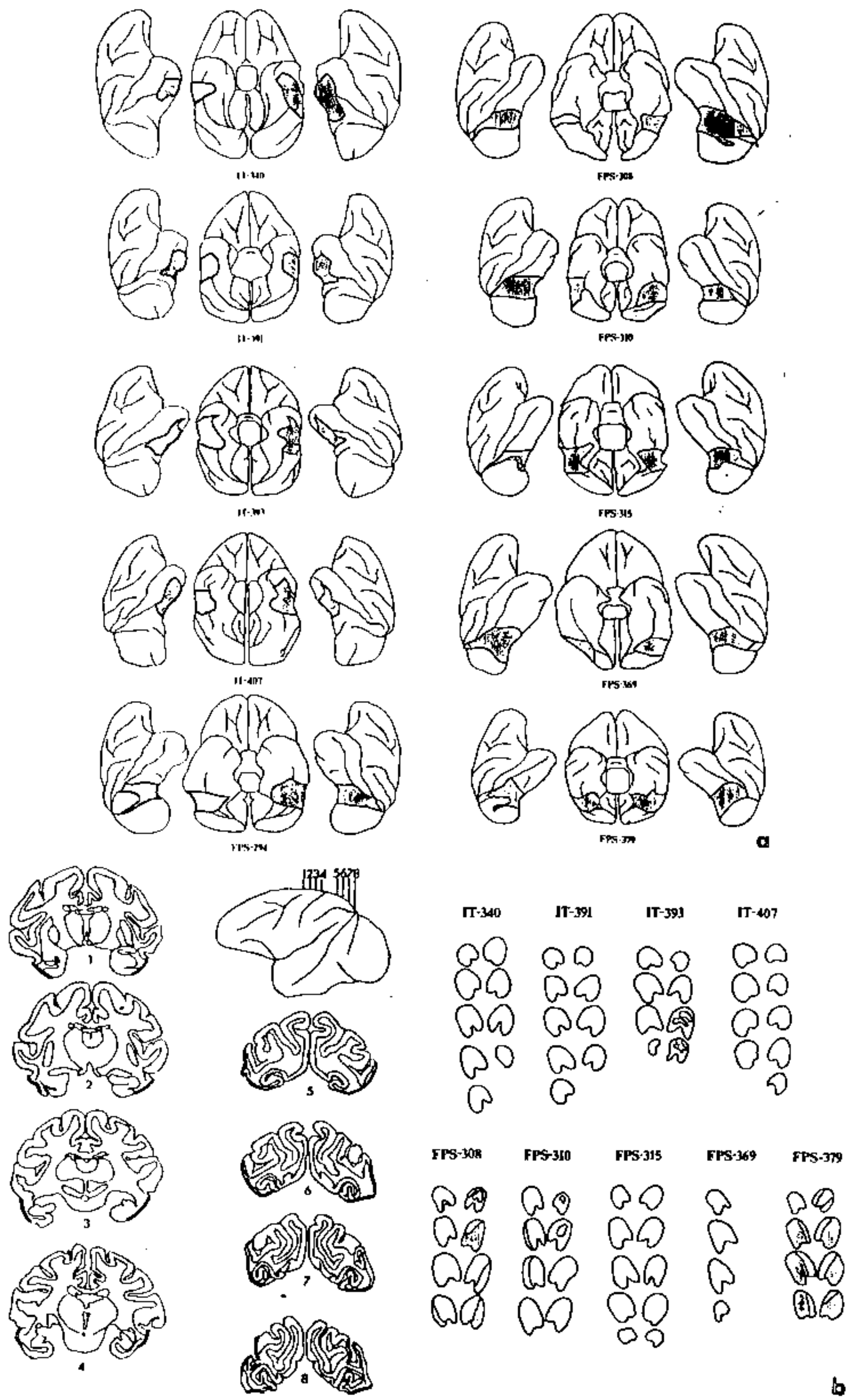

FIG. 1a and b. Reconstructions of lateral and ventral views of the experimental animals are represented in Figure 1a. Solid black indicates the area of lesion; stippled areas represent undercut tissue. Figure 1b shows coronal sections representative of lesions in the inferotemporal and foveal prestriate groups with the lesioned areas drawn in heavy lines. Degeneration of the lateral geniculate nucleus is represented in solid black. (Complete histology for FPS-369 and FPS-294 is not presented since these monkeys suffered unintentional geniculate damage after surgery subsequent to this experiment.)

TABLE I

TRIALS ACCUMULATED BY INDIVIDUAL ANIMALS DURING VISUAL DISCRIMINATION PERFORMANCE (SCORES DO NOT INCLUDE CRITERION TRIALS)

Animal	PREOPERATIVE 3 vs 8	POSTOPERATIVE 3 vs 8	POSTOPERATIVE 9 vs 6
N-337	250	0	100
N-338	227	50	372
N-339	150	0	150
N-342	200	0	50
N-343	414	50	350
X	248	20	204
FPS-294	50	1250	100
FPS-308	150	200	100
FPS-310	50	250	200
FPS-315	550	600	200
FPS-369	150	850	200
FPS-379	250	(2000)	1182
X	200	858	330
IT-340	250	(2000)	1350
IT-391	500	1550	1300
IT-393	450	1110	400
IT-407	400	800	100
X	400	1362	787

Parentheses indicate that training was stopped before criterion performance was achieved.

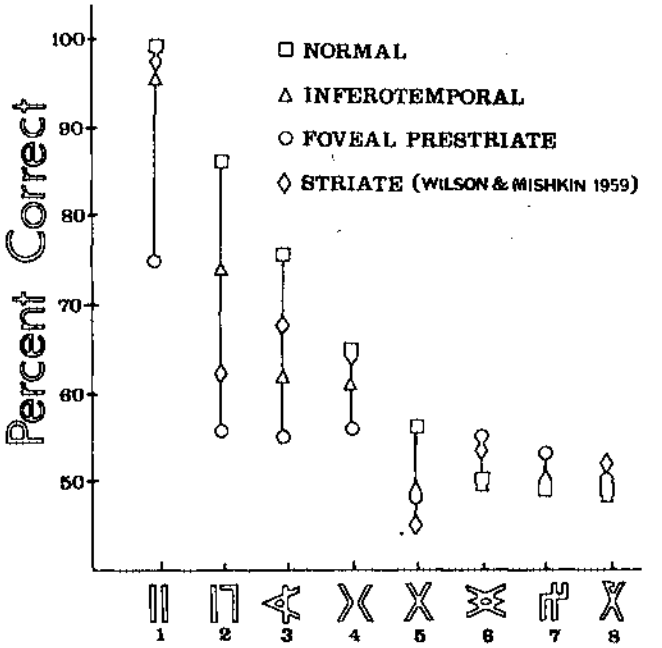

FIG. 2. Percent correct performance of normal, inferotemporal, foveal prestriate and lateral striate animals on individual patterns used in patterned string testing. Lateral striate scores are replotted from data reported by Wilson and Mishkin [18].

prestriate U = 0, $p<0.008$; inferotemporal U = 0, $p<0.028$). In addition, monkeys with inferotemporal lesions performed better than monkeys with foveal prestriate lesions (U = 2, $p<0.07$). The foveal prestriate group was impaired on problems which other animals accomplished with ease. There was no overlap in their performance and that of normal animals on any of the first three patterns (U = 0, $p<0.008$). They were also poorer than inferotemporal animals on patterns 1 (U = 0, $p<0.018$) and 2 (U = 1, $p<0.036$). The inferotemporal impairment was more diffuse. Although the monkeys with inferotemporal lesions accumulated significantly more total errors than normal monkeys, they were not significantly poorer on any single pattern.

DISCUSSION

Data presented here show that the magnitude of the initial postoperative retention deficit in monkeys with foveal prestriate and inferotemporal lesions is equal but that in subsequent postoperative acquisition of a discrimination problem, monkeys with foveal prestriate lesions, but not those with inferotemporal removals, are indistinguishable from normal monkeys. Thus, these findings do not support the results of other investigators [4, 7, 10, 11, 12] that removal of foveal prestriate cortex produces as severe a visual discrimination deficit as that seen after lesions of the inferotemporal cortex.

Can this discrepancy be explained by incomplete removal of foveal prestriate cortex in the monkeys reported here? We think not. Histological examination of our animals does reveal occasional sparing of islands of tissue in the depth of the inferior occipital sulcus but the amount of this sparing is less than that reported by Cowey and Gross [4]. Further, the tissue remaining in the sulcus usually is severed from adjacent structures, thus making it unlikely that differences in sparing of tissue in the inferior occipital sulcus are responsible for the differences in behavior observed in the different studies.

A second possibility for the discrepancy concerns a foveal striate projection onto the posterior portion of the superior temporal sulcus, an area which has been suggested to be an important way station to the inferotemporal cortex. This area, though removed by Cowey and Gross and to a large extent spared in the present experiment, also appears to have been spared in the experiment reported by Manning [10] whose monkeys showed deficits equivalent to those reported by Cowey and Gross. It is therefore unlikely, though not impossible, that the differences in removal of tissue in the depths of the posterior portion of the superior temporal sulcus are critically responsible for the discrepancies in the behavioral results.

How then, can the discrepancies be resolved? While we intend to explore the possibility that the foveal projection onto the superior temporal sulcus is an area critical for visual processing, at present our data support the hypothesis that lesions which remove foveal prestriate cortex produce severe and lasting impairments only when the ablation also includes the posterior portion of inferotemporal cortex. This hypothesis is suggested by the fact that all foveal prestriate lesions published from other laboratories [4, 7, 10, 11, 12] in which a lasting deficit in visual discrimination behavior was obtained have removed a large part of the posterior portion of inferotemporal cortex. Iwai and Mishkin [9] have shown that destruction of even the most posterior 5 mm strip of inferotemporal cortex is sufficient to produce visual discrimination impairments. This hypothesis would also explain a discrepancy in data collected in this laboratory; a larger retention deficit was observed in the foveal prestriate monkeys studied in this experiment whose lesions included some inferotemporal tissue than in the animals reported by Pribram, Spinelli and Reitz [16] where the encroachment on posterior inferotemporal cortex was less.

In addition the data to date suggest that the disruption of discrimination by the combined lesion is due to interference with two processes, one specifically related to discrimination behavior – the inferotemporal deficit – and a second which is more perceptual in nature – the foveal prestriate deficit. A perceptual deficit is suggested because monkeys with lesions of foveal prestriate cortex who showed initial retention deficits in this study are similar to monkeys with lateral striate lesions [18] in that they maintain a marginal discrimination impairment; they are slightly inferior to normal animals but significantly better than monkeys with inferotemporal resections. In addition, the removal of foveal prestriate cortex produces a patterned string deficit somewhat similar to that produced by ablation of lateral striate cortex. (See Fig. 2.)

The magnitude of the patterned string deficit observed in foveal prestriate animals is positively correlated with the extent of degeneration in the lateral geniculate nucleus (rho = .83), a finding which raises the possibility that the discrimination deficit seen after removal of this tissue might also be due to geniculostriate damage. However, the correlation between discrimination deficits and damage to the lateral geniculate nucleus is not significant (rho = .47). While alterations in sensory function may influence the visual behavior of monkeys with foveal prestriate lesions, this factor alone is insufficient to explain their marginal discrimination deficit.

In sum these findings suggest (1) that future examination of the effects on visual behavior of ablation of foveal prestriate cortex be studied in monkeys with lesions carefully restricted to the projection of foveal striate onto prestriate cortex and (2) that these experiments include studies of sensory and perceptual status as well as more complex visual behavior.

We are presently examining the eye movements of monkeys with this lesion to ascertain whether abnormalities can be discerned which provide evidence for perceptual dysfunction.

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