The selective attention "deficit" of monkeys with ablations of foveal prestriate cortex*

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Three monkeys with bilateral lesions of foveal prestriate cortex were compared to three with inferotemporal cortex lesions and three intact normals on a three-stage visual discrimination problem. In Stage 1, all monkeys learned a simultaneous color discrimination. In Stage 2, redundant size cues were added to these color cues. In Stage 3, only the size cues were present and the Ss were run until they learned this discrimination. No group differences were seen until Stage 3, where the inferotemporals, but not the foveal prestriates, learned more slowly than normals.

Several recent studies have demonstrated qualitative differences in the visual learning deficits that follow ablations of inferotemporal and foveal prestriate cortex. For example, foveal prestriate lesions produce a more severe impairment on difficult visual pattern discrimination tasks, while inferotemporal lesions result in worse deficits on concurrent object discrimination tasks (Iwai & Mishkin, 1968; Cowey & Gross, 1970). Attempts to specify the precise nature of these two deficits have just begun, but it has been suggested in several studies (Iwai & Mishkin, 1968; Cowey & Gross, 1970; Manning, Gross, & Cowey, 1971; Manning, 1971; Gross, Cowey, & Manning, 1971) that one might characterize the deficit following foveal prestriate lesions as one primarily affecting the attentional aspect of learning and that which follows inferotemporal lesions as one primarily affecting associative or mnemonic aspects.

The present experiment was addressed primarily to the first half of this hypothesis, that foveal prestriate lesions impair visual discrimination learning largely by disruption of the attentional phase of learning. Gross et al (1971) have reported that the addition of irrelevant color or brightness cues to a well-learned pattern discrimination produced a severe disruption in the performance of monkeys with foveal prestriate lesions, but not in those of intact monkeys or monkeys with inferotemporal lesions. On this evidence they suggested that animals with foveal prestriate lesions find it

particularly difficult to restrict their attention to a single visual feature or dimension. This explanation implies that there might be some special situations in which animals might be helped rather than hindered by a "broadening of attention." The present experiment was an attempt to devise such a situation. As in the experiment of Gross et al (1971), a new cue was added to a well-learned visual discrimination. In this case, however, the cue was relevant (New Stimulus A was always paired with S+ and New Stimulus B with S-). After three sessions with both cues present, the original stimuli were dropped and the Ss tested with only the added cues present. It was predicted that monkeys with foveal prestriate lesions would be more likely than those with inferotemporal lesions to attend to the added cue and therefore would perform better when the original cue was eliminated.

SUBJECTS

Nine rhesus monkeys (*Macaca mulatta*) were used. Three had previously received bilateral lesions of foveal prestriate cortex, three had received ablation of inferotemporal cortex, and three served as unoperated controls. Complete descriptions of these lesions have been published previously (Manning, 1971), along with details on surgical and histological procedures. Briefly, the inferotemporal lesions were all confined to Area TE as defined by von Bonin & Bailey (1947) but spared the rostral-most 5 mm. Caudally, the lesions extended to about 10 mm anterior to the ascending limb of the inferior temporal sulcus. The foveal prestriate lesions extended caudally from this point to the lunette sulcus and a line extending this sulcus down to the inferior occipital sulcus, dorsally to about 5 mm above the tip of the ascending limb of the inferior occipital sulcus, and ventrally to the lateral bank of the occipitotemporal

sulcus. All monkeys had participated in several discrimination experiments before the present one.¹

APPARATUS

All behavioral testing took place in a fully automated testing cage, 18 x 18 x 30 in., enclosed in a sound- and light-attenuating wooden box. The cage was illuminated diffusely from above, and a masking noise was presented during testing. Mounted on one wall, 12 in. from the floor, were two Gerbrands monkey response keys, 14 in. apart, backed by Industrial Electronic Engineers readout units, by means of which the discriminanda were projected onto the translucent response keys. Below and between the keys was a liquid dispenser with which reinforcements of 0.25 cc orange juice were presented.

PROCEDURE

The monkeys were tested daily while approximately 23 h water-deprived. Sessions consisted of 100 trials, with an intertrial interval of 5 sec. Both stimuli were presented on every trial, and a single press on either key extinguished both stimuli and ended that trial. Presses on the correct stimulus (S+), the position of which varied randomly, also produced an orange juice reinforcement. No correction trials were given.

The experiment proper consisted of three stages. In the first of these, all Ss were trained to discriminate two slightly different patches of green. No effort was made to measure the wavelength, brightness, or saturation of the stimuli. Human Os consistently reported the two as "lime" (S+) and "aqua" (S-). The monkeys progressed to Stage 2 upon reaching a criterion of 90 correct responses in a session. This stage consisted of overtraining on this color problem, but with two new stimuli added: superimposed on the lime stimulus (S+) was a set of 16 white dots arranged in a .75 x .75 in. square, and superimposed on the aqua (S-) stimulus was a set of 16 similar white dots arranged in a .50 x .50 in. square. This stage lasted 3 days (300

Table 1
Errors to Criterion by Each S in Each Stage of the Experiment

Group	S	Errors		
		Stage 1	Stage 2	Stage 3
Normal	GB	15	28	21
	Jerry	0	8	11
	Cain	23	27	37
Temporal	Granger	0	8	68
	Abel	0	25	42
	Eugene	32	15	62
Prestriate	Red	507	34	58
	Galen	21	5	34
	BB	0	0	18

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Fig. 1. Median errors to criterion of normal monkeys (N) and monkeys with inferotemporal (IT) or foveal prestriate (PS) lesions in each of the three stages of the experiment.

trials) regardless of performance. On the fourth day, the color cue was eliminated, leaving only the dot-squares. Ss were given 100 trials daily until they solved this dot-square discrimination, at which point Stage 3 and the experiment ended.

RESULTS

The findings of all three stages of the experiment are presented in Table 1, which shows the number of errors made by each animal in each stage. Figure 1 summarizes these data as group medians. No significant or suggestive differences or trends were found in either the first or the second stages, but in Stage 3, where the monkeys were tested for what they had learned about the dot-squares during overtraining on the lime vs aqua discrimination, the animals with inferotemporal lesions, and only the inferotemporals, made significantly more errors than did the normals (Mann-Whitney $U = 0$, $p = .05$). The foveal prestriates were intermediate between and did not differ significantly from either the normals or the inferotemporals.

DISCUSSION

The finding that the monkeys with foveal prestriate ablations were not impaired in the Stage 3 dot-square acquisition, despite the fact that the inferotemporals showed a significant retardation, suggests that these two groups were affected somewhat differently by the Stage 2 sessions.

Foveal prestriate lesions usually result in a larger deficit in pattern discrimination learning than do inferotemporal lesions (Iwai & Mishkin, 1968; Cowey & Gross, 1970). Previously published data from the present Ss (Manning, 1971) show that they are not exceptions to this generalization. Despite this, only the inferotemporals were impaired in Stage 3 of the present experiment. Assuming that exposure to the dot-square stimuli during Stage 2 was somehow involved in this peculiar finding, at least two explanations fit the data equally well: (1) the foveal prestriate monkeys benefited to an abnormally large extent from Stage 2 training with two relevant cues; or (2) that inferotemporal monkeys gained abnormally little from Stage 2 training.

The first of these alternatives, that the foveal prestriates benefited disproportionately from the sessions with two relevant cues, is based on earlier proposals (Gross et al, 1971; Manning et al, 1971) that foveal prestriate ablations cause monkeys to attend to more aspects of their visual environment than they normally would. In traditional discrimination learning situations, this tendency would result in increased errors as the monkey attended to various irrelevant stimuli, both programmed and unprogrammed, but in the present experiment one of these "extra"

stimuli was relevant. In this situation, the experience of the foveal prestriates (noticing the extra relevant cue during Stage 2) presumably was instrumental in eliminating (in Stage 3) the deficit shown by such Ss on visual pattern discriminations.

The second possible explanation offered, that inferotemporals gained disproportionately little from Stage 2, is also not without support. Butter (1968), for example, proposed, on the basis of pattern equivalence tests, that the learning impairment of monkeys with inferotemporal lesions was due to a defect in attending to less salient aspects of visual stimuli. Furthermore, demands put on the monkey in Stage 2 (gain information about the dot-squares while responding on the basis of color differences) are at least superficially similar to those of the concurrent (or serial) problem on which inferotemporals ordinarily show a larger impairment than foveal prestriates (Iwai & Mishkin, 1968; Cowey & Gross, 1970). A replication, with the addition of a matched set of nine animals learning the dot-squares problem without any previous Stage 2 exposure, should provide sufficient information to evaluate these two interpretations.

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NOTE

1. In conducting the research described in this report, the investigators adhered to the "Guide for Laboratory Animal Facilities and Care," as promulgated by the Committee on Revision of the Guide for Laboratory Animal Facilities and Care of the Institute of Laboratory Animal Resources, National Academy of Science—National Research Council.