Vision in tree shrews (*Tupaia glis*) after removal of striate cortex¹

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Three tree shrews (*Tupaia glis*) were trained to discriminate between horizontal and vertical stripes, and upright and inverted triangles. The striate cortex of both hemispheres was then ablated. All animals relearned the habits based on the discrimination of visual patterns. Histological study of the thalamus revealed a complete degeneration of the lateral geniculate bodies. On the basis of these findings and on the basis of the unlearned behavior of the operated animals in both familiar and unfamiliar circumstances it is concluded that pattern and object vision do not depend on the geniculostriate system in this particular species.

A comparison of the cortex of tree shrews with a prototypic eutherian mammal like the hedgehog provides a number of revealing contrasts and similarities. While both brains are clearly primitive, the dorsal thalamus and sensory neocortex in the tree shrew are greatly expanded and differentiated, especially the visual centers, the lateral geniculate bodies (GL) and the striate cortex. Evidently between the stages represented by a generalized mammalian type and an early primate there was an enormous increase in the functional significance of vision (Simpson, 1945). There is little doubt that these advances in structure and function had an influence throughout the course of primate evolution (Le Gros Clark, 1959).

Two years ago we began to study the striate cortex of the tree shrew—first by the method of thalamic retrograde degeneration to determine the organization of the projections of GL, and then with behavioral methods. This is a preliminary report of three cases in which we have complete anatomical as well as behavioral results.

Method

The three tree shrews were trained in a three choice Yerkes box before receiving surgery, first, to discriminate between black and white, and then, between two sets of visual patterns, vertical and horizontal stripes, and upright and inverted triangles. The criterion for learning was 19 correct responses in two successive 10 trial sessions. The patterns were cut from black and white paper, secured between 4 in. by 4 in. squares of glass, and inserted into the frame of a doorway. To change from a positive to a negative stimulus the glass insertion was simply rotated 90° or 180°. Fluorescent light bulbs behind the doors transmitted light through the white regions of the pattern.

Results

The chief behavioral finding is that, following the ablation of striate cortex, each of the three animals either retained or quickly relearned the habits based on the discrimination of patterns.

Further, the postoperative behavior of the three cases could not be distinguished from normal outside of the training apparatus. In their home cages the animals continued to circle from floor to wall to ceiling in a typical fashion. They would usually interrupt this vigorous activity long enough to seize a small piece of food held with a forceps inside the wire mesh of the cage. If now the food was quickly removed to a new location the movements of the experimenter's hand would be followed and the food taken at the new locus. The ability of the animals to follow moving objects was tested further by suspending a piece of food on a string and then swinging the bait back and forth inside the home cage. At the lowest part of the arc, the bait was just beyond the animal's outstretched hands, but with a well-timed leap the food could be snatched from the string. After observing the success of the operated animals on this and similar tasks, and after observing all animals avoid obstacles in an unfamiliar environment, such as on the floor of the colony room, we have been forced to conclude that visual cues remain important in their adaptation to the external world.

The simplest explanation for the postoperative behavior in and out of the training apparatus is that some part of the geniculostriate system had been preserved. According to Lashley (1939), rats are capable of discriminating patterns with only 700 normal cells remaining in GL.

The cortical lesions were reconstructed from frontal sections (50μ and stained with thionin) and every single section through GL was examined. No portion of the striate area remains preserved in any of the six hemispheres and, similarly, no portion of GL escapes complete retrograde degeneration (see Fig. 1). The degeneration in GL in these three cases resembles that found after hemidecortication: only nuclei of cells are clearly stained and most of these are readily identified as neuroglia. About two dozen degenerated neurons could be identified in GL of *Tupaia* 102, but this was hardly a basis for arguing that GL in this case was less severely affected than in the case of a hemidecortication. We therefore conclude that pattern vision in *Tupaia glis* does not depend on the geniculostriate system.

Discussion

This conclusion leads to two further interrelated questions: What central nervous system structures are responsible for pattern vision in the absence of the geniculostriate system? Is the tree shrew unique among experimental mammals? The exceptional size of the superior colliculus and the large proportion of optic fibers terminating there may reflect an unusual capacity

Fig. 1. The lesion in case 110 is the smallest of the three cases. Even so, the reconstruction of the surface lesion shows that the ablation extends beyond the striate area, the boundary of which is shown by dots. The frontal sections following the surface lesion indicate that the medial wall of the cortex has been removed to the limit of the hippocampus and that on the lateral wall, neocortex has been removed below the boundary of the striate area. Below are five sections through the thalamus in which complete degeneration is indicated by black, while moderate or slight degeneration is shown by dots. The chief point is that GL is totally degenerated throughout. Section 179 illustrates that a portion of VGL is continuous with the medial layer of GL. We have been able to identify this sector in the case of hemidecortication. Abbreviations: GM, medial geniculate; L, lateral group; MD, mediodorsal; Pul, pulvinar; R, reticular; SC, superior colliculus; TO, optic tract; V, ventral group; VGL, ventral lateral geniculate; VP, ventroposterior.

for the tectum to assume visual functions (Tigges, 1966). On the other hand, some portion of the pulvinar and its cortical target may be responsible for the visual capacity of the animals here described. If the pulvinar and the related lateral nuclei prove to be responsible for pattern vision in the tree shrew it would be worthwhile to reconsider some established results in other species. The loss of visual discrimination based on patterns in the rat may have resulted from removal of extrastriate cortex—the target of the lateral nuclei—in addition to striate cortex. The literature on the cat contains at least one report on the importance of extrastriate areas in pattern vision (Doty, 1961). Thus the preservation of the 700 cells in GL might just be coincident with the preservation of the lateral nuclei.

Whatever the final answer to these problems, we now have an opportunity to study the visual cortex by the method of ablation unhampered by the appearance after surgery of simple sensory defects. Surely the striate cortex did not develop simply to replace sensory functions that could be accomplished by the tectum. A clue

to the higher integrative functions of the cortex, those which have evolved beyond the level achieved by the midbrain, may be provided by a study of tree shrews who see quite well in the absence of the striate cortex.

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