

BEHAVIORAL STUDIES OF BINOCULAR COMPETITION IN CATS¹

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Abstract—Cats were raised with one eye sutured and the other removed. We wished to determine whether: (1) the deprived eye would develop a visual field of normal extent (135°) as might be expected on the basis of the competitive advantage that this eye enjoys within the geniculo-cortical pathways, or (2) the deprived eye, in the absence of pattern vision, would develop only 90° of vision, as happens in binocularly deprived cats. In these experiments the deprived eye developed only 90° of vision. This may represent a failure of normal geniculo-cortical development, a failure probably due to lack of a spatially patterned visual environment.

INTRODUCTION

In our previous studies we have shown that when a cat is raised with one eye sutured, visual orienting responses are lost for much of the visual field of the deprived eye (Sherman, 1973). When such a cat is tested with the deprived eye open, orienting responses are seen for only the monocular (peripheral) segment of the visual field (see Figs. 1A and B). This loss of visual responses in the binocular segment, and sparing in the monocular segment, corresponds to anatomical and physiological observations of monocularly lid-sutured cats. These observations indicate a loss of geniculate cell growth and of geniculo-cortical activity in the binocular segment of the visual pathways, but they indicate no loss in the monocular segment (Guillery and Stelzner, 1970; Sherman, Hoffmann and Stone, 1972). The difference between the monocular and the binocular segments of the visual pathways demonstrates that during development there is a competitive interaction between the two retino-geniculo-cortical pathways. When one eye is closed, its central connections appear to be at a disadvantage in this competition and, thus, the central connections of the sutured eye are not established in segments where they must compete with the central connections of the open eye. In the monocular segment there can be no competition between the two pathways, and so the pathways from the deprived eye are spared here.

The monocular sparing of geniculo-cortical development can also be demonstrated in segments of the visual pathways that are normally binocular. This is done by making a restricted retinal lesion in the open eye of a monocularly sutured cat, and thus creating an artificial monocular segment. Behavioral tests show visual sparing for the appropriate segment of the visual field of the deprived eye (Fig. 1C), and geniculate cell growth as well as geniculo-cortical activity show a parallel sparing within the artificial monocular

segment (Guillery, 1972; Sherman, Guillery, Kaas and Sanderson, 1974; Sherman, Wilson and Guillery, 1975).

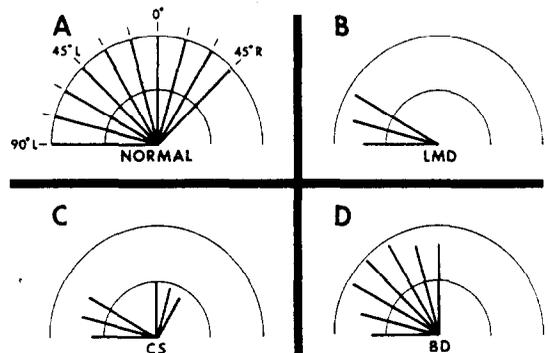


Fig. 1. Visual fields for left eye of cats raised in a variety of environmental conditions. The visual fields are represented by polar plots which show the response level in every 15° horizontal sector of visual field (see text). The outer semicircle represents the 100% response level; and the inner circle, the 50% level. Each is a typical result of behavioral testing with the right eye occluded and is redrawn from previously published data (Sherman, 1973, 1974a; Sherman *et al.*, 1974). These fields should be compared with those in Fig. 2 (see text). A: Field for a normally reared cat. Essentially, this field is also seen in a right-monocularly deprived cat. Normal monocular vision for the cat thus extends from 90° ipsilateral to 45° contralateral. B: Field for a left-monocularly deprived cat. The left eyelids were sutured closed from the 8th day until 9–12 months. Functional vision by this test appears to develop only in the monocular segment. C: Field for a “critical segment” cat. In this example the left eyelids were sutured shut from the 8th postnatal day until 9–12 months. Also on the 8th postnatal day a small lesion was placed in the right, nasal retina. This test demonstrates functional vision for the left eye in only two separate zones: the natural monocular segment and the artificial one created by the right retinal lesion. D: Field for a binocularly deprived cat. Both eyes were sutured closed from the 8th postnatal day until 9–12 months. Vision, as determined by these methods, has not developed functionally for the contralateral 45° of visual field (i.e. temporal retina).

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As the size of the artificial monocular segment is increased by an increase of the retinal lesion, so the size of the field that shows visual sparing might be expected to increase accordingly. In the extreme case, one might anticipate that removal of one eye would produce visual sparing in all parts of the other, sutured eye. That is, a cat raised with one eye closed and the other removed would be expected to show 135° of vision in the closed eye. This expectation is reinforced by the observations of Kratz and Spear (1976) who showed that cortical responses to visual stimulation of a deprived eye are improved when the other eye is removed at birth.

A strikingly different expectation can be based upon experiments in which cats were raised with both eyes sutured (Sherman, 1973). These cats develop only 90° of behaviorally demonstrable vision in each eye (Fig. 1D) and there appears to be a global loss of geniculate-cortical development in cats that are completely deprived of pattern vision in this way. This global loss is demonstrable in two ways. Electrophysiological studies show abnormalities throughout the lateral geniculate nucleus, including the monocular segment (Sherman *et al.*, 1972). Also, behavioral studies show that the orienting responses illustrated in Fig. 1D are due to retino-tectal mechanisms, since in these binocularly deprived cats cortical lesions do not produce a change in the extent of the visual fields of either eye, whereas tectal lesions create a permanent contralateral hemianopia (Sherman, in preparation).

The present experiment was designed to distinguish between the two alternative possibilities. We raised cats with one eye sutured and the other eye removed in order to determine whether the competitive advantage of the deprived eye in this situation would allow it to establish 135° of vision as in Fig. 1A, or whether a complete lack of a spatially patterned visual environment during development would produce a 90° field as in Fig. 1D.

MATERIALS AND METHODS

Five cats were studied with the use of previously described techniques (Sherman, 1973, 1974a). On the eighth postnatal day, three of the kittens (OED1, OED2 and

OED3) had the right eye removed and the lids of the left eye sutured. The other two kittens (OE1 and OE2) had the right eye removed and the left eye kept open. At 6–8 months of age, OED1, OED2 and OED3 had their left eyes opened and all five cats were then studied by a visual field test (Sherman, 1973, 1974a). Briefly, each cat fixated forward to a visual and auditory cue while a visual test stimulus was rapidly introduced into a limited portion of the visual field. Every 15° sector of visual field, measured horizontally, was tested over 70 times. The cats' orientation or lack of orientation to this test stimulus determined the horizontal extent of the functional visual field. As a control, the proportion of the orientations for each 15° sector of the visual field was compared to a baseline of spontaneous orientations that occurred in the absence of the test stimulus. These were the "blank" responses. The final response levels shown in Fig. 2 are a weighted % score, with the "blank" response level set at zero (see Sherman, 1974a).

RESULTS

Figure 2 shows that each of the experimental OED cats had only the 90° of visual field ipsilateral to the sutured eye. In contrast, the OE cats, which served as controls, had a normal field for the remaining left eye. That is, they saw 90° to the left and 45° to the right. The fields of the OED cats are clearly unlike those of a normal, non-deprived eye, and also unlike those of the deprived eye in a monocularly deprived cat (cf. Figs. 1A and B). However, the visual fields of the OED cats were indistinguishable from those of binocularly sutured cats (cf. Fig. 1D).

DISCUSSION

Our method measures a behavioral consequence of the competitive interaction that occurs between the two retino-geniculate-cortical pathways during the postnatal development of normal and monocularly deprived cats. If such an interaction had occurred, and if it had been expressed in the behavior we were testing, one would have expected the one-eyed, deprived (OED) cats to have shown a normal visual field such as that of the OE cats. That is, the visual field should have been demonstrable throughout the 45° contralateral to the deprived eye. It is reasonable

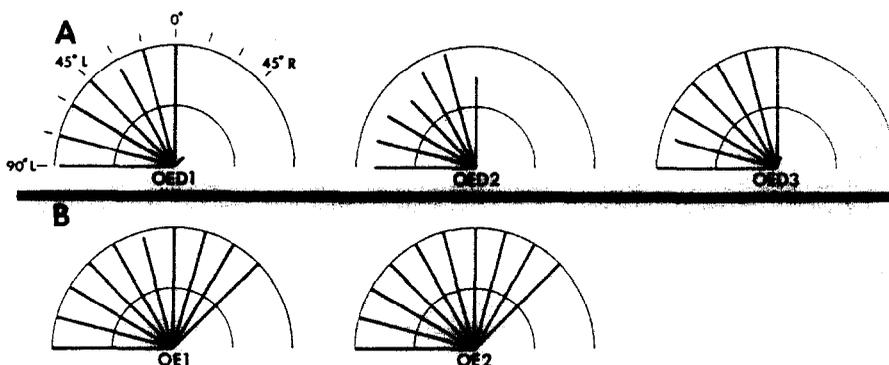


Fig. 2. Visual fields for remaining left eye of cats raised after removal of the right eye on the 8th postnatal day. The fields are represented as in Fig. 1. A: Fields for three cats whose left eyelids were sutured from the 8th day until the 6–8th month (several weeks before testing ensued). The test demonstrates a functional loss of the contralateral 45° of visual field. B: Fields for two cats whose left eyes were left open. The test demonstrates a normal extent of visual field.

to expect that the pathways from the sutured eye should dominate over those from the absent eye. In fact, Fig. 1C illustrates that a deprived segment of the geniculo-cortical pathway does dominate over a denervated one, that our behavioral test can demonstrate this domination, and specifically, that the domination is demonstrable for the contralateral visual field of a deprived eye.

Thus, our results, which show that removing one eye has no effect upon the visual field of a sutured eye, indicate either that the competitive interaction did not occur, or that if it did occur, it was not expressed by the behavior we were testing. It appears that the one-eyed, deprived cats developed like binocularly sutured cats. In both conditions the visual system is deprived almost entirely of patterned light. It could be argued that in the absence of patterned visual experience the competitive interactions do not occur in the geniculo-cortical pathways (Sherman, 1972). However, the observations of Kratz and Spear (1976) indicate that some competitive interactions can occur in one-eyed, deprived cats, and one is led to the conclusion that some form vision is necessary during development if the cortex is to develop appropriate links with the motor pathways that are being tested in these experiments.

The visual fields of Figs. 1D and 2A are similar to those of decorticate cats (Sherman, 1974b). That is, they are seen when subcortical mechanisms control the responses and when the cortex is not linked into the motor pathways. Thus, we conclude that in the one-eyed, deprived cats, as in the binocularly deprived cats, there may be a failure of the development of the cortically influenced motor pathways, and that this occurs because there is no possibility for form vision during development. In cats that have some form vision, behavioral orientations occur and the cortex influences them.

The experiment illustrated in Fig. 1C can demonstrate the competitive interaction during development provided that some form vision is allowed to occur during development. If the lesion extends to include

the whole eye, as in the present experiments, the visual sparing that corresponds to the retinal damage can no longer be demonstrated by our behavioral methods. We do not know how much retina, or what specific portions of the non-deprived retina must be intact for the visual sparing that corresponds to the retinal lesion to be demonstrable. Unfortunately, experiments to determine the critical size or location of normal retina in the non-deprived eye are likely to be extremely difficult.

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