

Behavioral, Electrophysiological and Morphological Studies of Binocular Competition in the Development of the Geniculo-Cortical Pathways of Cats¹

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ABSTRACT Cats were raised with one eye sutured and with a lesion in the retina of the other eye. In these cats the competitive interaction between the pathways that go to the cortex from each eye was tested by studying the behavioral capacities, the electrophysiological responses and the morphological appearance of the geniculo-cortical pathways.

Two parts of the visual system in which no binocular competition was possible were defined. One is the segment that receives inputs from the monocular crescent of the visual field, which has been called the monocular segment. The other is the artificial monocular segment created by the limited lesion of the non-deprived retina, and this has been called the critical segment.

In the binocular segments of the visual pathways we found, as have others, that: (1) behaviorally, cats do not respond to objects viewed by the deprived eye; (2) cortical cells tend not to respond to stimulation of the deprived eye; and (3) geniculate cells innervated by the deprived eye grow less than the normally innervated cells. However, we found that the deprived eye is more effective in driving neurons in contralateral than in ipsilateral cortex.

Within the monocular and the critical segments of the visual pathways we found: (1) that cats orient appropriately to visual stimulation of the deprived eye, (2) that cortical cells respond to visual stimulation of the deprived eye, and (3) that geniculate cells grow more than the deprived cells in the binocular segment of the nucleus. Thus, the deleterious effects of visual deprivation of one eye can, to some extent, be prevented by damage to the other.

If a kitten is raised with the lids of one eye sutured several abnormalities develop in the central visual pathways. Many of these abnormalities can be explained by assuming that during normal development there is a competitive interaction between the pathways that go from each eye to the striate cortex; suturing one eye upsets the balance of this competition, and the pathways from the open eye grow at the expense of those from the other, deprived eye. Evidence of such a competitive interaction has been obtained by electrophysiological studies of the visual cortex (Wiesel and Hubel, '63b, '65a) and of the lateral geniculate nucleus (Sherman et al., '72), by morphological studies of the lateral geniculate nucleus (Guillery and Stelzner, '70; Guillery, '72, '73) and by behavioral

studies of lid sutured kittens (Sherman, '73, '74a).

In the visual cortex of a cat raised with one eye sutured, most of the cortical cells are activated through the normal eye and, when the deprived eye is tested with the lids re-opened, the effective input to the cortex is found to be substantially less than normal (Wiesel and Hubel, '63b, '65a). In the lateral geniculate nucleus, the layers that are innervated by the deprived eye show a significant loss of large cells. Morphologically this is seen as a reduction in the mean cell size of the deprived geniculate cells (Wiesel and Hubel, '63a; Guillery and Stelzner, '70; Chow and Stewart, '72),

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while electrophysiologically one finds that activity of Y-cells, which are probably the largest of the geniculate cells, cannot be recorded (Sherman et al., '72). Behaviorally, the cat suffers from impaired vision while using only its deprived eye (Sherman, '73, '74a; Dews and Wiesel, '70; Chow and Stewart, '72).

All the changes described above occur only in the segments of the visual pathways that receive input from the binocular parts of the visual field and in which binocular competition can occur. The changes have not been found in the parts of the visual pathways that receive their inputs from the monocular crescents of the visual fields. These parts have been called the monocular segments of the visual pathways and, since only one ocular input is represented in these segments, there can be no binocular competition active in their development. Thus, in cats that have been raised with one eye sutured, cell growth is normal in the monocular segments of the lateral geniculate nucleus (Guillery and Stelzner, '70) and there is no detectable decrease of Y-cell activity in this part of the nucleus (Sherman et al., '72). When the visual fields of the deprived eye are tested behaviorally, the cats respond to objects only in the monocular crescent of the visual field (Sherman, '73, '74a). The response properties of cortical cells in the monocular segments have not been studied, but one can anticipate that they might be relatively normal.

While it seems reasonable to interpret the difference between the monocular and binocular segments as reflecting the absence of competition in the monocular segments, it is entirely possible that all of the results that have been summarized reflect a central:peripheral difference in the visual pathways, not a monocular:binocular difference. It can be argued that the central, binocular segments are more severely affected by pattern deprivation than the peripheral, monocular segments. A more stringent test of binocular competition can be produced by making an artificial monocular segment in the more central parts of the visual pathways. This has been done by placing a lesion within the binocular segment of one retina and suturing the lids of the other eye soon after birth (Guillery, '72). The artificial monocular seg-

ment created in this way has been called the "critical segment" of the central visual pathways, and it has been found that geniculate cell growth within this segment is greater than the cell growth in the adjacent parts of the deprived geniculate laminae.

The experiments to be reported here were designed to determine whether functional sparing for the deprived eye could be demonstrated behaviorally and electrophysiologically within an experimentally produced critical segment. The visual fields were mapped to determine the extent of visual sparing behaviorally, and microelectrodes were used to sample the activity of cortical neurons within the region of the critical segment. In addition, since no studies of cortical cell activity within the true monocular segment of monocularly deprived cats have been reported, we have looked at the activity of cortical cells in this region.

MATERIALS AND METHODS

1. *Surgical procedures*

Four cats were used for this study. They were anesthetized with ether at seven to nine days of age, and the lids of one eye were sutured, care being taken to ensure that lachrymal drainage from the medial corner of the eye was clear. The other eye was approached through an incision that avoided the conjunctival sac. This eye was rotated and a lesion was placed in the retina by inserting a small, bent knife through the back of the sclera and pressing the knife against the inside of the sclera around the point of insertion. The animals were given antibiotics post-operatively and they all recovered rapidly. The kittens were observed regularly to ensure that there was no blockage of lachrymal drainage, and to check that the sutured lids did not open. When they were 12 to 20 months of age two of these cats (CS1 and CS2) were used for behavioral testing; three cats (CS2, CS3 and CS4) were used for electrophysiological studies; and all four brains were prepared for neurohistological analysis (see below).

2. *Behavioral testing*

The tests used in this experiment have been fully described previously (Sherman, '73, '74a) and will be only briefly outlined

here. We tested for the extent of the visual field, for visual placing, and for visual following of moving objects. All tests were carried out in a small room illuminated at a photopic level. The cats were tested either monocularly, with an opaque occluder completely covering one cornea, or binocularly, with both eyes opened.

(a) *Visual field tests.* A table upon which radiating lines marked at 15 degree intervals was used for these tests. A food-deprived cat was placed at the center of these radiating lines and was taught to fixate on visual and auditory cues, consisting of food (the *fixation object*) held in forceps that were tapped on the table. While the cat fixated, a second visual stimulus (the *novel stimulus*: food or non-food objects were used interchangeably) was introduced vertically along one of the radiating guidelines. The cat was then released and its behavior noted. If it oriented to and approached the novel stimulus, this was scored as a positive trial for the direction of the novel stimulus. Any other behavior, which was usually a forward movement to the fixation object with no attention to the novel stimulus, was counted as a negative trial for this direction. When novel stimuli were presented immediately in front of the cat, no orientation was involved, so trials were scored somewhat differently: (1) if the cat bumped the novel stimulus and gave a startle response at the contact, this counted as a negative trial; (2) if the cat stopped and began to explore the novel stimulus before contacting it (the vibrissae were clipped), this counted as a positive trial; (3) the few responses that were not clearly one of the above (less than 10% of the total), were scored separately, and are not considered further here.

An important control consisted of a number of blank trials during which the cat was released without a novel stimulus being presented. If the cat immediately went forward to the fixation object, this counted as a negative blank trial. If the cat did anything else (almost always behaving as if searching for the absent novel stimulus), this counted as a positive blank trial.

The cats were tested several times weekly over a four month period, so that for all three viewing conditions (right- or left-monocular and binocular) at least 200 blank trials plus 100 trials for each guide-

line were scored. No obvious day to day variability was detected in the cats' behavior and the analysis was thus made by averaging results over many test sessions. Only regions in the visual field that had response levels higher than the blank positive level were considered as regions to which the cat attended visually. Thus, in figures 1 and 2 the guideline scores ($G\%$) are normalized with respect to the blank scores ($B\%$) in the following manner: if $B \geq G$, the normalized score is zero; if $G > B$, the normalized score is $(G-B)/(100-B)\%$.

It should be noted that the tests we have used define the horizontal extent of the visual field very well, but do not show the vertical extent so accurately. Since the novel stimulus was always introduced from above, visual losses that did not include the full vertical extent of the visual field were not easily recognized. Thus, the scotomata produced by the retinal lesions were not shown by the method, since in each cat there was intact retina below the damaged retina. However, one can expect that the method would successfully demonstrate sufficiently large patches of visual sparing (the critical segments), which are surrounded by large zones of visual loss. During testing the experimenters did not know the location of the retinal lesion in CS1 and CS2, so that no bias could be introduced into the estimates of the zones of sparing. For further details about the methods and the underlying assumptions see Sherman ('73, '74a).

(b) *Other visual tests.* Visual placing was tested by lowering the cat toward a table top and noting any anticipatory fore-leg extension. Visual following was tested by observing the cats' tracking of objects such as the novel stimulus moved through its visual field. The cats were also checked for strabismus by measuring the alignment of the pupil and the corneal reflex of a distant light source in each eye (Sherman, '72a).

3. *Electrophysiological methods*

Neuronal activity in areas 17 and 18 of the visual cortex was studied with micro-electrodes by methods that have been described in detail previously (Kaas and Guillery, '73). Receptive fields for clusters of nerve cells or, occasionally, single neurons,

were determined for three of the experimental cats. The cats were anesthetized with urethane, placed in a head-holder, and the dorsal aspect of the visual cortex was exposed. The cortex was protected by a pool of mineral oil in an open chamber of acrylic plastic. The eyelids were removed from both eyes and the eyes were held firmly by suturing the margins of the sclera to metal rings that were anchored to the headholder. The non-deprived eye, which had a restricted lesion of the retina, was centered within a translucent plastic hemisphere (60 cm diameter). The hemisphere served as a rear projection screen upon which visual stimuli consisting of small bars of light or shadow were presented. The deprived eye was slightly off center in the hemisphere, but since the interocular distance was small relative to the diameter of the hemisphere, no correction was made for the errors introduced by this eccentricity. The pupils were dilated with 2% cyclopentolate hydrochloride and the optic disc and the retinal lesion were projected onto the surface of the hemisphere by the method of Fernald and Chase ('71). Receptive field positions were recorded in terms of coordinates that were plotted for each eye as follows: the zero horizontal meridian was estimated in terms of distances from the center of the optic disc using the mean values given by Nikara et al. ('68) and the vertical meridian was mapped on the basis of receptive field positions recorded at the 17/18 border of the visual cortex (Hubel and Wiesel, '67).

Receptive field positions were determined by moving light or dark bars of varying shapes across the surface of the hemisphere. When the boundaries of a receptive field had been defined with both eyes open, we occluded each eye in turn and determined which eye had to be stimulated to produce the cortical response. We then looked for a second receptive field position for the other eye. The two eyes were deliberately misaligned so that receptive fields for the two eyes obtained at a single cortical locus would always lie some distance apart upon the hemisphere.

The procedure that was used for recording receptive field positions during any one electrode puncture introduced a sampling bias that tended to favor detection of inputs from the deprived eye, and the method will therefore be described in detail. The

electrode was advanced until it was 200–400 μm below the pia, and the receptive field for neurons at that site was recorded. The eye that activated these neurons was determined and a careful search was made for a second receptive field related to the other eye. The electrode was then advanced slowly and a search was made for (a) any significant change in receptive field position, and (b) a change in the eye that activated the cortical neurons. Another recording site was entered in the protocol only if a change in (a) or (b) occurred. Thus, since the majority of cortical cells were activated by the non-deprived eye, an electrode penetration that passed perpendicular to the pia often produced only one documented recording site. Penetrations passing down the medial wall of the hemisphere usually produced a series of documented recording sites which were generally 500–1000 μm apart, as the receptive fields from the non-deprived eye changed position by a significant amount. However, whenever a neuron or neuron group that responded to the deprived eye was detected, and there were relatively few of these, this was recorded as a recording site, except in the rare instances when two such groups were sufficiently close to each other in the cortex so that their receptive fields were also very close. In this way, many neurons activated from the non-deprived eye were ignored, since there was generally no significant shift of receptive field position as one passed from one neuron group to the next, but the great majority of the recorded nerve cells that were activated through the deprived eye were documented, since their receptive fields were relatively far apart.

Although it is possible that some recordings have been obtained from geniculocortical afferents, this cannot have been a frequent occurrence, and is not likely to have affected our conclusions. Activity was generally recorded from a range of depths relative to the cortical surface, including cortex above and below layer 4. Further, the recorded activity was dependent upon the cortical condition, and was absent in areas of damage or deteriorated blood flow.

4. *Histological methods*

During the electrophysiological experiments the electrode tracks were marked with small electrolytic lesions and at the end of each experiment the brains were

perfused with 10% formol saline and embedded in celloidin. Frontal sections were cut at 30 μm in the plane of the electrode tracks and were stained with buffered thionin. These sections included the whole of the lateral geniculate nucleus so that the zone of transneuronal degeneration that was produced in the nucleus by the retinal lesion could be identified and so that the adjacent critical segment of the deprived geniculate layers (Guillery, '72) could be plotted (figs. 4, 5).

Damage to the retina, especially where it involved the pigment epithelium, was seen at the time of the recording experiment and at this time the position of the retinal lesions was determined by the projection method described above. Later the lesion was checked by gross examination of the retina after it had been fixed. In each of the animals the retinal lesion could be seen readily. Since the zone of transneuronal degeneration that was found in the lateral geniculate nucleus corresponded closely, in terms of the available geniculate maps (Sanderson, '71; Guillery and Kaas, '71), to the position of the retinal lesion as defined grossly, no detailed histological plot of the retinal lesions has been made.

RESULTS

1. Behavior

(a) *Visual field tests.* Cats CS1 and CS2 both had a slight (approx. 15°) convergent strabismus; due to the vertical orientation of the pupils it was not possible to rule out even a slightly larger vertical strabismus. These squints, which could be due either to the monocular deprivation (Sherman, '72a) or to the extraocular surgery of the non-deprived eye, created the possibility that the cats fixated eccentrically (Sherman, '73).

The deprived eye (figs. 1B, 2B) showed patterns of visually responsive areas quite unlike any that have been described before. Each cat responded well to stimuli in the monocular segment (60°, 75°, 90°), and in this they behaved exactly like other cats raised with one eye sutured (Sherman, '73, '74a). However, in addition each of the cats also showed a second isolated portion of the visual field from which positive responses could be elicited. In both cats, this portion, which is the behaviorally defined critical segment of the visual field, was related to the temporal retina close to the

vertical meridian, and it was the only other portion of the visual field from which positive responses were obtained (figs. 1, 2). Therefore, in each cat one can anticipate a lesion in the nasal retina of the non-deprived eye close to the vertical meridian. Although the method of testing was not designed to plot the visual fields in terms of vertical co-ordinates, it was found that the critical segment was rather low in the visual field in both cats. By varying the height at which the novel stimulus was presented it could be crudely estimated that the upper margin of the critical segment was about 30° below the horizontal meridian (fig. 7). When the novel stimuli were presented only above the horizontal plane passing through both eyes the results were indistinguishable from those previously reported for cats raised with one eye sutured (Sherman, '73, '74a).

When the two cats were tested with both eyes open, they showed an apparently normal field of view. Thus, they did not differ from the monocularly deprived cats that have been reported previously, and this shows that even when these cats are given an opportunity to use the non-deprived eye, they do not ignore stimuli falling upon the monocular segment of the deprived retina.

(b) *Other tests.* On tests of visual placing and following, both cats appeared entirely normal when tested binocularly or with the non-deprived eye open. When the cats were tested monocularly with the deprived eye open, visual placing was noticeably below normal and resembled that seen in other monocularly deprived cats in every way (Sherman, '73, '74a). This placing is apparently the "visually elicited" component of placing described by Hein and Held ('67). When moving objects were kept close to eye level both cats gave responses much like those seen in monocularly deprived cats, and they followed only when the stimulus was in the temporal peripheral field of the deprived open eye. For objects moving much lower in the visual field (30°–50° inferior) the cats occasionally seemed to respond to the moving stimulus much nearer the midline and, in general, they could follow the stimulus more briskly and for longer periods without losing it.

2. Electrophysiological results

Recordings were obtained from the vis-

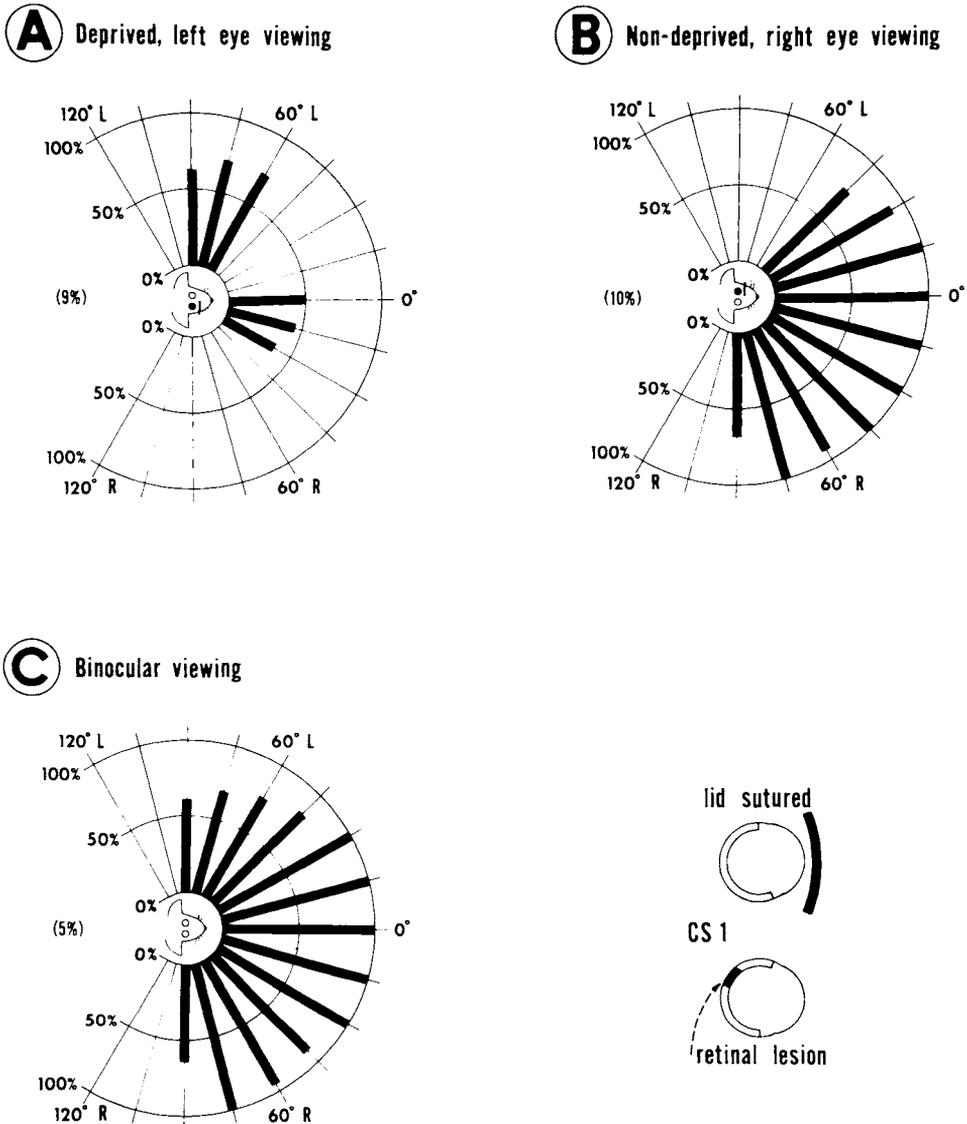


Fig. 1 Behavioral visual fields for cat CS1. The positive response levels for each visual field sector are shown as black bars. These levels are normalized against a background of blank positive responses (MATERIALS AND METHODS) which are indicated in parentheses for each graph. Every guideline was repeatedly tested and each bar represents a response level which is significantly higher than the blank positive level ($p < 0.001$ on a X^2 -test). For details see text. A: Field for the deprived, left eye. B: Field for the non-deprived, right eye. C: Binocular field.

ual cortex of three of the experimental cats, including CS2, which was one of the animals used for behavioral testing. The other behavioral subject (CS1) died before it could be studied electrophysiologically. It has been reported previously (Wiesel and Hubel, '63b; Ganz et al., '68; Chow and

Stewart, '72) that after a monocular deprivation cortical activity tends to be dominated by the input from the non-deprived eye, and this has also been found in each of the three cats studied here. However, while stimuli presented to the deprived eye were relatively ineffective in eliciting cor-

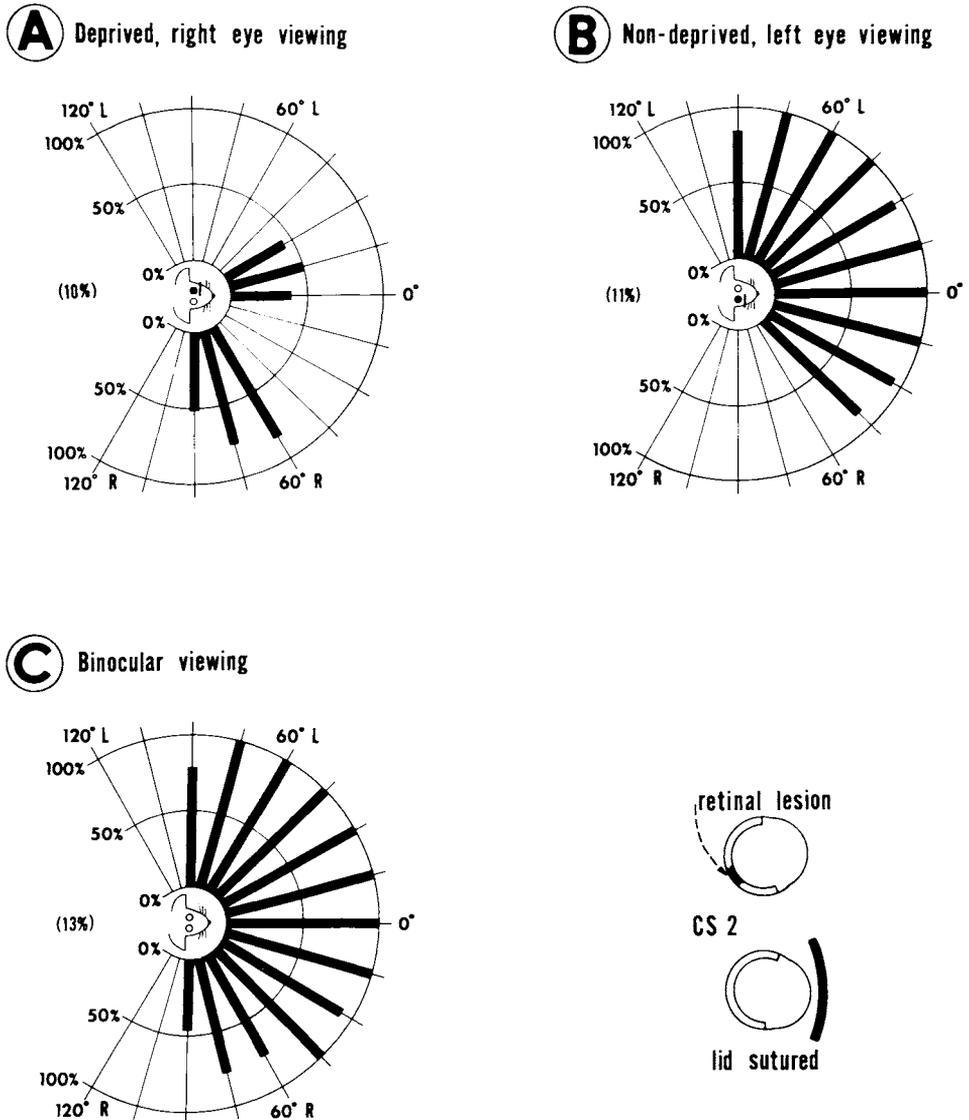


Fig. 2 Behavioral visual fields for cat CS2 shown as in figure 1. A: Field for the non-deprived, left eye. B: Field for the deprived, right eye. C: Binocular field.

tical responses, the reduced responsiveness was not uniform throughout the cortex. The change was less evident contralateral to the deprived eye than ipsilaterally and, further, we found no evidence that cells within the monocular or critical segments were made less responsive by the visual deprivation.

The difference between the two sides of the cortex will be considered first. This

comparison includes only those parts of the cortex in which binocular activation is theoretically possible (the potential binocular cortex). This excludes the monocular and critical segments of the cortex, which will be considered separately.

Of the 161 recording sites that were judged to be in potentially binocular cortex, 61 were ipsilateral to the deprived eye and 58 of these 61 were activated only by the

non-deprived eye. A reduced input from the deprived eye to the ipsilateral cortex has also been obtained previously in studies of monocular deprivation (Wiesel and Hubel, '63b, '65a; Chow and Stewart, '72). Only three recording sites were activated by the deprived eye, and it appeared that in each the electrode was within small groups of neurons that were activated exclusively from this eye. When the electrode was moved 50–100 μm , recordings were, again, obtained from the non-deprived eye. In these and other instances (see below) it was sometimes possible to place the electrode so that some activity could be produced by stimulation of either eye. However, with the methods we have used we never obtained clear evidence that a single neuron was responding to both eyes. Of the 100 recording sites that were in cortex contralateral to the deprived eye, 20 were activated by the deprived eye. These results suggest that the effects of monocular visual deprivation are considerably more marked in the cortex that receives an ipsilateral input from the deprived eye, than they are contralaterally.

Within the monocular segment of the striate cortex, which lies on the upper bank of the splenic sulcus and receives from the lateral 45° of the temporal hemifield of the contralateral eye (Sanderson, '71; Guillery and Kaas, '71; Woolsey, '71; Kaas and Guillery, '73) we recorded no obvious abnormalities in response properties that might have resulted from the monocular deprivation. In one cat (CS3) eleven electrode penetrations were made into the monocular segment of the cortex contralateral to the deprived eye. In each penetration neurons were activated by stimuli in the temporal crescent of the visual field of the deprived eye. The centers of the receptive fields of these neurons lay 42° to 75° temporal to the zero vertical meridian. For comparison, we made three electrode penetrations into the monocular segment of the cortex contralateral to the non-deprived eye. In terms of their responses to simple stimuli such as moving bars of light or shadow, and in terms of their receptive field sizes (4° – 8° in diameter), the neurons innervated from the non-deprived eye did not differ noticeably from those innervated by the deprived eye. However, details regarding the precise response prop-

erties of individual nerve cells have not been determined since most of the recordings were made from neuron groups rather than individual cells.

In a second cat (CS4), two electrode penetrations were made into the monocular segment of the striate cortex contralateral to the deprived eye and, again, it was found that nerve cells responded well to visual stimuli to the deprived eye. The responsiveness of these neurons to visual stimulation of the deprived eye appeared normal when compared to results obtained by the same methods in the monocular segment of the other hemisphere of the same cat or in other cats.

The final objective of our experiments was to record from cortex in the critical segment. In one of the cats (CS3), we were unable to record successfully from the region of the critical segment because the retinal lesion was not identified ophthalmoscopically and the relevant cortical region was not explored while the cortex was in a suitably responsive condition. In cat CS2 the retinal lesion was identified ophthalmoscopically and the cortex of the critical segment, which was on the medial wall of the right hemisphere, was explored systematically. The receptive fields in the general region of the critical segment are shown in figure 3. All recording sites with receptive fields around the projected lesion site were activated by the non-deprived eye only (receptive fields shown by solid lines in fig. 3). Thus, immediately above the projection of the retinal lesion one sees an almost horizontal row of receptive fields which were all activated from the non-deprived eye. In addition, receptive fields centered 5° or more medial and lateral to the projected lesion site were activated through the non-deprived eye.

In the immediate neighborhood of the projected lesion seven receptive fields are shown shaded, and these were all activated through the deprived eye. All except one of these receptive fields overlap the projection of the lesion. Six of these receptive fields were from recording sites in four electrode penetrations through the part of area 17 that lies along the medial wall of the hemisphere and the other one was recorded from a single penetration in area 18. Within the penetrations, the switch from neurons that were activated by the

ipsilateral eye to those that were activated by the deprived eye was always quite sharp.

Two points should be noted about the distribution of the receptive fields shown in figure 3. The first is that the shaded fields extend some way beyond the borders of the projected lesion site. To some extent this is, no doubt, due to an underestimate of the retinal damage. However, since there is an overlap between the receptive fields of the two eyes, the sparing of vision from the deprived retina must extend somewhat beyond the borders of the region that is homonymous to the lesion of the non-deprived retina. That is, the visual sparing extends somewhat beyond the borders of the critical segment. The second point is that receptive fields were not determined for the part of the visual field immediately below the projection of the lesion. Presumably in the corresponding upper part of the lesioned retina there were many ganglion cells whose axons were cut by the lesion

(Stone and Hansen, '66). It would have been of interest to record from cortex representing that part of the visual field, but in the relevant penetrations the electrode passed too far laterally to include the cortex of the medial wall.

Results similar to those obtained in CS2 were also obtained from CS4. However, the lesion was in the lower temporal retina, so that fewer recordings were obtained from the cortex of the critical segment, which was relatively inaccessible in the posterior parts of area 17. Further, since this cortex was contralateral to the deprived eye, a number of neuron groups that were activated from the deprived eye were found widely scattered in all parts of the visual field (see above) and so the sparing in the critical segment was demonstrated less dramatically than in CS2.

We conclude that the monocular and binocular segments of the visual cortex are not affected in the same way by a uni-

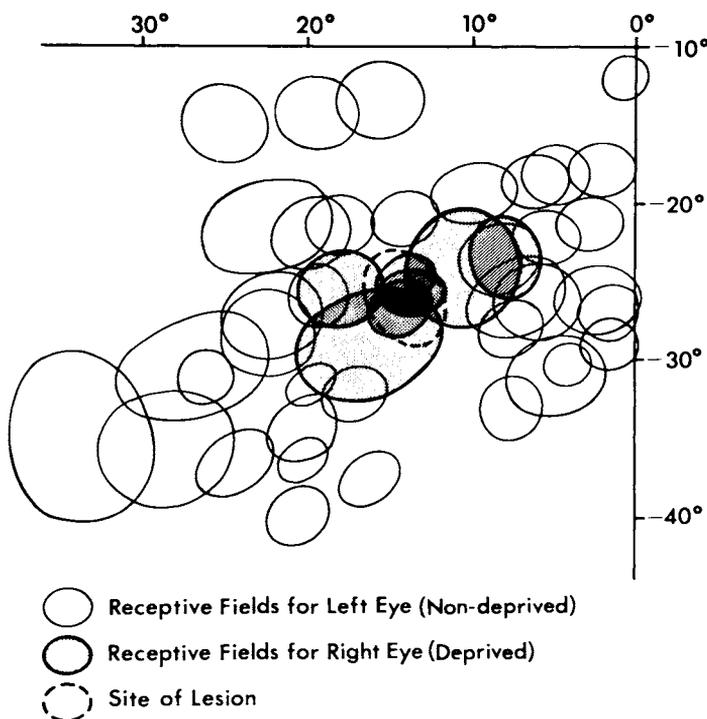


Fig. 3 The locations of receptive fields for recording sites in the visual cortex of the right hemisphere of cat CS2. This cat was reared with the right eye closed and a restricted left retinal lesion. The zero vertical meridian and the -10° horizontal parallel are indicated. Recording sites activated by the deprived eye all relate to receptive fields (shaded) near the projected lesion of the non-deprived eye (dashed line).

lateral lid suture, and that an artificial monocular segment behaves like the natural one. However, details of the specific response characteristics of nerve cells within deprived monocular segments of cortex remain to be studied.

3. Anatomical results

The morphological changes that can be seen in the critical segment of the lateral geniculate nucleus have been fully described and measured previously (Guillery, '72). Similar changes have been found in the present experiments although no measurements of the changes have been made. Figures 4 and 5 show the region of the critical segment in the lateral geniculate nucleus of cats CS1 and CS2 and figure 6 shows the position of the retinal lesion seen

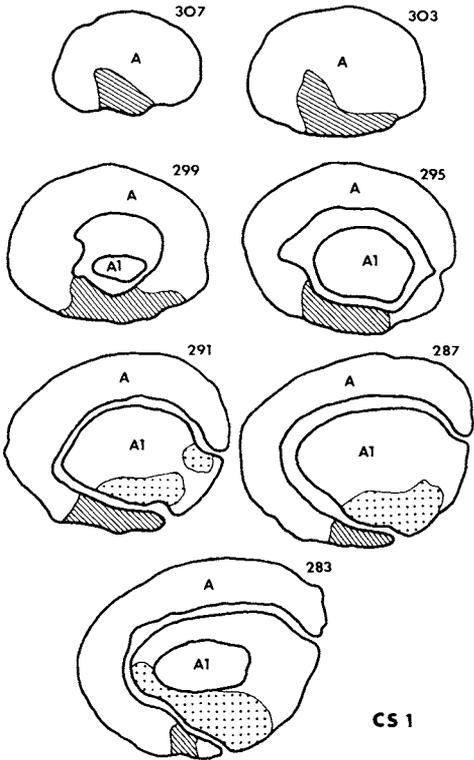


Fig. 4 Schematic outlines of the rostral part of the dorsal lateral geniculate nucleus of cat CS1 contralateral to the open (lesioned) eye. Oblique shading shows the zone of transneuronal degeneration in lamina A and the stipple shows the zone of cell sparing in the critical segment. Based on Nissl stained coronal sections. Medial is to the right, dorsal up.

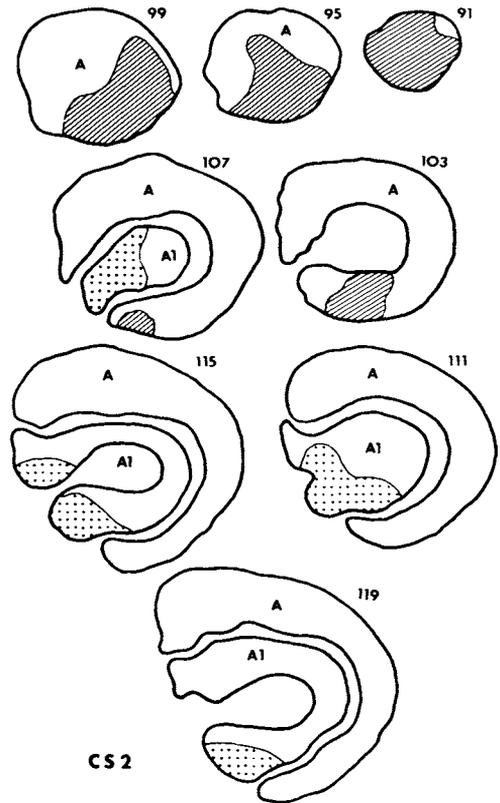


Fig. 5 Schematic outlines of the rostral part of the dorsal lateral geniculate nucleus of cat CS2 contralateral to the open (lesioned) eye. Medial is to the left, dorsal up.

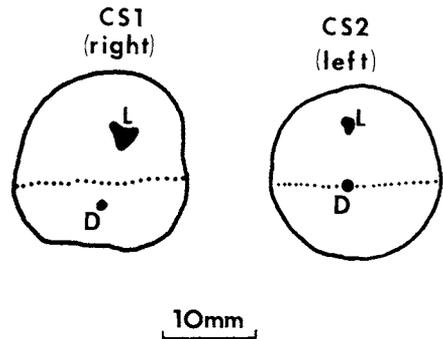


Fig. 6 Outline drawings of the lesioned retina in CS1 and CS2. D = optic disc; L = site of lesion. Obtained from a tracing of photographs.

in the fixed retinæ of these animals. As in the cats described previously (Guillery, '72), the survival of large cells within the critical segment is not striking and the borders

that have been drawn around the zone with surviving large cells are not sharp. However, in these animals, as in the ones that were studied in more detail, the lamina A1 zone that contains large cells extends beyond the region in lamina A in which transneuronal degeneration can be recognized.

That is, the sparing effect may extend beyond the borders of the critical segment. However, since we do not know how much the deafferented zone of the lateral geniculate nucleus shrinks during development, the amount of this extension cannot be defined anatomically.

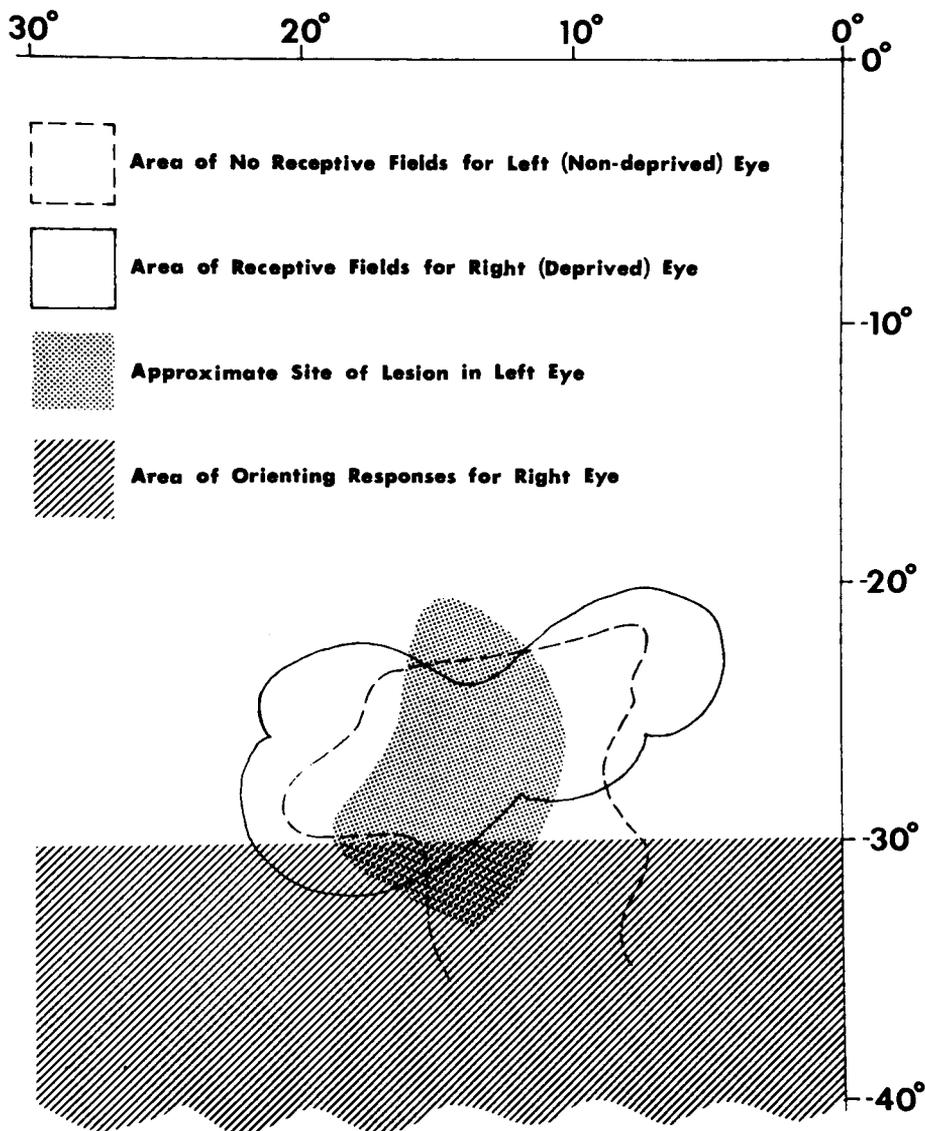


Fig. 7 Summary of critical segment data from cat CS2. The coordinate system represents the cat's visual fields with both visual axes passing through the origin. The lesion in the non-deprived, left eye (dotted area) is drawn as plotted by the technique of Fernald and Chase ('71). Corresponding to this is a region of field outlined by the dashed line in which stimuli to the left eye did not activate cortical neurons. The critical segment of cortex for the deprived, right eye determined both electrophysiologically (solid line) and behaviorally (cross-hatched area) substantially overlaps this region of visual field.

4. *A brief comparison of the behavioral and the electrophysiological approaches*

Figure 7 presents a summary of the results that have been obtained for the critical segment in cat CS2. It can be seen that in the horizontal dimension, the zone of visual sparing demonstrated behaviorally corresponds rather closely to the critical zone defined on the basis of the retinal damage. The matching here is quite good despite the error inherent in the behavioral method (approx. $\pm 10^\circ$). Along the vertical meridian the behavioral method is subject to greater errors, but in spite of this it provided a reasonable localization of the critical segment. In this cat, cortical cell activity also defined the critical segment. However, the area of the visual field from which cortical cells could be activated by the deprived eye is larger than the projection of the retinal lesion by a wide margin. The discrepancy is less if one plots the lesion in terms of the area of visual field from which no cortical responses could be elicited from the non-deprived eye (fig. 7), and this electrophysiological measure of lesion size is likely to be more accurate.

The most significant correlation is between the visual field segment from which cortical activity could be evoked through the deprived eye and the visual field segment within which it was possible to demonstrate visual sparing of the deprived eye behaviorally. Figure 7 shows this correlation for CS2. It should be noted that a similar correlation, not shown in figure 7, has also been found for the monocular segment, and that the same general correlations have been found in the other cats wherever comparable data were available.

DISCUSSION

We have shown that the visual loss produced when one eye is sutured in young kittens can be modified by damage to the other, normally open eye. This sparing of a part of the visual field of one retina, which results when the homonymous portion of the other retina is damaged, demonstrates clearly that there is a binocular interaction in the development of the visual pathways, that the interaction is competitive, and that this binocular competition acts to establish the visual functions of each retino-geniculo-cortical pathway.

1. *General considerations regarding the binocular competition*

The degree to which a competitive interaction can control the growth of lateral geniculate cells was earlier demonstrated within the monocular and critical segments of the lateral geniculate nucleus, and has been fully discussed before (Guillery and Stelzner, '70; Guillery, '72). However, the observation that relatively large cells survive within the critical and monocular segments of the nucleus gave no direct evidence about visual functions in these parts of the deprived pathways.

We have now shown that in the monocular and critical segments of cortex it is possible to record a significant amount of activation of nerve cells by visual stimulation of the deprived eye. In this respect the critical and monocular segments resemble each other and differ sharply from the binocular segments of the visual pathways.

Even the patterns of cortical activation that we have found in the monocular and critical segments do not, in themselves, give evidence of any functional visual sparing. They show the change that occurs in the relative dominance of the input from each eye, but they tell us nothing about what either input by itself can achieve in terms of the animal's visual abilities. Earlier behavioral studies (Sherman, '73, '74a) demonstrated directly that some visual sparing occurs in the monocular segments, and the observations we have made here suggest that the critical segment behaves essentially like another monocular segment.

2. *The asymmetry of the cortical deprivation effect*

Although cortical cells in the potentially binocular cortex show a general decreased responsiveness to stimulation of the deprived eye, we have found that this deprivation effect is more marked in the cortex ipsilateral to the deprived eye than in the contralateral cortex. While contralateral to the suture about 20% of the cortical recording sites could be activated by the deprived eye, ipsilaterally this number was only about 5% of the total. Because of the techniques we have used (MATERIALS AND METHODS) these figures are probably overestimates of the number of neurons driven by the deprived eye. Nevertheless, the sam-

pling bias in favor of the deprived eye does not obscure the asymmetry of the cortical activity. This asymmetry appears to reflect primarily an asymmetry of the deprivation effect. Thus, in normal cats and kittens (Hubel and Wiesel ('62, '63) found that the contralateral input dominates the ipsilateral to some extent, but that the majority of nerve cells are driven about equally by both eyes. We have found, under the conditions of our experiments, that in nine electrode penetrations made in two normally reared cats there was no evidence for any marked contralateral dominance.

The relative weakness of the deprivation effect contralateral to the deprived eye has not been found consistently in the past (e.g., Wiesel and Hubel, '63b, '65a; Hubel and Wiesel, '70). While in their early experiments Wiesel and Hubel ('63b) found that the overwhelming majority of neurons contralateral to the deprived eye were uninfluenced by the deprived eye (83 out of 84), in later experiments (Wiesel and Hubel, '65a) they found during two penetrations of cortex contralateral to the deprived eye as many as 12 cells that were influenced by that eye. Ganz et al. ('68), recording contralateral to the deprived eye, found many nerve cells that could be activated from the deprived eye, although the response was smaller and more readily fatigued than for activation from the non-deprived eye. Unfortunately, Ganz et al. recorded only from the side contralateral to the deprivation, so reported no asymmetry.

Perhaps the most striking evidence for an asymmetrical effect of deprivation upon the cortex comes from the observations of Blake et al. ('74). They raised kittens with alternating monocular deprivation and found that in one such cat 34 out of 39 monocularly driven neurons were activated only by the contralateral eye.

It is not easy to account for the different results that have been obtained in the past. The precise recording conditions and the particular region of cortex may determine the extent to which a contralateral dominance can be demonstrated. It should be noted that within the lateral geniculate nucleus the changes that are produced by a monocular deprivation affect both sides more or less equally. Thus cell growth is affected about as much in lamina A1 on

one side as in lamina A on the other (Wiesel and Hubel, '63a, '65b) and the loss of Y-cell activity is as great in lamina A as in lamina A1 (Sherman et al., '72). Since, in contrast to this, the deprived uncrossed pathway to the cortex is more severely affected than the deprived crossed pathway, it is necessary to postulate some mechanism that can operate at cortical levels but that has not been seen in studies of the geniculate levels.

Three possibilities arise: The first is that the C layers of the lateral geniculate nucleus (Hickey and Guillery, '74), within which the contralateral retinal afferents outnumber the ipsilateral afferents, may serve to trip the effects of deprivation in favor of the crossed pathways. The second possibility is related to the first. The superior colliculus sends some fibers to the C layers of the lateral geniculate nucleus (Graybiel and Nauta, '71) and also has a projection to the peristriate cortex through the pulvinar (Graybiel, '72). Thus perhaps the tectal system, which receives a predominantly crossed retinal input (Sterling, '73; Kaas et al., '74) is responsible for the balance in favor of the crossed geniculocortical pathways from the deprived eye. It is known that the direct retino-tectal pathways are not severely affected by deprivation (Sterling and Wickelgren, '70; Hoffmann and Sherman, '74) although the cortico-tectal pathways are. In the tectum, as in the cortex, one finds that stimulation of the deprived eye can activate many more cells contralaterally than ipsilaterally (Hoffmann and Sherman, '74).

The third possibility is that the contralateral dominance may be produced by lateral interactions within the geniculocortical pathways. There is some evidence that such an interaction may play a part in the development of the cortical part of the visual system (Kaas and Guillery, '73). If adjacent segments within the system do influence each other, then the contralateral retinal input would tend to dominate near the peripheral, monocular segments (in which there is no ipsilateral input), while one would expect a more even balance between the two ocular inputs for regions that represent the central retina. Since the contralateral dominance has been found in the cortex and not in the lateral geniculate nucleus (see above) one must argue

that the postulated lateral interaction is primarily cortical, not geniculate; and this is also the conclusion suggested by earlier studies (Kaas and Guillery, '73).

3. *The nature of the cortical response to visual deprivation*

In our cats the monocular and critical segments of the cortex were completely deprived of patterned visual inputs. In spite of this we were able to show that nerve cells in these cortical segments responded to stimulation of the deprived eye and that the cat was able to use activity of deprived nerve cells for visual orientations. It should be noted that the behavioral responses we have found in the critical segment are not likely to represent subcortical mechanisms. Decorticate cats react to the tests we have used either as though they were blind, or, if the tectal commissure has been split, as though they are seeing with the nasal retina only (Sprague, '66; Sherman, '74b).

Although we have shown that the monocular and critical segments of the cortex were functional in our cats, we do not know how well developed the visual functions were. It is known that deprivation *per se* does affect the structure of the visual cortex (Guillery, '74; Guillery and Kaas, '74b) and that the response properties of nerve cells in the visual cortex do depend upon the visual environment (Blakemore and Cooper, '70; Hirsch and Spinelli, '70; Pettigrew, '74). It will obviously be of interest to make a more detailed study of the response properties of individual cortical cells in the critical and monocular segments after a monocular deprivation, in order to determine exactly how these neurons differ from normal cortical nerve cells.

Further studies of the behavioral capacities of cats like those described here may also prove valuable, since they may provide a fuller picture of the capacities of visually deprived cortex. They may also give a better correlation between the electrophysiological responses of cortical cells and the behavioral responses of the cat. It should be noted that contralateral to the deprived eye we recorded activity driven from the deprived eye at about 20% of the recording sites. At present there is no indication whether such cells have any functional connections with motor pathways, and it is not known to what extent these cells

may be responsible for some of the visual behavior that survives visual deprivation (Dews and Wiesel, '70; Rizzolatti and Tradardi, '71; Chow and Stewart, '72).

It is possible that the discrimination learning that can be demonstrated through the deprived eye after a monocular deprivation depends to some extent upon the sparing of the monocular segment (Sherman, '73). If this is so, then adding a critical segment to the monocular segment should improve this discrimination. As the size of the critical segment is increased, so the amount of the responsive cortex will increase, and the best behavioral responses will be obtained when the critical segment is largest. The critical segment is largest when the normal eye is removed, and this leads to the prediction that such a "critical eye" cat, that is a cat with one eye sutured and the other removed, will develop relatively normal vision for the sutured eye. However, observations of binocularly sutured cats suggest a different result.

Cats that are raised with both eyes sutured show no orienting response to stimuli falling upon the temporal retina. That is, they behave as though they were using retino-tectal pathways and as though the geniculo-cortical pathways had not developed the functional capacity for such responses (Sherman, '72b, '73, '74b). Such an interpretation of the development is supported by the observation that, in cats raised with both eyes sutured, Y-cell activity cannot be recorded to any extent even in the monocular segments of the lateral geniculate nucleus (Sherman et al., '72). Thus, the development is abnormal in the whole of the lateral geniculate nucleus, even in the parts where there can be no competition, and in this the binocularly deprived cats differ strikingly from those that are monocularly deprived. The view that the geniculo-cortical system develops very little after a binocular suture (Pettigrew, '74), whereas it develops on the basis of binocular competition after a monocular suture, is further supported by the effect of cortical lesions, which can severely influence orienting behavior in monocularly deprived but not in binocularly deprived cats (Sherman, unpublished observations).

A segment of cortex, such as the critical or monocular segment, which is completely deprived, but which lies next to cortex that still receives a monocular input, is, there-

fore, functionally quite different from a segment of cortex that forms a part of a completely deprived visual cortex. The difference is probably due to the type of interaction referred to above. Presumably, the function of neurons in the critical or monocular segments depends upon their position adjacent to cortex that is receiving normal inputs. Apart from such a possible "neighborhood" or "transcortical" effect, there can be no differences between the monocular segment of cortex in a monocularly deprived and a binocularly deprived cat.

4. *The borders of the competitive interaction*

It has been found that in the lateral geniculate nucleus the zone of large cell survival in the deprived geniculate lamina extends beyond the borders of the zone of transneuronal degeneration in the adjacent, non-deprived lamina (figs. 4, 5; Guillery, '72). Correspondingly, in terms of cortical cell activity the region of visual sparing in the deprived eye extends beyond the borders of the visual loss in the lesioned eye (fig. 3).

This overlap region is difficult to evaluate in terms of geniculate histology because there may have been considerable shrinkage within the zone of transneuronal degeneration. However, it has been found quite consistently in this and in other studies that the zone of large cell survival in the monocular segment of lamina A overlaps the lateral border of lamina A1. Thus, the overlap of cortical receptive fields probably corresponds to the overlap of geniculate cell sparing. Even though the overlap noted in the cortical records of the critical segment may owe something to experimental errors, such as residual eye movements, it is reasonable to conclude that some of the overlap we have observed demonstrates that the binocular competition is not strictly limited by the lines of projection.

Further and more accurate studies of this overlap phenomenon are justified. Our cortical records are not sufficient to show the extent to which the monocular sparing overlaps into the binocular segment of the geniculo-cortical system, but one can expect to find that cortical records will show an overlap corresponding at least to the geniculate histology.

The occurrence of an overlap zone demonstrates that at some level, either within the lateral geniculate nucleus or in the cortex, the pathways from the two eyes can compete across the lines of projection that represent single points in the visual field. It is possible that this represents an overlap between the normal pathways from each eye, and such an overlap would be consistent with Bishop's ('73) theory that cortical receptive field disparities form a basis for stereopsis in the cat (Barlow et al., '67; Nikara et al., '68; Joshua and Bishop, '70). The overlap zone that we have found is approximately the size to be expected on the basis of this theory (Joshua and Bishop, '70). However, it is also possible that the overlap is produced by abnormal axonal growth occurring after the retinal lesion has been made.

5. *The representation of the optic disc*

If there is a competitive interaction, one can ask whether it affects the parts of the visual system within which the blind spot is represented. Within lamina A of the lateral geniculate nucleus the blind spot is represented as a cell free zone (Kaas et al., '73), and the cells that lie in lamina A1 opposite this zone would probably not be involved in any binocular competition. So far we have found no strong evidence that there is any sparing for the deprived eye in the critical segment that would correspond to the optic disc of the normal eye. There is no good evidence that geniculate cell growth is affected (Guillery, '72) and in this study we have found no sparing in electrophysiological or behavioral terms. It is possible that the relevant region is so small that it was missed, or perhaps the overlap effect discussed in the previous section produces a graded effect at the edge of the critical segment. Thus, it may be that more subtle methods will be needed to reveal such a small critical segment and that only critical segments significantly larger than the width of the overlap zone itself can produce a zone of sparing that is readily identifiable with the methods used so far.

The nature of the competitive interaction

Although our results demonstrate quite clearly that there is a competitive interaction, they do not provide much evidence

about the nature of this interaction. The simplest hypothesis is that geniculo-cortical axons compete for synaptic space upon cortical cells and that, by some undefined mechanism, axons coming from non-deprived geniculate cells are favored over axons that come from deprived cells. The pattern of cortical activity recorded after a monocular deprivation originally suggested such a hypothesis (Wiesel and Hubel, '63b, '65a) and no subsequent observations have provided evidence against it. Other mechanisms, involving translaminar pathways within the lateral geniculate nucleus or corticogeniculate feed-back pathways cannot be excluded (Guillery and Stelzner, '70; Guillery, '72). It is possible that the process by which one set of connections is favored over another involves complex intracortical circuits, but nothing is known about this process.

The evidence that has been obtained in terms of geniculate cell growth suggests that the largest geniculate cells are involved in the competitive interaction, and the observations of Y-cell activity lead to the same conclusion. There is some evidence that these large geniculate cells project to areas 17 and 18 in the cat (Garey and Powell, '67) and the same is true of Y-cells (Stone and Dreher, '73). It is thus of interest to note that most of our recordings of activity in the critical segment were obtained from area 17. We do not know where the primary competition is occurring; it may be in both areas 17 and 18, or it may involve one area primarily and this area may then modify the other, either through direct pathways or via the lateral geniculate nucleus.

At present the most complete evidence about binocular competition in the development of visual pathways comes from studies of cats. The cell shrinkage that occurs following monocular deprivation of infant squirrels (Guillery and Kaas, '74a), tree shrews (Casagrande et al., '74) or dogs (Sherman and Wilson, '74) has been studied and this shows the same pattern of change as in cats: within the binocular segments the geniculate cells are abnormally small, but within the monocular segments they are unaffected. Monocular deprivation in dogs produces the same pattern of visual loss as in cats: for the de-

prived eye there is visual sparing in the monocular segment and a loss in the binocular segment. Thus, it is probable that the phenomenon we have demonstrated in cats will be found more generally in other species that have binocular geniculo-cortical pathways.

The geniculate cell changes that are produced by monocular deprivation in infant monkeys have also been investigated recently (von Noorden, '73; Headon and Powell, '73). While both studies demonstrated that the deprived cells are smaller than the non-deprived cells, neither looked at the monocular segment, presumably because this is very small in monkeys (Kaas et al., '72) and hard to define in frontal sections. Headon and Powell point out that in the monkey, cortical cells in layer IV do not receive a binocular input. Instead, geniculo-cortical axons end within discrete monocular columns of the cortex (Hubel and Wiesel, '72). Headon and Powell argue that, therefore, the geniculate changes seen in the monkey cannot reflect a binocular competition occurring at cortical levels, and that the competition is likely to be an interlaminar competition occurring at geniculate levels.

The data presented by Headon and Powell do not themselves demonstrate any binocular competition. To identify binocular competition, it is simplest to compare the effects in the monocular segment with those in the binocular segment. If binocular competition is demonstrated in monkeys, then it remains to be determined at what level it is occurring. It is entirely possible that geniculo-cortical axons compete for cortical columns in the monkey, while they compete for individual cells in the cat. It would then be easier to look for histological evidence of the cortical competition in monkeys, because the cortical columns can be demonstrated by degeneration methods (Hubel and Wiesel, '72), and this may prove to be a particularly useful way in which to look for evidence of competition at cortical levels.

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