

Effects of Early Monocular Lid Suture on Spatial and Temporal Sensitivity of Neurons in Dorsal Lateral Geniculate Nucleus of the Cat

STEPHEN LEHMKUHLE, KENNETH E. KRATZ, STUART C. MANGEL, AND S. MURRAY SHERMAN

Department of Physiology, University of Virginia School of Medicine, Charlottesville, Virginia 22908

SUMMARY AND CONCLUSIONS

1. We measured spatial and temporal contrast thresholds for 70 X- and 40 Y-cells in the lateral geniculate nucleus of cats raised with monocular eyelid closure. Of these cells, 52 X-cells and 30 Y-cells were located in the deprived laminae (i.e., the laminae of the lateral geniculate receiving input from the previously lid-sutured eye). The stimulus display employed to measure contrast thresholds was a vertically oriented counterphased sine-wave grating (see Ref. 21).

2. The spatial contrast sensitivity functions were measured at a temporal frequency of 2 cycles/s. These functions for deprived X-cells revealed a sensitivity loss to higher spatial frequencies. At lower spatial frequencies, these deprived X-cells exhibited normal sensitivity. The spatial resolution of deprived X-cells, which was the highest spatial frequency to which a cell responded at 0.6 contrast, was approximately one-half of that measured for nondeprived X-cells at all retinal eccentricities; this included cells located in the monocular segment. The few deprived Y-cells that were studied in the binocular segment and all in the monocular segment exhibited normal spatial sensitivity.

3. The temporal contrast sensitivity functions were measured with the spatial frequency at which each cell exhibited the lowest contrast threshold. The temporal contrast sensitivity functions for deprived X-cells revealed no effects of deprivation. Consequently, temporal resolution, which

was the highest temporal frequency to which the cell responded at 0.6 contrast, was roughly equivalent for deprived and nondeprived X-cells at all retinal eccentricities. The few temporal functions measured for deprived Y-cells were also within the range observed for nondeprived Y-cells.

4. Receptive-field center sizes for deprived X-cells were not different from those of nondeprived X-cells. This was true for estimates of center size based on hand plotting, as well as those based on area-response functions. The area-response functions indicated that the major receptive field property of X-cells that was altered by lid-suture deprivation was the sensitivity of the center to small stimuli.

5. We conclude in monocularly sutured cats that the development of Y-cells is primarily governed by binocular competition, whereas the development of X-cells is mainly influenced by a mechanism that does not involve binocular competition.

INTRODUCTION

Two physiological effects are evident in the lateral geniculate nucleus of cats that have been raised with the lids of one eye sutured closed. First, the proportion of recordable Y-cells relative to X-cells is abnormally low in the deprived laminae of the nucleus (23, 25, 33), and second, the spatial acuity or resolution of X-cells in the deprived laminae is reduced (20). We define spatial resolution as the highest spatial fre-

quency stimulus to which the cell responds (see preceding paper, Ref. 21). The purpose of this paper is to extend these observations in several ways.

First, we wished to determine if deprived X-cells have an abnormally low spatial resolution at all retinal eccentricities, including the monocular segment.¹ The reduction of recordable Y-cells is confined to the binocular segment of deprived geniculate laminae. If deprivation has a similar effect on X-cell development, then the spatial resolution should be normal for X-cells in the deprived monocular segment of the lateral geniculate nucleus. Second, since lid suture nonselectively attenuates all spatial frequencies in the visual environment,² it could be predicted that a cell deprived in such a manner during development would lose sensitivity to all spatial frequencies within its normal range. Currently, it is known that deprived X-cells have a reduced sensitivity to high spatial frequencies (20), but it is unknown whether sensitivity at low spatial frequencies is also impaired. Third, in the binocular segment of deprived laminae, Y-cells are rarely encountered with a microelectrode; however, visual responses can be measured for these cells (33). We wished to determine if these surviving Y-cells had normal spatial and temporal sensitivity. Likewise, we were interested in such sensitivity of Y-cells in the deprived monocular segment.

To answer these questions, we measured contrast thresholds for sine-wave grating patterns of different spatial and temporal frequencies. We compared sensitivities measured in this way among deprived, non-

deprived, and normal X- and Y-cells with receptive fields representing a number of retinal eccentricities.

METHODS

Twelve cats were born and reared in the laboratory. Each cat had the lids of one eye sutured at 5–8 days of age (i.e., before natural eye opening), and they were maintained in this fashion until the time of recording at 7–28 mo of age (mean age of 21 mo). The kittens were inspected daily to ensure there were no openings in the lids, and the deprived eye was opened just prior to the terminal recording session. Physiological methods were identical to those described in the preceding paper (21). Also, see this paper (21) for descriptions of spatial and temporal contrast sensitivity functions, area-response functions, etc.

RESULTS

Response properties were determined for 70 X-cells and 40 Y-cells from laminae A and A1. Their receptive fields were all within 25° of the horizontal zero parallel and ranged from area centralis to 85° eccentric. Of these cells, 52 X- and 30 Y-cells were located in the deprived laminae. Complete spatial contrast sensitivity functions were determined for 42 deprived and 13 nondeprived X-cells and for 21 deprived and 7 nondeprived Y-cells. Complete temporal contrast sensitivity functions were determined for 39 deprived and 11 nondeprived X-cells and for 18 deprived and 7 nondeprived Y-cells. No differences between deprived cells located in laminae A and A1 were found for any of the response properties measured. Thus, data from these laminae were pooled (see, however, Ref. 11).

Normal versus nondeprived X- and Y-cells

There were no discernible and statistically significant differences on these tests between X-cells in normally reared cats and X-cells located in the nondeprived laminae of the monocularly deprived cats; this was also true for Y-cells (21). Since these two cell groups were indistinguishable, we combined normal and nondeprived cells to increase the data base against which deprived X- and Y-cells could be compared. Therefore, in the remainder of this section, the

¹ The binocular segment of the central visual pathways (including striate cortex) is the portion whose neurons have receptive fields within the binocularly viewed portion of the cat's visual field. The monocular segments contain neurons whose receptive fields are in the peripheral, monocularly viewed crescents of the visual field (see also Refs. 7, 33).

² It is assumed here that the eyelid is a diffuser and attenuates equally the contrast of all spatial frequencies. Informal observations suggested to us that the eyelid of the cat is a nearly perfect diffuser. For instance, we were unable to resolve through the eyelid of an adult cat a bright, low spatial frequency, square-wave grating of nearly 100% contrast. Also, it is known that the eyelid of the cat reduces the overall luminance from 1 to 3 log units (26).

cells referred to as nondeprived include observations from the nondeprived laminae of monocularly deprived cats and from both laminae of normal cats (normal data from Ref. 21).

Spatial contrast sensitivity

X-CELLS. The spatial contrast sensitivity functions of three typical deprived X-cells are shown in Fig. 1. Deprived X-cells, like nondeprived X-cells, exhibited an attenuation in sensitivity to low spatial frequencies. This was a clear trait of every deprived X-cell located in binocular segment. However, not every X-cell in the monocular segment exhibited an attenuation in sensitivity to low spatial frequencies. This has

also been observed for normal X-cells located in the monocular segment (21).

The effect of deprivation on X-cells was seen only at higher spatial frequencies as abnormally low sensitivity. At lower spatial frequencies, contrast sensitivity was not reduced. Furthermore, the spatial frequency with the lowest contrast threshold (i.e., peak sensitivity) was located at a lower spatial frequency for deprived than for nondeprived X-cells ($P < 0.01$ on a Mann-Whitney U test). These results can be seen in Fig. 1D, in which the average spatial contrast sensitivity functions are shown. These functions were averaged for 17 deprived and for 11 nondeprived X-cells whose receptive fields were located within

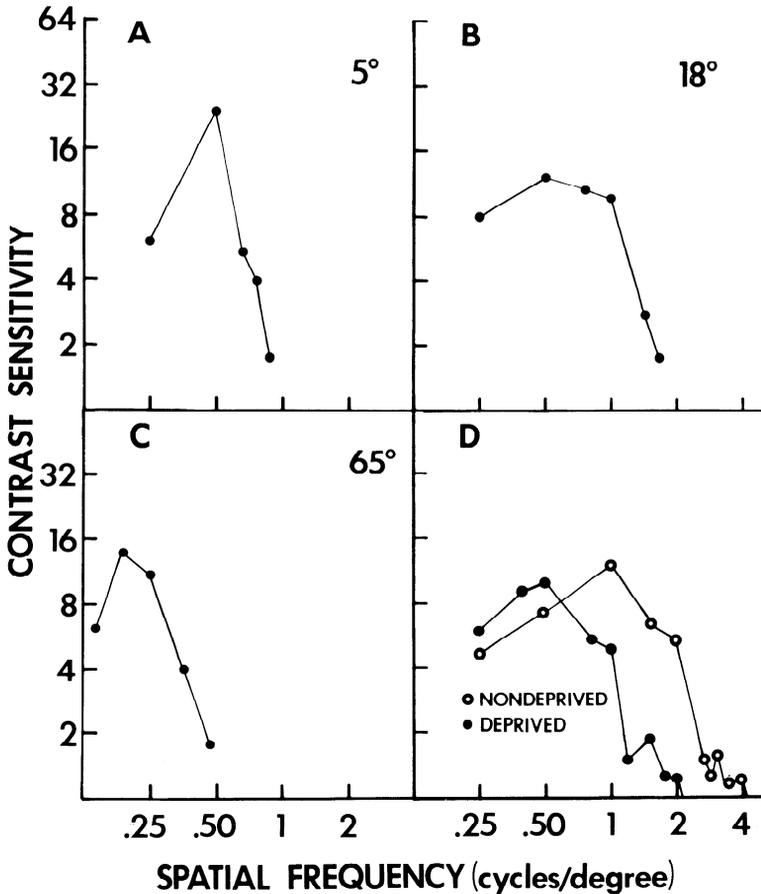


FIG. 1. Spatial contrast sensitivity functions of deprived X-cells. *A, B, C*: spatial functions for three typical X-cells in deprived laminae. The number with each function indicates the receptive-field eccentricity from area centralis. *D*: average functions for 17 deprived and 11 nondeprived X-cells with receptive fields within 10° of the area centralis. Open circles denote the average sensitivities for the nondeprived X-cells; filled circles, for the deprived X-cells.

the central 10° of visual space. The difference between deprived and nondeprived X-cells is further illustrated in Figs. 2 and 3. In Fig. 2 (upper), the mean spatial resolution (± 1 standard error) is plotted as a function of retinal eccentricity for deprived and nondeprived X-cells. Figure 3 shows the deprived and nondeprived X-cell distributions of spatial resolution, both for the entire population and for each eccentricity group. Although the spatial resolution of deprived and nondeprived X-cells declines with increasing retinal eccentricity, at each retinal eccentricity, deprived X-cells have a lower

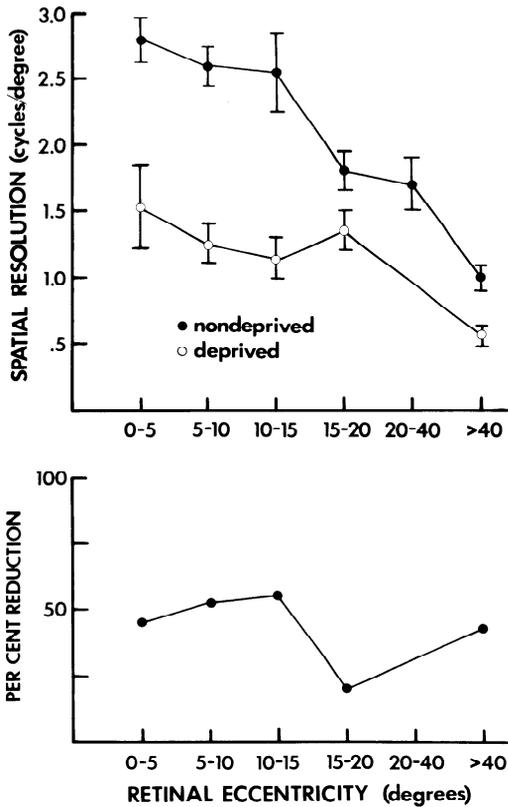


FIG. 2. Mean spatial resolution of deprived and nondeprived X-cells plotted as a function of receptive-field eccentricity from area centralis. These were measured using a sine-wave grating of 0.6 contrast, counter-phased at 2 cycles/s (see text for details). Bars in the upper part of the figure indicate ± 1 standard error of the mean. Filled circles denote means for nondeprived X-cells; open circles, for deprived X-cells. The bottom part of the figure plots the percent reduction in spatial resolution as a function of retinal eccentricity. The number of cells in each group can be inferred from Fig. 3.

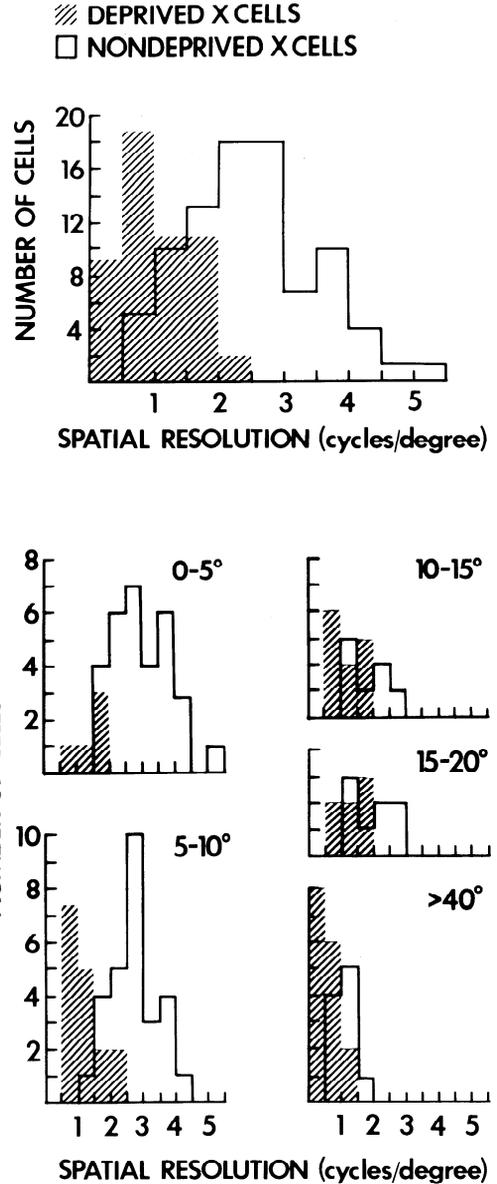


FIG. 3. Cell frequency distributions of spatial resolution for deprived and nondeprived X-cells. The frequency distributions combining all observations are shown in the upper part of the figure. The frequency distributions for six retinal eccentricity groups are separately shown in the lower part of the figure. Open frequency histograms denote distributions for nondeprived X-cells; crosshatched, for deprived X-cells.

spatial resolution ($P < 0.001$ on a Mann-Whitney U test), and the proportion of this reduction is not strongly related to eccentricity (Fig. 2, lower). In other words, X-cells in the monocular segment seem as af-

ected by lid suture as are those in the binocular segment.

Y-CELLS. The spatial contrast sensitivity functions of three typical deprived Y-cells are shown in Fig. 4. There seemed to be no effect of deprivation on spatial contrast sensitivity of deprived Y-cells, and neither deprived nor nondeprived Y-cells exhibited reduced sensitivity to lower spatial frequencies. This result is shown in Fig. 4D, which depicts the average spatial contrast sensitivity functions for deprived and nondeprived Y-cells. These functions were averaged for four deprived and seven nondeprived Y-cells whose receptive fields were located within 20° of the area centralis.

This apparent normality of deprived Y-cells is further illustrated in Fig. 5. This shows the distributions of spatial resolution for deprived and nondeprived Y-cells located within the binocular segment (upper) and within the monocular segment (lower). The difference between the spatial resolution of deprived and nondeprived Y-cells are statistically significant in neither the binocular nor monocular segment ($P > 0.10$ on a Mann-Whitney U test).

Temporal contrast sensitivity

X-CELLS. The temporal contrast sensitivity functions of three typical deprived X-cells are shown in Fig. 6A-C. As mentioned earlier, these functions were gener-

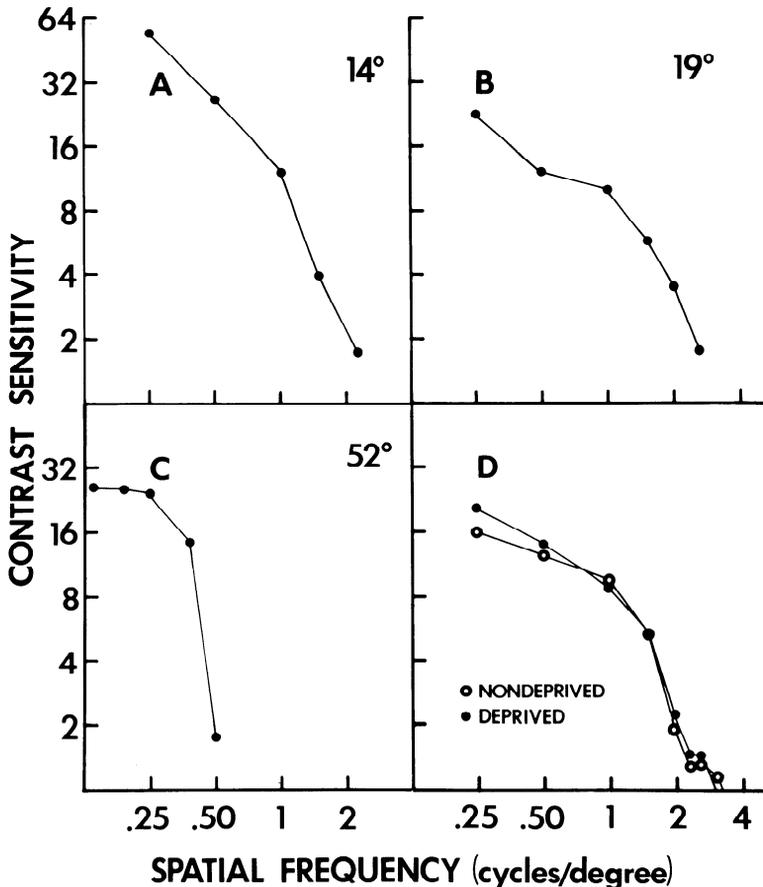


FIG. 4. Spatial contrast sensitivity functions of deprived Y-cells. A, B, C: spatial functions for three typical Y-cells in deprived laminae. The number with each function indicates the receptive-field eccentricity from area centralis. D: average functions for four deprived and for seven nondeprived Y-cells with receptive fields within 20° of the area centralis. Open circles denote the average sensitivities for nondeprived Y-cells; filled circles, for deprived Y-cells.

ated using the spatial frequency to which the cell was most sensitive. As for nondeprived X-cells, sensitivity systematically decreased with increasing counterphase rates, and no low temporal frequency attenuation was seen. We found no effect of deprivation on the sensitivity of X-cells to any temporal frequency. This result is shown in Fig. 6D, which shows complete overlap in the average temporal contrast sensitivity functions of the deprived and nondeprived X-cells. These temporal functions were averaged from 14 deprived and 9 nondeprived X-cells whose receptive fields were located within 10° of the area centralis.

Consequently, the temporal resolution of deprived X-cells also seemed normal. In Fig. 7, the mean temporal resolution (± 1 standard error) is plotted as a function of retinal eccentricity for both deprived and nondeprived X-cells. Figure 8 illustrates the distributions of temporal resolution both for the entire neuronal population and for groups based on receptive-field eccentricity. There was no statistical difference in the temporal resolution between deprived and nondeprived X-cells either at any eccentricity or for the entire population ($P > 0.10$ on a Mann-Whitney U test).

Y-CELLS. There also seemed to be no effect of deprivation on the temporal sensitivity of Y-cells. In Fig. 9A–C, three representative temporal contrast sensitivity functions from our sample of deprived Y-cells are shown. The shape of these functions appeared normal in that there was no attenuation in sensitivity to lower temporal frequencies and a systematic decrease in sensitivity to higher temporal frequencies. The average temporal functions, which are shown in Fig. 9D, reveal no marked difference in sensitivity at any temporal frequency. These contrast sensitivity functions were averaged for four deprived and for six nondeprived Y-cells whose receptive fields were located within 20° of the area centralis.

The temporal resolution for deprived Y-cells was also similar to that found for nondeprived Y-cells. This result is shown in Fig. 10, in which cell distributions of temporal resolution are shown for deprived and nondeprived Y-cells located within the binocular segment (upper) and monocular segment (lower) of the nucleus.

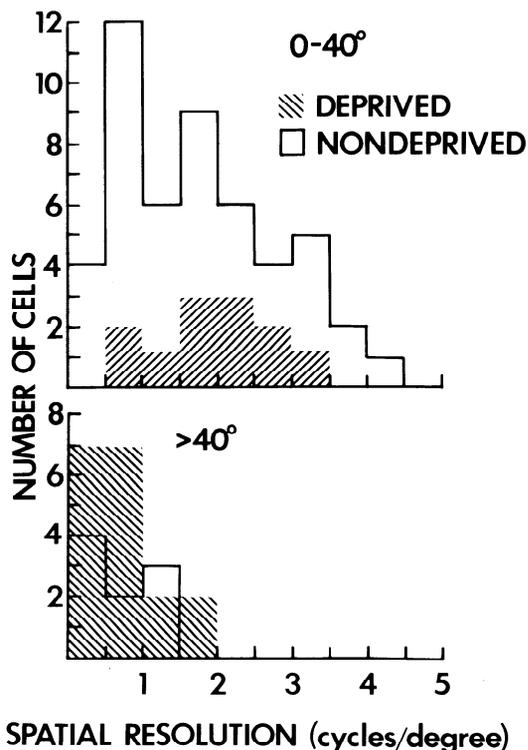


FIG. 5. Cell frequency distributions of spatial resolution for deprived and nondeprived Y-cells. The frequency distributions for deprived and nondeprived Y-cells with receptive fields in the binocular segment of visual field are shown in the upper part of figure. The frequency distributions for these cell groups with receptive fields in the monocular segment of visual field are shown in the lower part. Open frequency histograms indicate the distributions for nondeprived Y-cells; crosshatched, for deprived Y-cells.

Relationship between center size and spatial resolution

X-CELLS. There was a correlation between size of the receptive-field center, as determined by hand plotting (21), and the inverse of spatial resolution (expressed as deg/cycle) of deprived X-cells. The correlation for deprived X-cells ($r = 0.41$; $P < 0.01$) was similar to that observed for nondeprived X-cells ($r = 0.55$; $P < 0.01$), and the two correlations do not significantly differ ($P > 0.10$ on a Z test). Nor did the slopes of the regression lines for normal and deprived X-cells statistically differ ($P > 0.10$ on an F test). However, the intercepts of these regression lines were statistically different ($P < 0.001$ on an F test). Furthermore, hand plotting failed to reveal

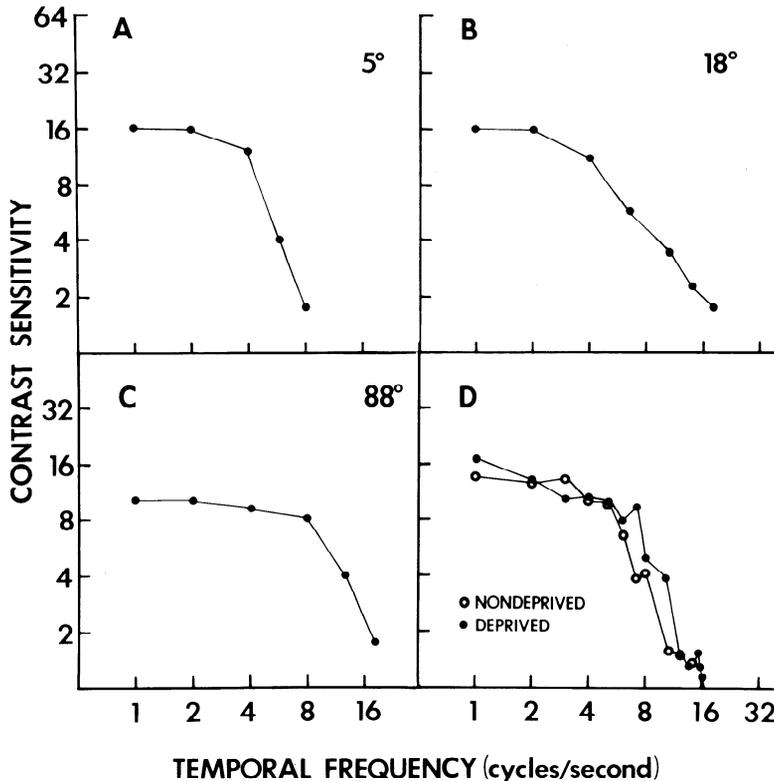


FIG. 6. Temporal contrast sensitivity functions of deprived X-cells. A, B, C: temporal functions for three typical X-cells in deprived laminae. The number of each function indicates the receptive-field eccentricity from area centralis. D: average functions for 14 deprived and for 9 nondeprived X-cells with receptive fields within 10° of the area centralis. Open circles denote the average sensitivities for the nondeprived X-cells; filled circles, for the deprived X-cells.

any difference in center sizes between deprived and nondeprived X-cells ($P > 0.10$ on a Mann-Whitney U test; see Ref. 33). In other words, deprived X-cells have normal center sizes even though, when compared to nondeprived X-cells, they display poorer spatial resolution and a similar relationship between spatial resolution and center size.

However, we were concerned about the relative imprecision of hand-plotting methods since the receptive fields of X-cells are relatively small and tiny differences among receptive-field centers may not have been resolved. Therefore, for nine deprived X-cells, we adopted a different and more quantitative measure of center size based on area-response functions. These functions measured neuronal response as a function of the area of a flashing spot carefully

centered on the receptive field, and the spot size that evoked the maximum discharge was taken as the center size. For details concerning this method, see the previous paper (21). We failed with this method, as well, to reveal any significant difference between center sizes of deprived and nondeprived X-cells ($P > 0.10$ on a Mann-Whitney U test). Nevertheless, the spatial resolution of the deprived X-cells in this sample was markedly lower than the nondeprived X-cells ($P < 0.001$ on a Mann-Whitney U test).

A typical example of an area-response function of a deprived X-cell is shown in Fig. 11A. The striking feature of this area-response function is the relatively small response elicited by the cell to small spot sizes, and this was generally true for the deprived X-cells. This is further illustrated in Fig. 11B, in which averaged area-re-

sponse functions are shown for nine deprived and nine nondeprived X-cells. Deprived X-cells tended to elicit a smaller response to spot sizes less than the size of the center of the receptive field. However, there were no consistent differences between the responses of deprived and nondeprived X-cells to spot sizes larger than the center, since both groups exhibited response attenuation to larger spot sizes.

Y-CELLS. There was a small correlation between center size estimated by hand plotting and the inverse of spatial resolution of deprived Y-cells. This correlation was similar to that observed for normal Y-cells. There was no difference in center sizes of deprived and nondeprived Y-cells ($P > 0.10$ on a Mann-Whitney U test). We measured area-response functions for only three deprived Y-cells in the binocular segment, since few could be located there (33). However, each area-response function was indistinguishable from the area-response functions of normal Y-cells (see previous paper, Ref. 21).

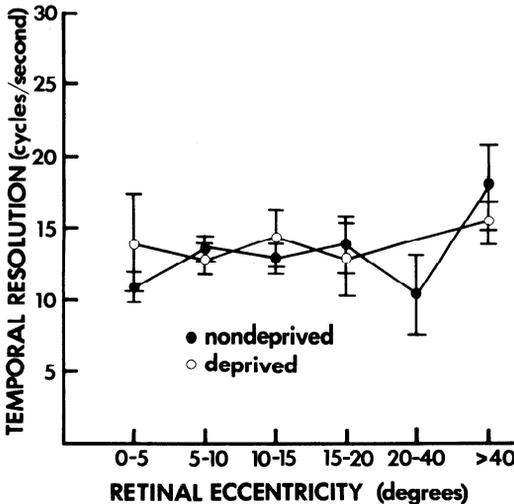


FIG. 7. Mean temporal resolution of deprived and nondeprived X-cells plotted as a function of receptive-field eccentricity from area centralis. The temporal resolutions were measured using a sine-wave grating of 0.6 contrast, at a spatial frequency for which the cell exhibited the lowest contrast threshold (see text for details). Bars indicate ± 1 standard error of the mean. Filled circles denote means for nondeprived X-cells; open circles, for deprived X-cells. The number of cells in each group can be inferred from Fig. 8.

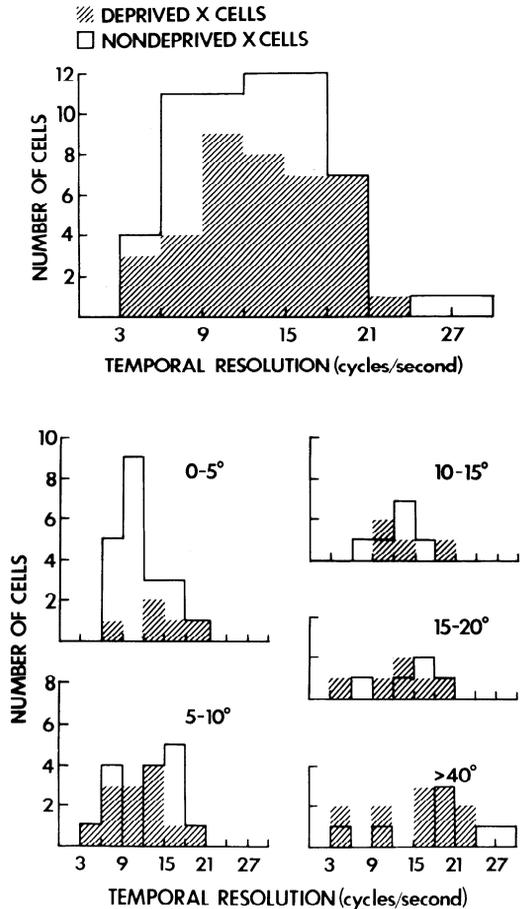


FIG. 8. Cell frequency distributions of temporal resolution for deprived and nondeprived X-cells. The frequency distributions for all retinal eccentricities are shown in the upper part of the figure. The frequency distributions for six different retinal-eccentricity groups are separately shown in the lower part of the figure. Open frequency histograms indicate distributions for nondeprived X-cells; crosshatched, for deprived X-cells.

DISCUSSION

Early lid suture affects the development of spatial and temporal sensitivity in geniculate X- and Y-cells in different ways. In this section of the paper, these effects are summarized and discussed; some theoretical implications of these findings concerning development of X- and Y-cells are presented; and finally, the findings are compared with similar observations made in strabismic cats.

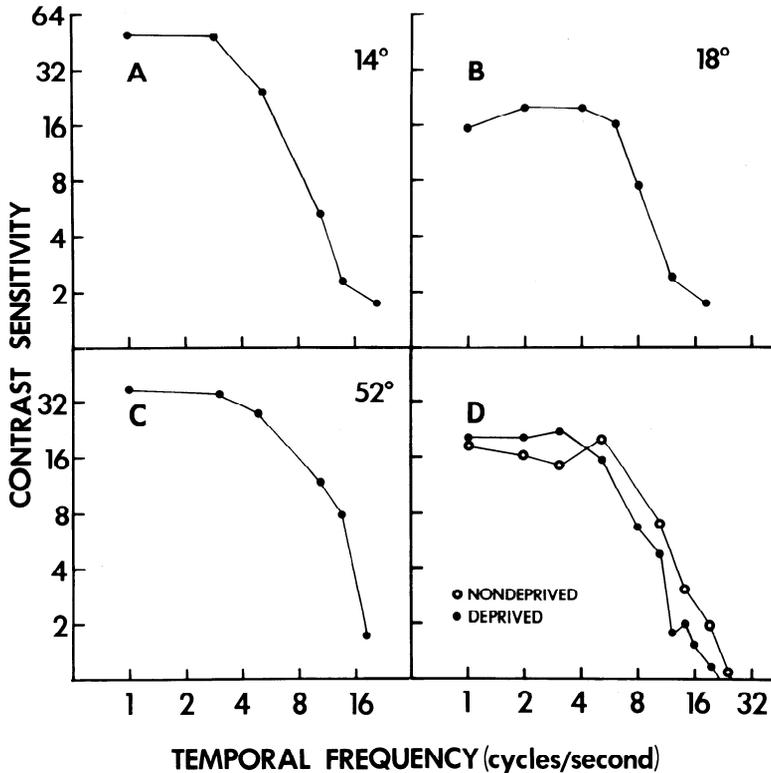


FIG. 9. Temporal contrast sensitivity functions of deprived Y-cells. *A, B, C*: temporal functions for three typical Y-cells in deprived laminae. The number with each function indicates the receptive-field eccentricity from area centralis. *D*: average functions for four deprived and six nondeprived Y-cells with receptive fields within 20° of area centralis. Open circles denote the average sensitivities for nondeprived Y-cells; filled circles, for deprived Y-cells.

Physiological effects of deprivation on X-cells

We have recently shown that monocular deprivation affects the development of X-cells (20). The present data extend this finding to show that rearing with lid suture impairs the sensitivity of X-cells only at higher spatial frequencies. At lower spatial frequencies, contrast sensitivity seems normal, although there may be a shift downward in the spatial frequency that evokes the lowest threshold response. This selective deficit in spatial contrast sensitivity cannot be explained simply by the nature of the deprivation, since lid suture limits the transmission of all spatial frequencies during development (see footnote 2). That is, loss of high spatial frequency sensitivity is not due simply to deprivation selectively eliminating high spatial frequencies. The loss of sensitivity to high spatial frequencies

occurs for X-cells located throughout the nucleus, including those X-cells located in the monocular segment. This is in direct contradistinction to the effect deprivation has on Y-cells, and the theoretical implications of this difference will be discussed in a subsequent section.

Although there seems to be a loss in sensitivity to higher spatial frequencies, this deficit is not accompanied by an obvious change in the size of the center of deprived X-cells. Center sizes of these cells, estimated either by hand plotting or by area-response functions, are indistinguishable from center sizes of normal X-cells. In addition, the surround antagonism of the center response, as revealed by the area-response functions, is unchanged. One observation that supports indirectly the contrary notion that center sizes of deprived X-cells are slightly larger is the finding that

deprived X-cells seem to exhibit a peak sensitivity to lower spatial frequencies than do normal X-cells. This assumes, of course, that the spatial frequency that elicits the peak sensitivity and center size are closely related (see footnote 3 in previous paper, Ref. 21; see also Table 1 of Ref. 17). Nevertheless, if there is a change in center size for deprived X-cells, it must be quite small since we were unable to detect one with more direct measures of center size.

The major effect of deprivation on the area-response functions of X-cells observed in these experiments is to reduce the sensitivity of the center response to small flashing spots. Since the spot size needed to evoke a threshold response in these cells was abnormally large, it would seem that the spatial summation characteristics of the center were altered by deprivation. This also suggests that the spatial summation characteristics of the center are important for spatial acuity, and that the size of center is less directly related to spatial resolution.

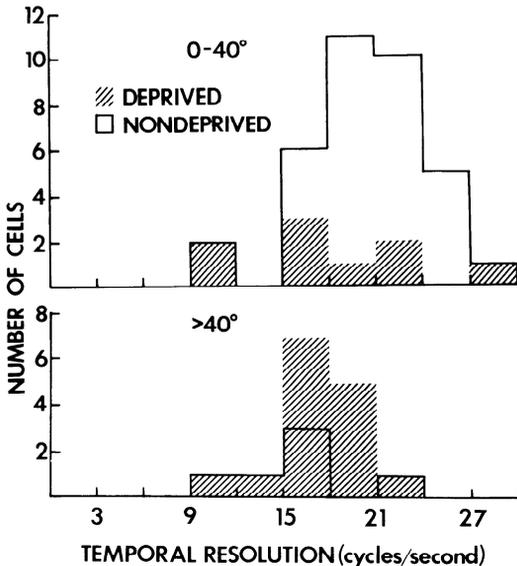


FIG. 10. Cell frequency distributions of temporal resolutions for deprived and nondeprived Y-cells. The frequency distributions for deprived and nondeprived Y-cells with receptive fields in the binocular segment of visual field are shown in the upper part of the figure. The frequency distributions for these cell groups with receptive fields in the monocular segment of visual field are shown in the lower part. Open frequency histograms indicate distributions for nondeprived Y-cells; crosshatched, for deprived Y-cells.

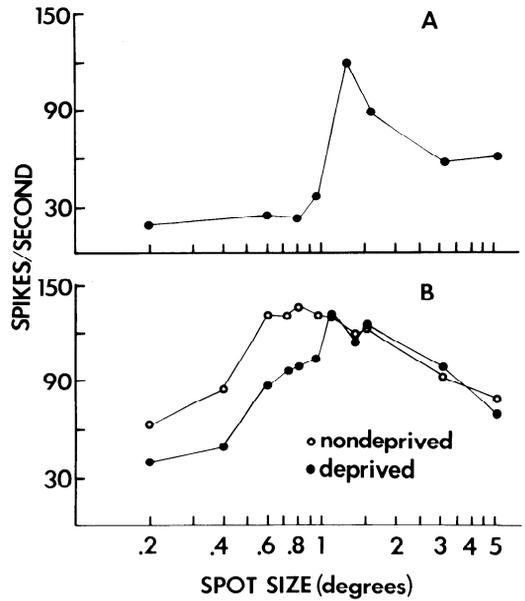


FIG. 11. Area-response functions for deprived and nondeprived X-cells. These functions plot response magnitude (spikes/s) as a function of spot size (degrees of visual angle). A: area-response function measured for a deprived X-cell. B: area-response functions that have been averaged for nine nondeprived and for nine deprived X-cells. Open circles denote averages for the nondeprived X-cells; filled circles, for the deprived X-cells.

Two observations support this notion. First, as already mentioned, deprived X-cells have a lower spatial resolution but have centers of roughly normal size. The second observation is the disparity between the sizes of the center and of a bar of a grating the cell is able to resolve. On the average, the width of a bar of a grating at the highest spatial frequency to which the cell responds is more than 3 times smaller than the diameter of the center of a normal X-cell (see the previous paper, Ref. 21).

Unlike spatial sensitivity, the development of temporal sensitivity seems to be unaffected in deprived X-cells. The observation of normal temporal contrast sensitivity functions for deprived X-cells in the present experiments extends an earlier observation that temporal resolution of X-cells is unaffected by deprivation (20). It is important to note, however, that the apparent temporal normality of deprived X-cells is dependent on selecting a spatial frequency for which a deprived cell exhibits maximum

contrast sensitivity. This spatial frequency for deprived X-cells tended to be lower than that for nondeprived X-cells (see above). If, for example, we had employed the same spatial frequency (i.e., 1.0 cycles/deg) to measure the temporal contrast sensitivity of all cells, deprived X-cells on average would have exhibited a lower sensitivity at all temporal frequencies than would have nondeprived X-cells.

Physiological effects of deprivation on Y-cells

In these experiments, there were no obvious abnormalities in either the spatial or temporal contrast sensitivity functions of the few deprived Y-cells from which we were able to record. Furthermore, the few area-response functions we obtained from these cells also appeared normal. Although we were unable to uncover any effects of deprivation on any of these tests, other data indicate rather severe deprivation effects on geniculate Y-cells in the binocular segment, including their functional loss (5, 23–25, 33, 34). From the present work, it appears that those Y-cells from which we were able to record appeared to have normal spatial and temporal sensitivities.

Binocularly competitive and noncompetitive mechanisms of visual development: effects of deprivation on X- and Y-cells

It has been suggested that during rearing with monocular lid suture, cells related to the closed eye are at a competitive disadvantage and, consequently, cells related to the open eye dominate central visual pathways (6, 7, 31–34, 36). This hypothetical mechanism of development has been referred to as binocular competition. Binocularly noncompetitive forms of development are implicated if the deficits observed for a cell following monocular deprivation are attributed simply to the eye's deprivation per se and not to any imbalance between central pathways related to each eye. These two hypothetical mechanisms of visual development can often be distinguished in monocularly lid-sutured cats by comparing the abnormalities seen in the binocular and monocular segments of the nucleus (6, 7, 29, 32–34). If binocular competition alone controlled development,

deprived cells only in the binocular segment should suffer from the effects of deprivation. Deprived cells in the monocular segment, since they are exempt from binocular competition, should escape the deleterious effects of being placed at a competitive disadvantage and would thus develop normally. If mechanisms unrelated to binocular competition operated, cells throughout the nucleus, including cells in the monocular segment, should be equally affected by the deprivation. The data from the present experiment implicate both types of developmental mechanisms, and this is shown schematically for both X- and Y-cells in Fig. 12.

It has been previously reported that the effects of deprivation on Y-cells follows the rules of binocular competition (33, 34). The percentage of Y-cells in the binocular segment of the deprived laminae is abnormally low, whereas the percentage of Y-cells in the monocular segment is normal. Since Y-cells in the deprived monocular segment have normal spatial and temporal sensitivity, binocular competition alone is sufficient to account for the development of Y-cells. The few surviving Y-cells in the deprived binocular segment might represent cells with projections to purely monocular cortical cells, which are occasionally seen in normal kittens and adult cats (9, 10, 28). For deprived X-cells, spatial resolution is reduced both in the binocular and monocular segments. This suggests that a mechanism unrelated to binocular competition significantly influences the development of X-cells, and no evidence is apparent for binocular competition in X-cell development.³

These different mechanisms of development may explain why the effect of deprivation seems more severe for Y-cells than it does for X-cells (see also below). Other explanations for the differences in the

³ Although X-cells seem to develop without influences of binocular competition, competitive mechanisms involving other hypothetical interactions within deprived laminae (i.e., between deprived A- and C-laminae, between interneurons and relay cells, and many others) can also affect X-cell development. Whether or not X-cell development is completely unaffected by competitive mechanisms and dependent solely on afferent input activity cannot be addressed by our available data.

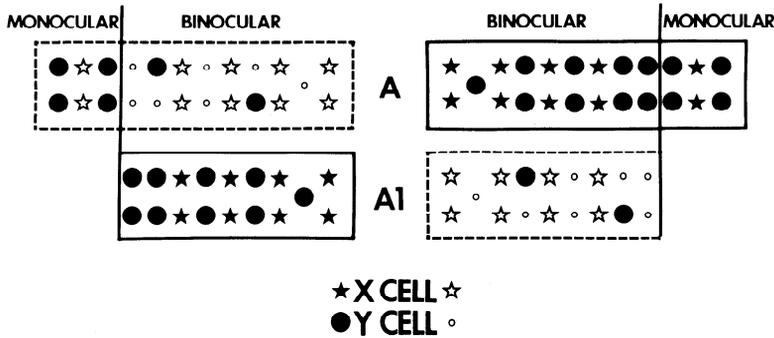


FIG. 12. Schematic summary diagram of effects of early lid suture on development of geniculate X- and Y-cells. Laminae A and A1 and the binocular and monocular segments are labeled. This is drawn as if the lids of the right eye were sutured, so that left lamina A and right lamina A1 (dashed outlines) are deprived. Normal X- and Y-cells are represented by filled symbols (stars and circles, respectively). Abnormal cells in deprived laminae are indicated by open symbols. Open stars indicate X-cells with reduced sensitivity to higher spatial frequencies. Small open circles represent the functionally lost (or unrecordable) Y-cells. The pattern of Y-cell deficits suggests a mechanism of binocular competition; that for X-cells, a deprivation mechanism not involving binocular interactions (see text).

severity of the effect of lid suture on X- and Y-cells may be related to differences in the time courses of their developments. It has been reported recently that Y-cells develop later than do X-cells (2, 27). Since Y-cells mature later than X-cells, this places the Y-cell period of susceptibility at a time when these cells can be more dramatically influenced by the visual environment.

Comparison of lid suture and esotropic strabismus

X-CELLS. Ikeda and Wright (18) have recently reported that, in the lateral geniculate nucleus of cats raised with an esotropic strabismus, X-cells⁴ driven by the misaligned eye exhibit abnormally low spatial resolution. At lower spatial frequencies, the responses of these cells seem normal. These results closely parallel our findings for the spatial contrast sensitivity functions of deprived geniculate X-cells in lid-sutured cats. However, an important difference is that, in strabismic cats, the loss of sensitivity to higher spatial frequencies occurs only for X-cells located in or near area centralis. In lid-

sutured cats, lower spatial resolution was observed for X-cells located at all retinal eccentricities.

This loss in X-cells of sensitivity at higher spatial frequencies has been attributed to the defocused images that result from the abnormal patterns of fixation and accommodation adopted by the strabismic eye (14, 15, 18). Ikeda and Wright suggest that, as a result, the contrast of the retinal image of the misaligned eye is attenuated (but for higher and not lower spatial frequencies). Only cells that normally develop sensitivity to these higher spatial frequencies are affected by this sort of deprivation, and they would be X-cells concentrated in the area centralis. These cells are inadequately stimulated by defocused images (15) and, as a consequence, their development of sensitivity to higher spatial frequencies is arrested. Defocused stimulation achieved by other means, such as paralysis of accommodation or hypermetropia, have also been shown to arrest the normal development of sensitivity of a cell to higher spatial frequencies (3, 12). Since lid suture attenuates the contrast of all spatial frequencies in the retinal image, X-cells located both in peripheral, as well as central regions, are deprived of normal spatial stimulation. This sort of deprivation could account for the observation that deprived X-cells located at all retinal eccentricities have a lower spatial

⁴ Ikeda and Wright have classified geniculate cells mainly in terms of response dynamics and labeled cells accordingly as either sustained or transient cells. Sustained and transient cells are assumed here to be X- and Y-cells respectively, since X-cells tend to have sustained responses, and Y-cells tend to have transient responses (19).

resolution following lid-suture rearing. That is, X-cells with peripheral fields, which do not normally attain sensitivity to higher spatial frequencies, would receive normal spatial stimulation during moderate defocus but not during lid suture.

The normal sensitivity of X-cells to low and moderate spatial frequencies in esotropic cats can also be attributed to the nature of the deprivation, since the contrast of lower spatial frequencies in the defocused retinal image is relatively unattenuated. Yet, even though X-cells during lid suture are deprived of low and moderate spatial frequency stimulation, they develop normal sensitivity to these spatial frequencies. This observation suggests that this sensitivity of X-cells cannot be modified by the environment. Perhaps sensitivity to low and moderate spatial frequencies is already developed and fixed before the onset of the critical period. Indeed, it has been reported that the contrast sensitivity of X-cells to lower spatial frequencies is at adult levels at 3 wk of age (13). It follows, then, that the normal sensitivity at lower spatial frequencies observed for X-cells driven by the misaligned eye in strabismic cats is not completely due to the nature of the defocused stimulation, but rather, it may be a nonmodifiable property of the cell.

The fact that normal sensitivity at lower spatial frequencies develops in X-cells following lid suture also suggests that their failure to develop sensitivity at higher spatial frequencies during moderate defocus may be due to factors other than the attenuation of specific spatial frequencies in the retinal image. For instance, because X-cell sensitivity is normally attenuated at low spatial frequencies, lid suture and defocus (which permits only low spatial frequency stimulation) may both substantially reduce the general activity of developing X-cells. Their inactivity during the critical period may preclude further development. If it is assumed that the sensitivity of X-cells to lower spatial frequencies is already present at this time, then the effects of either defocus or diffusion would be evident only at higher spatial frequencies.

Another similarity between esotropic strabismus and lid suture is the lack of effect these rearing conditions have on the tem-

poral sensitivity of X-cells. Ikeda and Wright (18) report that cells driven by the misaligned eye have normal temporal sensitivity as measured by critical flicker fusion. The temporal contrast sensitivity functions for deprived X-cells in lid-sutured cats also seem to be normal.

This lack of effect of esotropic strabismus on temporal sensitivity may be accounted for in part by the nature of the deprivation, since temporal stimulation of the misaligned eye is unrestricted. However, in the lid-sutured cat, X-cells develop a normal temporal response, even though stimulation of the lid-sutured eye is temporally restricted.⁵ This finding does suggest that the development of temporal sensitivity of X-cells is insensitive to environmental modifications and, like the sensitivity of these cells to lower spatial frequencies, their temporal sensitivity may also be a fairly nonmodifiable neuronal property.

Y-CELLS. Esotropic strabismus and lid suture have quite different effects on Y-cells. In esotropic cats, there seems to be no loss of normal Y-cells in the laminae related to the misaligned eye, whereas few normal geniculate Y-cells are found in the deprived binocular segment of lid-sutured cats. The absence of any effect of esotropia on Y-cells has been attributed to the fact that the response of these cells does not critically depend on the state of focus of the stimulus (15) and, as a consequence, the optical image quality in the misaligned eye's retina is sufficient to allow normal activity and development of this cell type. That is, unlike X-cells, Y-cells are sensitive to low spatial frequencies that would not be attenuated during moderate defocus. Since lid suture attenuates all spatial frequencies in the retinal image, this condition may be insufficient to stimulate the normal development of Y-cells. Accordingly, an effect on Y-cells

⁵ In an evenly illuminated room, such as the rooms in which our cats were raised, the main source of temporal stimulation of receptive fields is the movement of spatial patterns across the retina. However, since a sutured lid acts as a diffuser and attenuates all spatial frequencies, no such spatial patterns fall upon the retina. This source of temporal stimulation is thus precluded by lid suture. Nonpatterned temporal frequency stimulation probably occurs rarely when shadows (from cage bars, etc.) fall intermittently across the lids.

following rearing with lid suture but not strabismus would be expected.

However, any hypothesis based on the nature of the deprivation cannot alone account for the observation that the Y-cells within the monocular segment are not affected by early lid suture. Rather, as has been previously suggested, Y-cell development seems to rely largely on competition between the pathways related to the two eyes (33, 34). The main reason for the absence of any effect of esotropic strabismus on Y-cells may be the failure of this rearing condition to establish a competitive imbalance in visual activity between Y-cells related to each eye.

CONCLUSIONS

In the preceding paper (21), we suggested that Y-cells were implicated in the processing of low spatial frequencies, which are essential to spatial pattern vision. This conclusion stems from the sensitivity attenuation seen in X-cells but not Y-cells to low spatial frequencies. It might thus be possible to account for the severe amblyopia in lid-sutured cats (see Refs. 4, 30) on the basis of the functional loss of geniculate Y-cells. We know, for example, that the psychophysically derived spatial contrast sensitivity functions for monocularly sutured cats while using the deprived eye indicate severe visual losses for low spatial frequencies, losses that are at least as great as those for high frequencies (22). It is unlikely that severe amblyopia can result from selective deprivation effects on X-cells, as has been recently suggested (16), for two reasons: *a*) normal Y-cell development should provide sensitivity to low and moderate spatial frequencies for useful spatial pattern vision; and *b*) lesions of area 17 in normal cats, which effectively eliminate the X pathways without damage to much of the Y pathways, result in only relatively

mild postoperative acuity losses (see preceding paper, Ref. 21; see also Refs. 1, 35).

These suggestions can also be applied to certain observations concerning human amblyopia. Where development of both X- and Y-cells is affected (i.e., in certain forms of strabismus, congenital cataracts, etc.), severe amblyopia results. Where only X-cell development is indicated (i.e., certain forms of strabismus, anisometropia, astigmatism, etc.), mild amblyopia, involving only the higher spatial frequencies or finest details, results. Perhaps this is the etiology that underlies the observation that certain amblyopic patients exhibit profound psychophysical contrast sensitivity losses for all spatial frequencies with very poor vision, whereas others demonstrate only high frequency losses with fairly good vision (8). That is, whenever the visual environment favors normal development of Y-cells (i.e., with lower spatial frequency stimulation as in anisometropia), fairly good vision will develop, but if the environment cannot support Y-cell development (e.g., without lower spatial frequencies, as in lid suture or severe cataract formation), poor vision results.

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Address reprint requests to: Dr. S. Murray Sherman, Dept. of Anatomical Sciences, SUNY, Stony Brook, School of Basic Health Sciences, Health Sciences Center, Stony Brook, New York 11794.

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