Effects of Early Monocular Lid Suture upon Neurons in the Cat's Medial Interlaminar Nucleus

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ABSTRACT Single unit extracellular recordings, cell size measurements, and cell packing density measurements were made in the medial interlaminar nucleus (MIN) of nine adult cats that had been monocularly deprived by lid suture prior to natural eye opening. The electrophysiological properties of neurons in the nondeprived regions of MIN (areas receiving input from the nondeprived eye) remained unaffected by monocular lid suture. The latencies to optic chiasm stimulation and receptive field properties, including receptive field center size, were essentially the same as those found for MIN neurons of normal adult cats. In contrast, cells in the deprived regions were severely affected by monocular deprivation. We encountered in the deprived regions of MIN only about one half as many active neurons per mm of electrode penetration as we did in the nondeprived regions. Of the physiologically active cells remaining, about one half had abnormal receptive field and/or response properties. This resulted in a sampling density of 5.1 normal Y-cells per mm of penetration in nondeprived regions of MIN compared to 1.0 normal Y-cell per mm in deprived regions of MIN.

Histological effects of deprivation were also seen. Deprived regions of MIN were distinguished from nondeprived regions in four cats by autoradiography following intravitreal injection of tritiated proline into the deprived or nondeprived eye (2 cats each). The mean cell size of deprived regions of MIN was 34% smaller than that of nondeprived regions. We did not find a difference in cell packing density between these two regions.

It appears that the effects of monocular lid suture upon MIN are in most respects similar to the effects of monocular lid suture previously reported for the A laminae. Since MIN is composed solely of Y-cells, these data support the idea that the Y-pathways are more severely affected by visual deprivation than are the X-pathways. Further, since MIN projects largely outside the striate cortex, these data give the first clear demonstration of a primary effect of early lid suture upon extrastriate visual pathways.

A cat raised with monocular eyelid suture develops anatomical and physiological abnormalities in its geniculostriate pathways. In striate cortex, cells become dominated by the nondeprived eye instead of the normal pattern of balanced, binocular activation (Wiesel and Hubel, '63a; Kratz et al., '76; Wilson and Sherman, '77). In the lateral geniculate nucleus, a number of deficits have been described for deprived laminae (i.e., those which receive direct retinal afferents from the deprived eye). The mean cross-sectional area of cells in deprived laminae is roughly 30% smaller than that in the nondeprived laminae (Wiesel and Hubel, '63b; Guillery and Stelzner, '70; Hickey et al., '77). Also, while X-cells seem relatively unaffected by lid suture, the Y-cells are severely affected by such deprivation (Sherman et al., '72). For instance, in nondeprived laminae A and A1, 50-60% of the neurons sampled with microelectrodes are Y-cells, but in deprived laminae, only about 10% of sampled neurons are Y-cells. Similar histological and electrophysiological deficits have

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been reported for the monocularly deprived tree shrew (Norton et al., '77).

Deprivation induced effects have not been described for the cat's medial interlaminar nucleus (MIN), which is a subdivision of the dorsal lateral geniculate nucleus (see preceding paper, Kratz et al., '78). There are at least two reasons why such a description seems important. First, major projections exist from MIN to cortical areas 18, 19, and to the lateral suprasylvian cortex (Rosenquist et al., '74; Maciewicz, '74, '75; Gilbert and Kelly, '75) and no *primary* deficits have been described beyond the geniculostriate system in lid sutured cats. That is, abnormalities in the superior colliculus are thought to be secondary to deficits in the geniculostriate pathways (Wickelgren and Sterling, '69; Hoffmann and Sherman, '74, 75; Berman and Sterling, '76); and a similar argument could be applied to reports of deficits noted in area 18 of visually deprived cats (Singer and Tretter, '76). Second, MIN represents an essentially pure population of Y-cells (see previous paper, Kratz et al., '78), and in the laminar region of geniculate (lamLGN), Y-cells seem to be relatively selectively affected by early lid suture (Sherman et al., '72).

We studied MIN neurons in cats reared with monocular lid suture and found abnormalities in this region which are very similar to abnormalities reported for Y-cells in deprived laminae of lamLGN. That is, deprived MIN cells were smaller, and very few had normal receptive fields (Kratz et al., '76).

METHODS

Most of the methods used were identical to those of the preceding paper (Kratz et al., '78). Only a brief outline plus an indication of differences in procedure will be presented here.

Nine cats, born and reared in the laboratory were used in this study. Each had the lids of one eye sutured at five to eight days of age (before natural eye-opening), and they were maintained in this fashion until their study as adults at least 12 months later. The kittens were inspected daily to ensure that no lid openings exposed the pupil (Loop and Sherman, '77).

Seven of the kittens were studied with electrophysiological techniques. Their deprived eyes were opened immediately prior to the recording session. The electrophysiological methods were identical to those described in the preceding paper (Kratz et al., '78). In all of the above cats, histological techniques were used to localize electrode penetrations.

Geniculate cell size measurements were made in four cats (two following electrophysiological recording and two others used solely for cell size measurements). These four cats had one eye (the nondeprived eye in two cats and the deprived eye in the other two) intravitreally injected with 100 μCi of tritiated proline ten days before sacrifice, and subsequent autoradiography delineated terminal zones of retinal axons. Histological procedures and sampling methods for cell measurements are described in the preceding paper (Kratz et al., '78). In addition, MIN cell density measurements for the same four cats were estimated by counting the number of MIN neurons with clearly visible nucleoli within a 130 $\times$ 130 μm grid. Since the sections were 40 μm thick, each sampled zone had a volume of 6.8 $\times$ 10^5 μm^3. Five such separate volumes each were sampled for the deprived and nondeprived regions of MIN in both hemispheres (i.e., a total of 20 sampling volumes per cat).

RESULTS

Electrophysiology

The results of the recording experiments in MIN indicate three general effects upon MIN cells following early eyelid suture. First, the nondeprived segment of MIN appears normal in terms of the number of functional cells and also the receptive field and response properties of these cells. Second, there is a dramatic decrease in the number of responsive cells in the deprived segments of MIN. Finally, of those responsive cells found in the deprived segments of MIN, most have abnormal electrophysiological properties.

A total of 39 penetrations were made through the MIN of the seven cats from which we recorded. Of these penetrations, 27 passed through nondeprived segments, and 23 passed through deprived segments. Since there was no suggestion of an ipsilateral/contralateral difference in either the deprived or nondeprived segments, these data will be considered together and pooled throughout this report.

Nondeprived segments

Equal numbers of normal Y-cells were found in MIN of normal animals (6.8 cells per mm; data from the preceding report, Kratz et al., '78) and in the nondeprived segments of

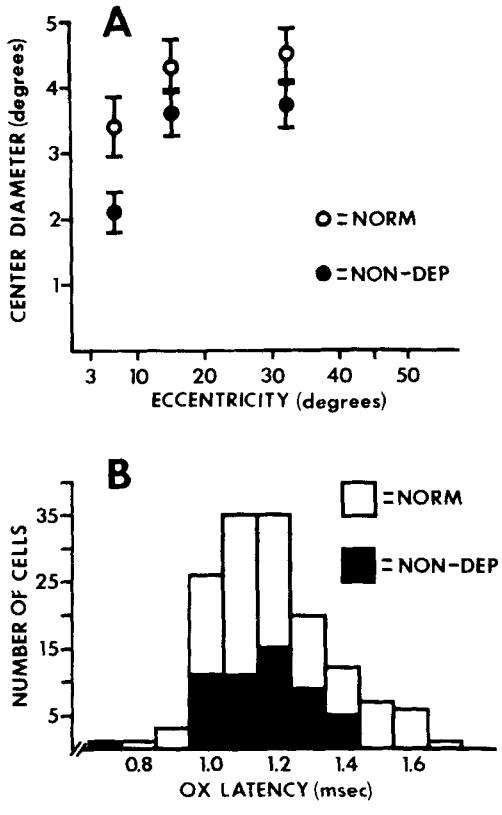


Fig. 1 Comparison of properties of MIN cells in normal cats and in nondeprived zone of monocularly deprived cats.

A Receptive field center sizes (mean ± one standard error) for MIN cells from normal cats and for MIN cells driven by the nondeprived eye in monocularly lid sutured cats. Although none of the comparisons (normal versus nondeprived) differ at the 0.01 level of significance, the 3-10° values do differ at the 0.05 level (on a t-test).

B Comparison of latencies to optic chiasm (OX) stimulation of MIN units from normal cats and MIN units driven by the nondeprived eye from monocularly lid sutured cats.

the monocularly deprived animals (5.2 cells per mm). Further, the electrophysiological properties of these nondeprived MIN Y-cells were indistinguishable from those of normal MIN Y-cells. Figure 1 illustrates this equivalence for receptive field sizes and response latencies to optic chiasm shock. Table 1 shows that 52 of 54 cells driven by the nondeprived eye were normal Y-cells, and the ratio found in normal cats (101/102; taken from Kratz et al., '78) is not significantly different ($p > 0.1$ on a X^2-test). As suggested earlier (Kratz et al., '78), the few cells recorded in MIN which were not Y-cells could be interneurons (cf. Lin et al., '77).

Deprived segments

The situation in deprived segments of MIN was quite different from that in nondeprived segments. Few cells were encountered in deprived segments, and of these, most were abnormal in their response and/or receptive field properties. A weak, low amplitude "swish" could usually be elicited by stimulation of the deprived eye, and this was frequently the only indication that the penetration was in fact going through deprived segments of MIN. Figure 2 is a series of photomicrographs of a typical electrode penetration through MIN of one of the monocularly deprived cats. In this cat, the nondeprived (contralateral) eye had an injection of tritiated proline eight days before the recording session, and the autoradiography has labelled the nondeprived (contralateral) segment of MIN. The vitreal injection of proline had no detectable effect upon the normal functioning of the injected eye, since normal cells were recorded both in the lamLGN and in the segment of MIN receiving input from this eye. In this particular penetration, little unit activity

TABLE 1

Electrode sampling density of single units in deprived and nondeprived segments of MIN

MIN segment	No. cats	No. [1] pens	Distance mm [1]	No. total [1] units	$\bar{X}$ units/mm [2]	S.E.	No. normal [1] Y-cells	(%)	$\bar{X}$ normal [2] units/mm	S.E.
Non-dep	7	27	10.2	54	5.2	±0.7	52	(96)	5.1	±0.7
Dep		23	7.8	21	2.8	±0.7	9	(43)	1.0	±0.4

[1] Pooled values combined from all seven cats.

[2] These values were calculated as follows. For each of the seven monocularly deprived cats in both deprived and nondeprived segments of MIN, a mean was calculated and considered a single measurement. For each segment is shown the mean ± one standard error for these seven single measurements. These values then, unlike the absolute number of units, takes into consideration interanimal variability.

was recorded after the electrode left lamLGN and entered what was suspected to be the ipsilateral (deprived) segment of MIN. Approximately half-way through MIN, the electrode isolated normal Y-cells which responded to stimulation of the nondeprived eye. Responsive cells were encountered until the electrode passed out of the nucleus. Electrolytic lesions were then placed at the depths corresponding to what was suspected to be the lamLGN/MIN border, the deprived/nondeprived border within MIN, and the medial border of MIN. As seen in figure 2, the lesion locations are as predicted. A reconstruction of this penetration is presented in figure 3C. Additional electrode penetration reconstructions are presented in figure 3 which indicate that few normal Y-cells were encountered in deprived segments.

For each cat, the mean number of units per millimeter of electrode penetration was calculated separately for penetrations through deprived and nondeprived segments of MIN. The means ± standard errors of these data are presented in figure 4. We encountered significantly fewer cells per millimeter in deprived segments of MIN than in the nondeprived segments ($p < 0.02$ on a Mann-Whitney U-test). At the sampling rate for nondeprived segments (5.2/mm), 41.3 cells should have been found for the distance of travel through deprived segments of MIN. Instead, only 21 units or 50% fewer than expected were encountered. Often the units encountered in deprived segments occurred close to the border of the nondeprived segments (fig. 3B). However, we did not encounter any binocularly influenced cells or unusual intermingling of monocular responses along this border.

As mentioned earlier, of the units encountered in deprived MIN, most were abnormal in their receptive field properties and/or responses. As shown in table 1, while 96% (52 of 54) of the units encountered in nondeprived segments were normal Y-cells, only 43% (9 of 21) of the units encountered in deprived segments of MIN appeared to have normal Y-cell characteristics ($p < 0.001$ on a X^2-test). The abnormal cells had a variety of characteristics which included one or more of the following: (1) four neurons tested were inconsistently or poorly responsive to repeatedly presented visual stimuli; (2) three neurons had latencies to optic chiasm stimulation that were abnormally long (> 1.8 msec); (3) three neurons had receptive field centers that were abnormally large (> 10°); (4) four neurons were unresponsive to fast target movements; (5) two neurons had receptive field centers that were "on" and "off" instead of one or the other; and (6) three neurons gave a tonic instead of a phasic response. For reasons given below, it seems unlikely that many of these cells could have been normal interneurons.

Figure 4 and table 1 also summarize the total electrophysiological effects of monocular deprivation on MIN, by taking into consideration both the paucity of units encountered and the abnormal cells among those units. In nondeprived segments, 5.1 normal Y-cells per millimeter were recorded, whereas 1.0 normal Y-cell per millimeter was recorded in deprived segments of MIN ($p < 0.001$ on a Mann-Whitney U-test).

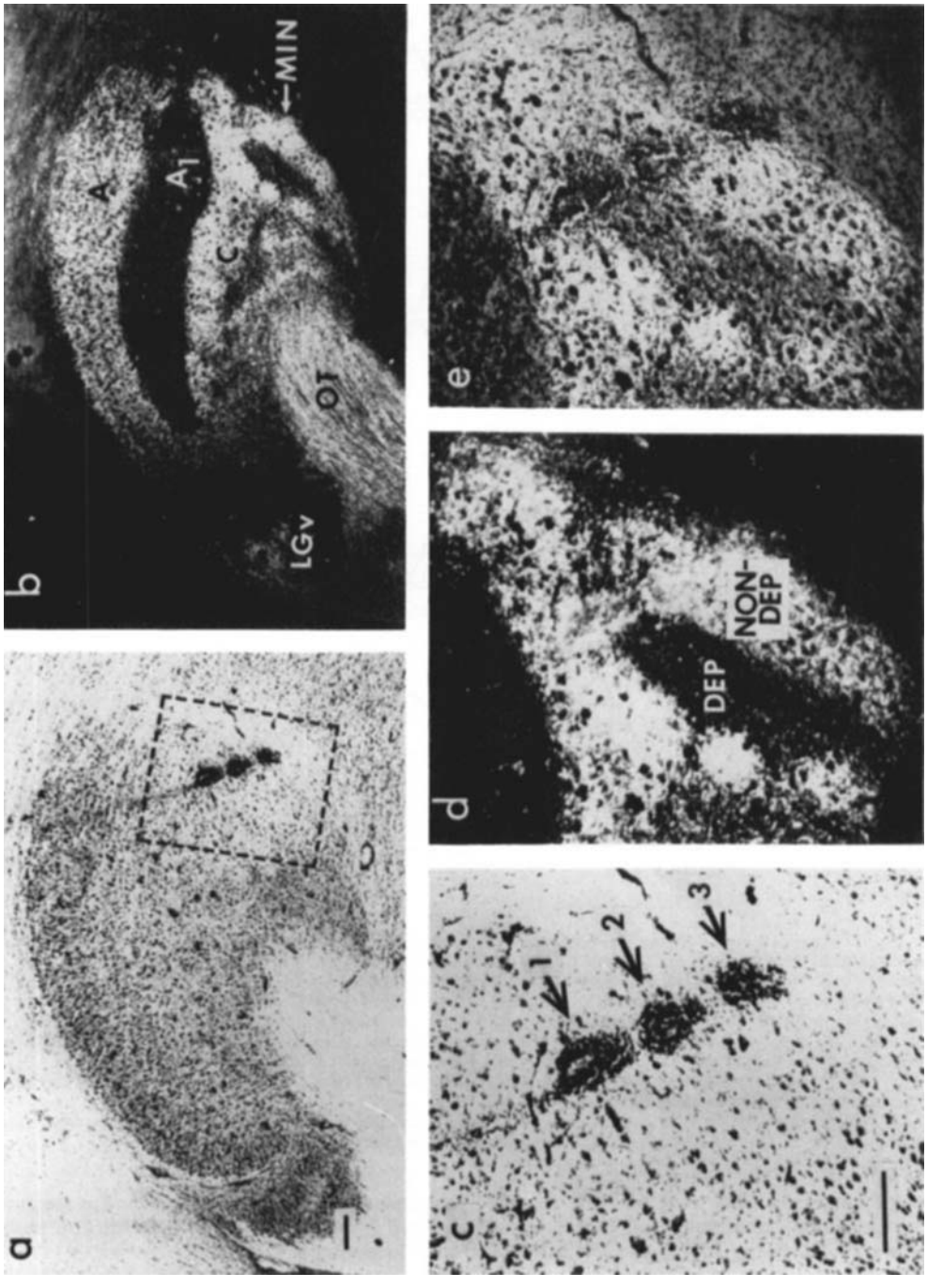
Cell sizes

In each of four monocularly deprived cats, one eye was injected intravitreally with tritiated proline eight to ten days prior to sacrifice. In two cats, the deprived eye was injected, and in the other two, the nondeprived eye was injected. No detectable effect of the injection on cell size was seen. As is illustrated by figure 5, subsequent autoradiography permitted us to measure MIN cell cross-sectional areas from deprived and nondeprived zones independently. Sampling procedures were identical to those described in

Fig. 2 Photomicrographs of a coronal section through the lateral geniculate nucleus of a monocularly lid sutured cat. This animal had its right (nondeprived) eye injected with tritiated proline seven days prior to recording, and autoradiography was performed on the brain sections.

a,b Photomicrographs, brightfield and darkfield, respectively, showing the A laminae, C laminae, medial interlaminar nucleus (MIN), optic tract (OT), and ventral lateral geniculate (LGv). Outlined area in a represents field of view shown in c, d, e at higher magnification. Electrode track with lesions in MIN can be seen passing ventromedially at a 30° angle from vertical through the lamLGN and MIN. The scale in a indicates 500 μm for a and b.

c-e Medial aspect of the lateral geniculate nucleus as outlined by the dashed rectangle in a. Brightfield, darkfield, and brightfield/darkfield double exposures are shown, respectively. The marking lesions in MIN are indicated by numbered arrows in c. Hidden lamination of MIN is evident in d where the nondeprived segment is labelled by autoradiography and the deprived segment remains unlabelled. Unfortunately, the lesions are not clearly seen in darkfield illumination. In e note that lesions are located: (1) at the border of the C laminae and the deprived segments of MIN; (2) at the border of the deprived and nondeprived segments of MIN; and (3) at the medial border of the nondeprived segment of MIN (see text, and reconstruction of this penetration in fig. 3C). The scale in c represents 500 μm for c-e.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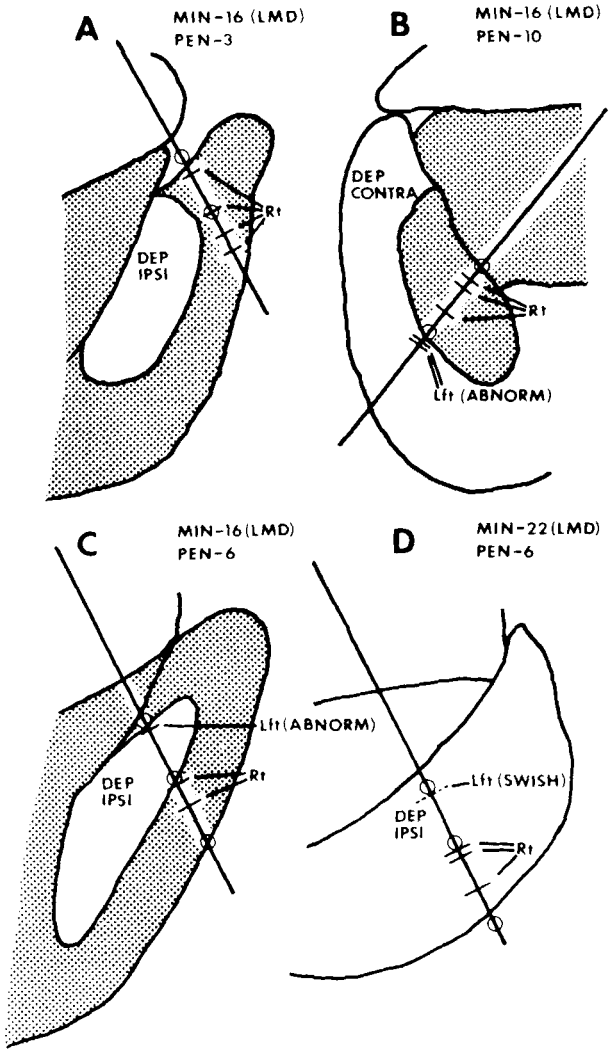

Fig. 3 Reconstructions of four penetrations through the MIN of monocularly deprived cats. Cat MIN-16 had the right (nondeprived) eye injected with tritiated proline and projection areas of this eye are indicated by stippling. Segments of MIN receiving input from the deprived eye are indicated on each reconstruction. Electrode penetrations are represented by the solid line passing at an angle through MIN. Units driven by either the left (Lft) or right (Rt) eyes, encountered along the penetration, are indicated by slash marks. Lesions were made at various depths at the completion of the penetration to aid in reconstruction of the penetrations. These lesions are indicated as circles on the electrode track reconstructions.

A-C Reconstructions of penetrations for cat MIN-16. Note the correspondence of neuronal ocular dominance zones with the autoradiography.

D Reconstruction of a penetration for cat MIN-22 (left eye deprived). Although no autoradiography was available for this cat, the ocular dominance of neurons is as expected.

the previous paper (Kratz et al., '78), except that independent deprived and nondeprived zones were chosen in MIN, and both hemispheres of each cat were sampled.

Figure 6 summarizes these data which are presented as the mean ± standard error from the means of the four cats used. The data presented for lamina A, A1, and for the monocular segment of lamina A are essentially the same as reported by previous studies (Guillery and Stelzner, '70; Hickey et al., '77). In the binocularly represented segments of lamina A

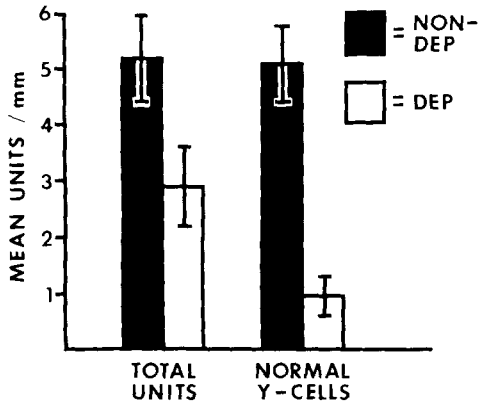

Fig. 4 Comparison of electrode sampling density of units in deprived and nondeprived segments of MIN. For each of seven monocularly deprived cats in both deprived and nondeprived regions of MIN, a mean was calculated and considered a single measurement. For each region is shown the mean ± one standard error for these seven single measurements. Total units refers to all single units isolated, whether normal or abnormal in receptive field characteristics, and normal Y-cells refer to only those single units isolated and classified as normal Y-cells. In normal cats (see previous paper, Kratz et al., '78, we sampled 6.8 normal Y-cells per mm in MIN, and this value is not significantly different from the sampling rate in nondeprived portions of MIN (see text).

and A1, the mean cell size is approximately one-third smaller in the deprived than in the nondeprived laminae (28% and 35%, respectively, for lamina A and A1). No difference was obtained in cell sizes for these animals between the deprived and nondeprived monocular segments. This result for the monocular segment is not in agreement with Hickey et al. ('77) even though the animals in the present study are of ages where a difference in cell size between monocular segments was obtained by Hickey et al. This discrepancy, however, is slight, and may result from subtle differences in sampling procedures (cf. Hickey et al., '77).

Figure 6 also shows that, in MIN, the mean cell size of the deprived segment is 34% smaller than the mean cell size of the nondeprived segment ($p < 0.01$ on a Mann-Whitney U-test). This difference is essentially the same as that found for the A laminae. No ipsilateral/contralateral differences were found in the MIN cell measurements, and they are therefore pooled in figure 6. Note that in nondeprived regions, MIN cells are not obviously larger than A laminae cells as they are in normal cats (see preceding paper, Kratz et al., '78). It has been demonstrated that nondeprived cells in the A laminae actually hypertrophy (Sherman and Wilson, '75; Hickey et al., '77), and the present results therefore suggest that nondeprived MIN cells show less hypertrophy than nondeprived cells of laminae A and A1.

Cell packing density

Only a small, nonsignificant difference was found in cell packing density between deprived and nondeprived segments of MIN. We counted all cells with visible nucleoli within a proscribed volume and found 1.1×10^4 cells per mm^3 in deprived portions of MIN compared to 1.2×10^4 cells per mm^3 in nondeprived portions of MIN. This finding differs from that in laminae A and A1. Guillery and Stelzner ('70) report an increase in cell packing density for the deprived A laminae. Apparently, cell numbers are normal after deprivation, but the reduced volume of the deprived A laminae result in more dense cell packing in these areas. We found no evidence from our autoradiographic material of a difference in volume between deprived and nondeprived MIN regions. This, plus presumably normal neuronal numbers of the deprived portions, results in normal cell densities in these areas. However, the smaller somata imply more space between cell bodies as a result of deprivation (fig. 5).

DISCUSSION

The effects of early monocular lid suture upon MIN are quite clear. Both electrophysiologically and morphologically, the nondeprived segment of MIN appears unchanged from MIN in normal animals. In contrast, compared to the nondeprived segment, the deprived segment of MIN contains fewer normal Y-cells and its cell bodies are smaller.

Comparison of effects of lid suture upon MIN and lamLGN

The effects observed in MIN are similar to the effects of monocular lid suture upon the A laminae. In deprived laminae of lamLGN, Sherman et al. ('72) encountered many fewer Y-cells (9% of the total) compared to normal or nondeprived laminae (50-60%). This is a reduction of about 80% in the relative percentage of Y-cells encountered. We found a similar reduction in the encounter rate of normal Y-cells in deprived segments of MIN (1.0/mm) compared to that in nondeprived segments (5.1/mm). Again this is a reduction of about 80%. An important difference should be noted

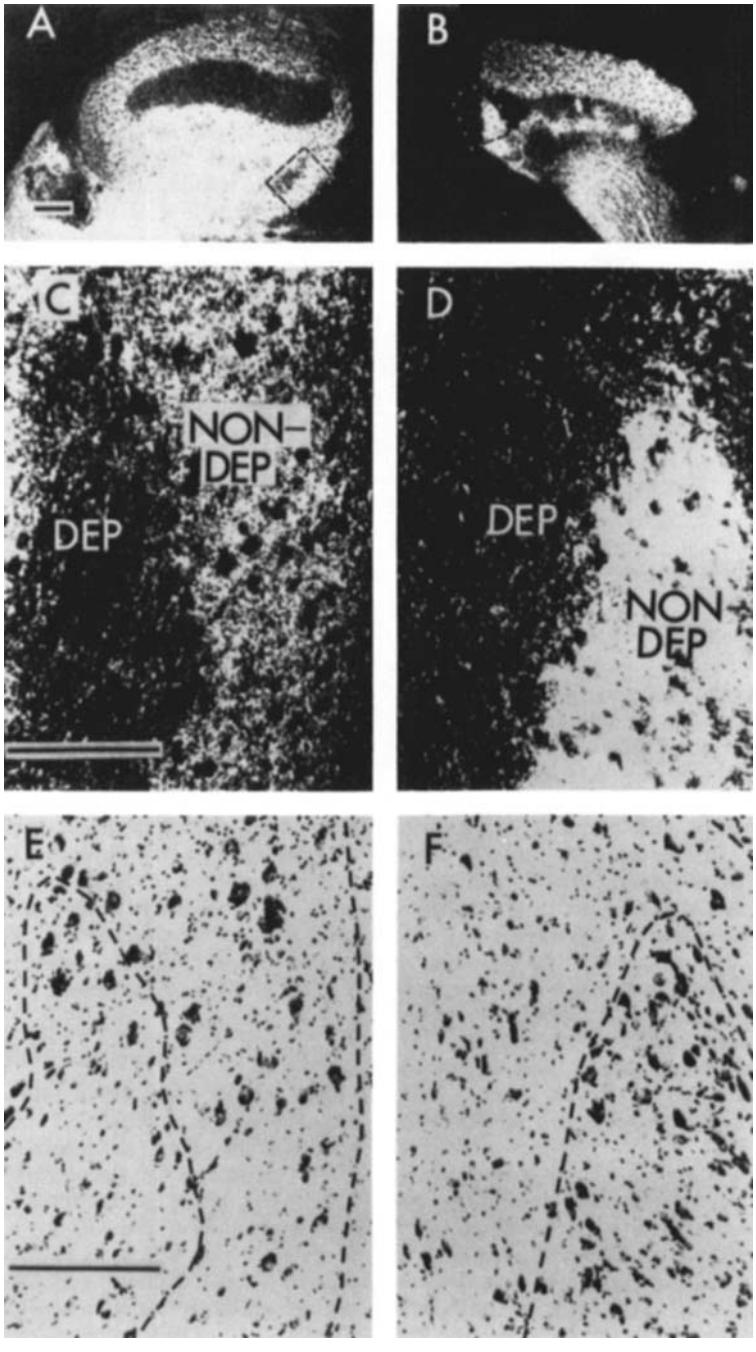

Figure 5

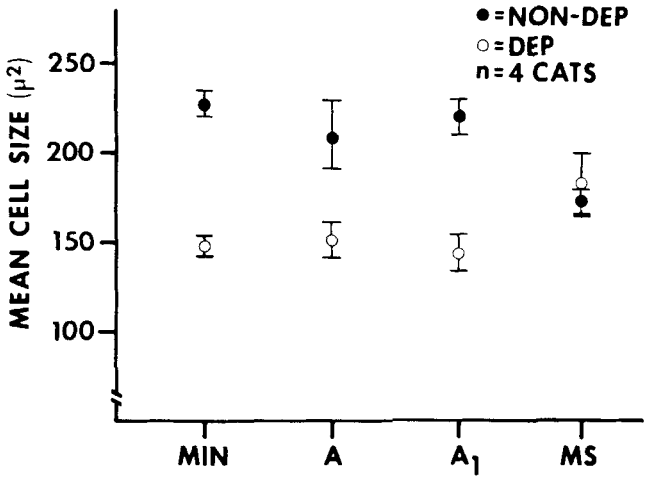

Fig. 6 Comparison of mean cell sizes in deprived and nondeprived regions in the lateral geniculate nucleus of monocularly deprived cats. Thirty to sixty cells were measured in deprived and nondeprived areas of the medial interlaminar nucleus (MIN), binocular segment of lamina A, lamina A1, and the monocular segment of lamina A(MS). For each of four monocularly deprived cats and each sample area, a mean was calculated and considered a single measurement. For each sampling area is shown the mean ± one standard error for these four single measurements.

between the results found in MIN and the A laminae. In deprived regions of MIN many abnormal cells were observed, while such cells were not reported in the deprived A laminae (Sherman et al., '72). However, abnormal cells similar to those found in deprived MIN regions have been recorded in deprived geniculate laminae of monocularly lid sutured tree shrews (Norton et al., '77).

The effects of monocular lid suture upon MIN are also similar to the effects of monocular lid suture upon the A laminae in that the mean cell size of deprived regions of MIN is 34% smaller than the mean cell size in nondeprived regions. This is comparable to the difference in mean cell size between deprived and nondeprived A laminae (fig. 6; see also Wiesel and Hubel, '63b; Guillery and Stelzner, '70; Hickey et al., '77). An important difference in these cell size measurements is that the effects in MIN refer to an essentially pure Y-cell population (Kratz et al., '78, preceding paper), whereas the effects in the A laminae refer to a mixed population of X- and Y-cells. Available evidence (LeVay and Ferster, '77; Garey and Blakemore, '77) suggests that deprived lamLGN Y-cells in monocularly lid sutured cats are more severely reduced in mean cell size (by 42-55%) than are deprived lamLGN X-cells (by 10-15%). This further suggests that lamLGN Y-cells may be affected to a slightly greater extent by monocular lid suture than are MIN Y-cells. This latter suggestion must remain tentative since a direct comparison by the same investigators has not been made.

Two effects of monocular deprivation have been described: namely a pure deprivation effect due to the lid suture, and a competitive effect (i.e., binocular competition) due to the imbalance of activity among cells related to each eye (Wiesel and Hubel, '65; Guillery and Stelzner, '70; Guillery, '72; Sherman et al.,

Fig. 5 Photomicrographs of the lateral geniculate nucleus from a monocularly lid sutured cat; same animal as illustrated in figure 2. This animal had the right, nondeprived eye injected with tritiated proline and autoradiography was performed on the brain sections.

A, B Darkfield photomicrographs of the left (A) and right (B) lateral geniculate nuclei. Outlined regions in A and B represent the field of view shown at higher magnification in C, D, E and F. The scale in A indicates 500 μm for A and B.

C-F: The identical region of the left MIN, as outlined in A, is shown in C (darkfield) and E (brightfield), and the identical region of the right MIN outlined in B is shown in D (darkfield) and F (brightfield). Labelled regions in C and D indicate zones receiving input from the nondeprived eye (NON-DEP), while unlabelled regions indicate zones receiving input from the deprived eye (DEP). Corresponding zones are shown in D and F. Note the larger size of cells in nondeprived segments compared to deprived segments. Some large cells appear in the dorsal aspect of the deprived segment of the left MIN (D). However, since some labelling is present (C) the border in this region is unclear.

'74; Kratz and Spear, '76; Wilson and Sherman, '77). Of these two effects, the binocular competitive effect seems to be of greater significance for lamLGN Y-cells. This follows because, whereas Y-cells are lost from the deprived, binocularly represented segments, they are normal in number and properties in the deprived monocular segments (Sherman et al., '72, '75); only in the monocular segments can these cells escape the consequences of binocular competition, although the deprived eye's activity is equally reduced in binocular and monocular segments. The results of the present experiment cannot address the issue of whether the effects of monocular deprivation on MIN are the result of a pure deprivation effect and/or binocular competition. In order to answer this question, it will be necessary to investigate the monocular segments of MIN in monocularly deprived cats with an experimental approach analogous to that used by Sherman et al. ('72, '75) in lamLGN.

Electrode sampling bias

Throughout this paper we have referred to the decreased encounter rate of Y-cells in deprived regions of MIN as a Y-cell "loss," although we emphasize that such an observation may represent the consequence of electrode sampling and may not represent a true functional loss.

Sherman et al. ('72) in fact qualified their interpretation of a Y-cell loss in deprived lamLGN by noting that their findings could have resulted from a large shift of electrode sampling characteristics brought about by cell shrinkage. However, LeVay and Ferster ('77) concluded that deprived X- and Y-cells are of roughly equal size (instead of Y-cells being larger as in normal laminae), so that electrodes should have sampled many more Y-cells if they were normally responsive. Furthermore, Kratz et al. ('77) reported a severe loss of Y-cells in the A laminae of dark reared kittens, despite the fact that cell sizes were normal in these animals. Again, the apparent loss of Y-cells in dark reared kittens cannot simply be attributed to electrode sampling biases. While the evidence strongly supports a functional loss of Y-cells in the deprived A laminae, electrode sampling biases must also be considered in interpretation of the MIN data.

Several points can be made, all of which support the conclusion that deprived segments of MIN suffer a true functional Y-cell loss. First, many abnormal deprived MIN neurons were found, which offers direct evidence of an effect of deprivation upon the developing Y-cells, since practically all MIN cells normally are Y-cells (Kratz et al., '78, preceding paper). It seems highly unlikely that these abnormal cells are normal cells (i.e., perhaps interneurons) found rarely in normal animals. We found only one such neuron (0.1/mm) in normal cats (Kratz et al., '78). As can be deduced from table 1, we found only two such cells (0.2/mm) in nondeprived MIN regions in the lid sutured cats, yet sampled 12 (1.8/mm) in deprived MIN regions. There is no reason to expect the sampling frequency of rare normal cells to increase so dramatically. Second, the deprived MIN cells, while abnormally small, are still fairly large. In fact, the size distribution of deprived MIN cells is not significantly different from that of normal lamina A neurons (compare fig. 6 of this paper with fig. 9 of the previous paper, Kratz et al., '78). Although lamina A cells are more densely packed than are deprived MIN cells, it seems unlikely that this alone could explain the large difference between these areas in the probability of sampling normal receptive fields (table 1). Third, Lin and Sherman ('78) report that large cortical injections of horseradish peroxidase in lid sutured cats label significantly fewer neurons in deprived than in nondeprived regions of MIN, and this supports the conclusion that the deprived MIN Y-cells are functionally affected by early lid suture. Taken together, these points argue strongly that the results of the present experiment cannot be attributed simply to changes in electrode sampling biases, but instead indicate a severe functional effect of early lid suture upon MIN Y-cells.

Conclusions

The results of the present experiment extend the conclusion of the preceding paper (Kratz et al., '78) that MIN Y-cells and lamLGN Y-cells should be considered subgroups of the same population; since both subgroups of Y-cells are affected by lid suture in essentially the same fashion. Consequently, these results extend previous studies of lateral geniculate neurons in deprived cats (Sherman et al., '72; Sherman et al., '75) and suggest that development of all groups of geniculate Y-cells are retarded by visual deprivation, whereas deprived X-cells develop relatively normally. Furthermore, since MIN projects

largely outside of the geniculostriate system to areas 18, 19 and the lateral suprasylvian cortex (Rosenquist et al., '74; Gilbert and Kelly, '75; Maciewicz, '74, '75; Holländer and Vanegas, '77; LeVay and Ferster, '77), this is the first clear demonstration of a primary effect of early lid suture upon extrastriate visual pathways.

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