

Further Evidence for an Early Critical Period in the Development of the Cat's Dorsal Lateral Geniculate Nucleus

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ABSTRACT The concept of an early postnatal critical period of development for the lateral geniculate nucleus was assessed by determining in adult cats whether previously established properties of geniculate neurons could be altered by varying the cats' visual experience. The analysis was limited to lamina A1 and the binocular segment of lamina A, and the properties studied were the percentage of physiologically recorded Y-cells and cell soma size. Eleven experimental cats in four groups were studied, and three cats reared normally plus three cats reared with continuous monocular lid suture served as controls. Two cats raised first with monocular suture followed by a prolonged period in adulthood with both eyes open had cell size distributions and Y-cell proportions that were indistinguishable from cats raised with continuous monocular suture. Four cats raised first with one eye sutured underwent a reverse suture procedure in adulthood (i.e., the originally sutured eye opened and the other closed) and were maintained in this fashion for a prolonged period. These cats also had geniculate cell size distributions and Y-cell proportions that were indistinguishable from cats raised with continuous monocular suture. Two cats were raised first with binocular suture followed by a prolonged period in adulthood with one eye opened. Their geniculate cell size distributions and Y-cell proportions showed no effect of the adult monocular deprivation and were indistinguishable from previously published data concerning cats raised with continuous binocular suture. Finally, three normally raised cats underwent a prolonged period of monocular suture in adulthood. Their geniculate cell size distributions and Y-cell proportions showed no effects of the adult monocular deprivation. From these data, we conclude that an early critical period of development occurs for geniculate cell sizes and Y-cell proportions. Adult visual environments, whether normal or abnormal, had no detectable effect on geniculate neurons for these previously developed properties, whether normal or abnormal.

A cat raised with the lids of one or both eyes sutured together develops certain abnormalities in its geniculocortical pathways. Studies of striate cortical neurons indicate that such deprivation induces abnormalities only during an early critical period (Hubel and Wiesel, '70; Blakemore and Van Sluyters, '74), and that these abnormalities are relatively permanent (Wiesel and Hubel, '65b; Chow and Stewart, '72; Hoffmann and Cynader, '77; see, however, Kratz et al., '76).

The issues concerning a critical period for and permanence of deprivation-induced abnormalities are less clear at the level of the lateral

geniculate nucleus. Anatomically, the geniculate cell bodies in deprived laminae (i.e., those receiving direct retinal afferents from the deprived eyes) are abnormally small (Wiesel and Hubel, '63, '65a; Guillery and Stelzner, '70; Cragg et al., '76; Hickey et al., '77). Several studies have found this effect on cell size to be permanent after at least 14 weeks of closure (Wiesel and Hubel, '65b; Cragg et al., '76; Dursteler et al., '76). However, Chow and

This work was accomplished in part while the authors were at the University of Virginia Medical School, Department of Physiology, Charlottesville, Virginia 22908.

Stewart ('72) reported that the effects of early lid suture on geniculate cell sizes could be substantially ameliorated or even reversed by appropriate visual environments during adulthood. Two other studies (Garey and Dursteler, '75; Spear and Hickey, '79) reported similar results in monocularly deprived cats after enucleation of the open eye at 3 months of age. Physiologically, Sherman et al. ('72) reported a deficit after early lid suture (namely, a reduction in the proportion of geniculate Y-cells recorded). Hoffmann and his colleagues have more recently reported that this physiological deficit in monocularly deprived cats can be changed by a reverse suture at 8–10 months of age even though these same cats displayed no change in their previously developed soma size distribution (Hoffmann and Cynader, '77; Hoffmann and Hollander, '78).

Therefore, it is not completely clear to what extent the concept of an early critical period applies to the development of geniculate neurons, particularly with respect to cell size and Y-cell proportions. Our only object in this initial study was to explore the ability of visual environments during adulthood to modify these geniculate properties. The failure of these environments to affect geniculate neurons would imply that a proscribed, relatively early critical period of development occurred for these properties. No attempt was made here to access the dynamics of the possible critical period for geniculate development.

We addressed this problem by determining cell sizes and Y-cell proportions in four experimental groups of cats. These were raised to at least 4 months of age (i.e., past the classical critical period as determined for striate cortex) with an initial visual environment, and this was followed by at least 5 months of a second visual environment. These groups were: (1) initial monocular lid suture followed by binocular viewing (i.e., the sutured eye was opened); (2) initial monocular suture of one eye followed by reverse monocular suture (i.e., the initially sutured eye was opened and the contralateral eye was sutured); (3) initial binocular suture followed by monocular suture (i.e., one eye was opened); and (4) initial normal binocular viewing followed by monocular suture. Control groups consisted of cats raised normally or with continuous monocular suture.

We found no evidence that the second rearing condition in any way affected geniculate cell size or Y-cell proportions expected from

the initial rearing condition. Our data support the concept of an early critical period for geniculate development, at least as far as these rearing conditions are concerned, and thus the lateral geniculate nucleus and striate cortex seem to share this phenomenon.

MATERIALS AND METHODS

Subjects

Seventeen cats were used in this study. Figures 1, 2, 6, and 8 summarize each cat's history of eyelid suture before the terminal experiments for physiology and/or histology. Six of the cats (N1, N2, N3, ALMD1, ALMD2, and ARMD3) were purchased as adults of unknown age with presumably normal visual development. Cats N1, N2, and N3 served as normal controls. Cats ALMD1, ALMD2, and ARMD3 had the lids of one eye sutured as adults and were anatomically and/or physiologically studied 2–3 years later. The other 11 cats were born and raised in the laboratory. Two of these kittens (BD7 and BD9) had both eyelids sutured before normal eye opening (i.e., 5–12 days postnatal) and were used to study the permanence of abnormalities induced by early binocular deprivation. At 4–6 months of age (after the presumptive critical period), each had the lids of the right eye parted, and the right eye alone was kept open for an additional 11–12 months until the final experiments were performed. The other nine kittens (RMD1, RMD2, LMD16, LMD27, RMD26, LMDR1, LMDR2, LMDR3, and RMDL) had the lids of one eye sutured before normal eye opening and were used to study the permanence of effects of early monocular deprivation. Cats RMD1 and RMD2 had their deprived eyes opened at 9 or 12 months, respectively, and thereafter both eyes were open until final study 22 or 9 months later. Cats RMDL, LMDR1, LMDR2, and LMDR3 underwent reverse suture operations whereby the previously deprived eye was opened and the other closed; they were maintained in this condition until final study. The ages of reverse suture and final study were 12 and 22 months for RMDL; 7 and 31 months for LMDR1; 24 and 36 months for LMDR2; and 14 and 19 months for LMDR3. Cats LMD16, LMD27, and RMD26 underwent no further ocular manipulations until their study at 10–12 months of age and thereby served as controls for the other monocularly deprived cats.

Cats RMD1, RMD2, LMDR1, RMDL, BD7, and BD9 were studied behaviorally before sac-

rifice, and these data were presented elsewhere (Sherman, '74). Not all of the cats were studied both electrophysiologically and anatomically. Single cell recordings of geniculate neurons were performed on cats RMD1, RMD2, LMDR1, LMDR2, BD7, BD9, and ALMD1. geniculate cell measurements were taken from all cats except RMD2.

Electrophysiology

Techniques were used for single cell recording that have been described previously (Hoffmann et al., '72; Sherman et al., '75). Criteria for X- and Y-cell identification included response latency to optic chiasm shock, responsiveness to large rapidly moving targets appropriate for surround stimulation, receptive field size, and the tonic or phasic nature of the response to appropriate standing contrast (Hoffmann et al., '72). Varnished tungsten microelectrodes or 4M NaCl-filled micropipettes (10–20 M Ω at 500 Hz) were used to record extracellular activity from single geniculate neurons. Since both types of electrodes provided similar results these data were pooled. The receptive fields were plotted on a tangent screen 114 cm in front of the eyes, and their positions were noted relative to the projections of the optic discs (Fernald and Chase, '71).

Histology

The cats were anesthetized and sacrificed by transcardial perfusion of saline followed by 10% formol-saline. The brains were stereotaxically blocked, embedded in egg yolk, and cut frozen at 40 μ m in the coronal plane. Every third or fourth section was stained with cresylecht violet. We used our previous methods (Sherman and Wilson, '75) to measure the cross-sectional area of individual geniculate cell bodies. Only cells in the binocular segment of laminae A and A1 (cf., Guillery and Stelzner, '70) are included in this study. The cells were traced onto graph paper by means of a microscope with a drawing-tube attachment. We used an oil immersion 100 \times objective (N.A. = 1.32) to achieve 1,000 \times magnification. The area of each cellular outline was calculated and calibrated into square micrometers by means of a micrometer scale drawn onto the paper with the same optical system.

Sampling errors were minimized by applying our previously described methods (Sherman and Wilson, '75). Briefly, 50 neurons with visible nucleoli were randomly sampled for measurement in a zone. Four such zones per

cat were available, one each from lamina A and A1 in each hemisphere. These were matched among cats by choosing a standard anteroposterior level (halfway through the nucleus) on each side and sampling neurons near the middle of the binocular segment (corresponding to the mediolateral middle of lamina A1).

RESULTS

Electrophysiology

Normally reared cats exhibit geniculate X- and Y-cells which are electrophysiologically sampled in roughly equal numbers. However, cats reared with early binocular or monocular lid suture suffer a loss of or fail to develop Y-cells that can be recorded in the deprived geniculate laminae (Sherman et al., '72). We were unable to alter this pattern in any significant manner with a variety of adult environments. We recorded from a total of 258 geniculate X- and Y-cells in seven cats. All of these neurons were from the binocular segment of laminae A and A1. We routinely sampled both hemispheres (see below) but have pooled our data according to ocular dominance for simplicity, since we found no suggestion that lamina A populations in one hemisphere differed from those in the opposite lamina A1 (see, however, Sireteanu and Hoffmann, '79).

Early binocular deprivation

Cats BD7 and BD9 were raised with both eyes shut until the fourth or sixth postnatal month, and then the right eyes were opened for the remaining 11–12 months. We reasoned that if changes in geniculate Y-cell proportions could occur beyond the early critical period, then a larger proportion of geniculate Y-cells should be driven by the right eye than by the left in each cat. Geniculate cells in each cat were sampled from both hemispheres. Figure 1 provides a summary of the data. A total of 73 X-cells and 33 Y-cells (31% Y-cells) were found in the two cats. Of these, the left eye (closed during adulthood) drove 39 X-cells and 20 Y-cells (34% Y-cells) and the right eye (opened during adulthood) drove 34 X-cells and 13 Y-cells (28% Y-cells). These ratios are not statistically different ($P > 0.10$ on a χ^2 -test). Figure 1 also shows that, in a previous study using identical techniques (Sherman et al., '72), three cats raised with continuous binocular suture yielded a geniculate sample of 73 X-cells and 29 Y-cells (28% Y-cells). Thus, the addition of monocular suture following early binocular suture in the present study had no observable

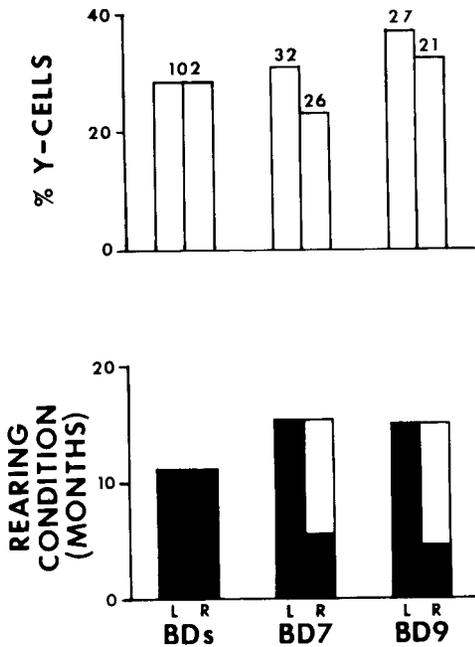


Fig. 1. Percentage of geniculate Y-cells from cats reared initially with binocular lid suture; all data are from the binocular segment of the A laminae. The lower histograms indicate the rearing conditions: L or R refers, respectively, to left or right eye; solid portions indicate the periods of lid suture, and open portions, periods of eye opening. BDs refers to previously published data (Sherman et al., '72). The upper histograms show the relative percentages of Y-cells (the remainder were X-cells) relative to each eye, since data were pooled between laminae A and A1 in opposite hemispheres. The numbers above the histograms refer to the total number of X- and Y-cells recorded.

effect upon Y-cell proportions recorded in the A laminae.

Early monocular deprivation

We recorded from both hemispheres in cats RMD2, LMDR1, and LMDR2, but only the right hemisphere in cat RMD1. Figure 2A shows that, for each cat, the originally deprived eye drove proportionately fewer geniculate Y-cells than did the originally open eye. The differences were statistically significant for each cat except cat LMDR2 (on a χ^2 -test; $P < 0.001$ for RMD2 and LMDR1; $P < 0.02$ for RMD1). The data from cat LMDR2 are in line with those from the others, but too few neurons were sampled¹ for statistical relevance ($0.05 < P < 0.1$ on a χ^2 -test). Figure 2B shows that pooled data from these four cats compared with those from four other cats raised with continuous monocular suture from birth until the final recording sessions (data

from Sherman et al., '72). Again, we found no evidence that the adult visual environment could alter the geniculate pattern developed earlier.

Late monocular deprivation

Single units were recorded from only one of the adult lid-sutured cats (ALMD1) during a very brief recording session. The results showed that the late-deprived eye drove practically the same percentage of Y-cells (33%; 8 X- and 4 Y-cells) as that of the nondeprived eye (31%; 11 X- and 5 Y-cells). Thus, no advantage was given to the nondeprived eye at the age of 1 year when the other eye was lid-sutured. The overall percentage of Y-cells from either eye of this one cat were lower than previously reported (Hoffmann et al., '72), and we cannot explain this observation, but our sample size was small due to technical problems (see footnote 1). However, no differential effect of the lid suture was seen on the proportion of Y-cells recorded for each eye, and histological results (see below) also suggest no effects of the adult suture.

Histology

Histological data based upon geniculate soma sizes were obtained from 16 cats, and 200 cells per cat were measured. As with the physiology, we combined data from lamina A in one hemisphere with those of lamina A1 in the other. This was done for simplicity. Any differences between the effects of deprivation upon laminae A and A1 were quite small or insignificant in our data, and the normal tendency for cells in lamina A1 to be slightly larger than those in lamina A is balanced by our pooling procedure (cf. Sherman and Wilson, '75; Hickey et al., '77). Pooled data from each lamina A and the contralateral lamina A1 are illustrated for each cat as a mean soma size in the figures. As above for electrophysiology, we found no evidence that adult environments could alter geniculate soma sizes established by earlier rearing conditions.

Early binocular deprivation

Geniculate cell measurements were taken both from cats BD7 and BD9. Any lack of growth or atrophy caused by early lid suture might be reversed, at least partly, by the adult

¹In this and several other cats, technical problems (e.g., difficulty in locating the lateral geniculate nucleus with functioning electrodes) led to a low yield of sampled neurons.

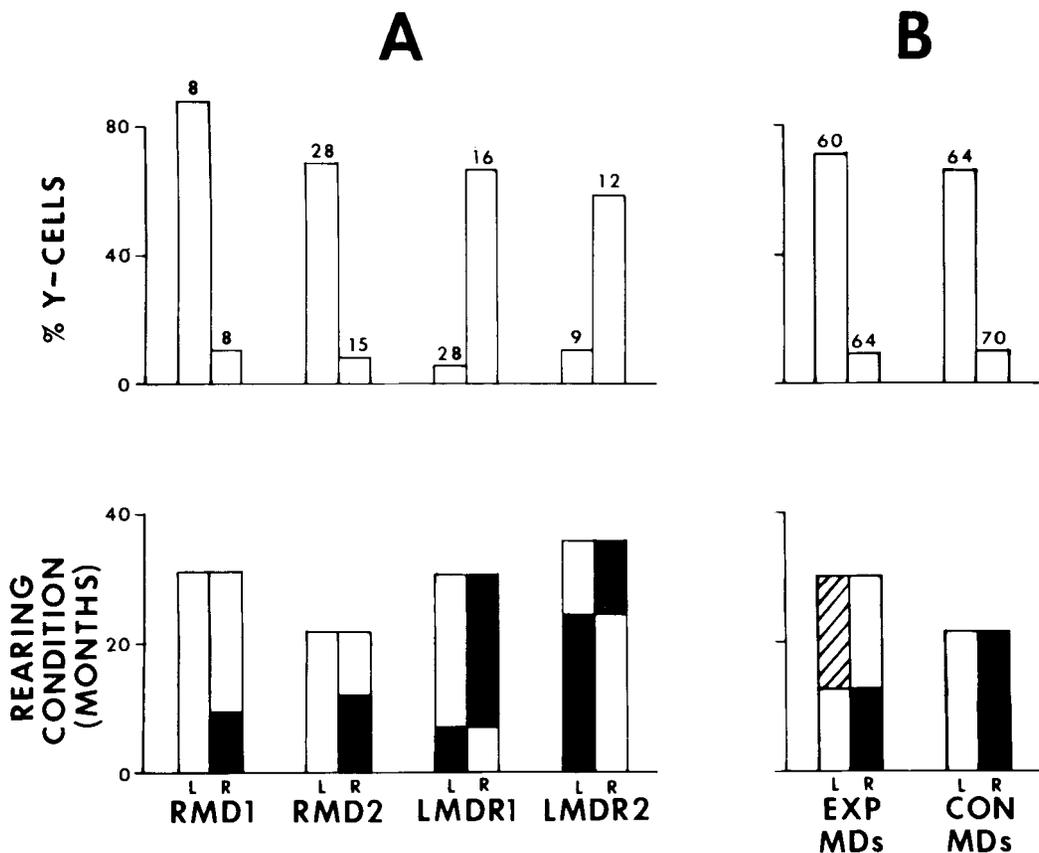


Fig. 2. Percentage of geniculate Y-cells from cats reared initially with monocular lid suture: all data from binocular segment of the A laminae. A. Data from individual cats, conventions as in Figure 1. B. Pooled data. Exp MDs refers to the four cats in A. For convenience, all cats are pooled as if the right eye were sutured originally; thus the histograms are reversed between L and R for LMDR1 and LMDR2. The cross-hatching indicates either an open eye (for RMD1 and RMD2) or sutured eye (for the others). CON MDs refers to previously published data (Sherman et al., '72).

experience for the cells related to the right eye; since the left eye was placed at a competitive disadvantage, geniculate cells related to it might atrophy. If so, cells in left lamina A and right lamina A1 should be larger than those on the opposite side. However, a general inspection of the tissue showed no evidence of interlaminar differences in cell size. Figure 3 illustrates this for cat BD9. We measured 50 cells from each of the four zones in the binocular segment as described in Materials and Methods. Figure 4 summarizes the resultant data, and these indicate that, for each cat, cells related to the right eye (i.e., left lamina A and right lamina A1) were no larger, on average, than those related to the left eye (i.e., right lamina A and left lamina A1). The slight differences were not statistically significant ($P > 0.1$ on a t-test). The three

normal cats also showed, as expected, no difference in geniculate cell size based upon ocular input (see below, and Fig. 8B). Overall differences between BD7 and BD9 probably obtain from an artifact due to differential tissue shrinkage (Guillery, '73), and in any case each cat served as its own control. These data do not support the notion that, after the critical period, asymmetrical experience between the two eyes leads to differences in geniculate cell sizes.

Early monocular deprivation

Many studies have shown that cats reared with continuous monocular suture develop, in the binocular segment of nondeprived geniculate laminae, neurons which are considerably larger than their deprived counterparts (Wiesel and Hubel, '63; Guillery and

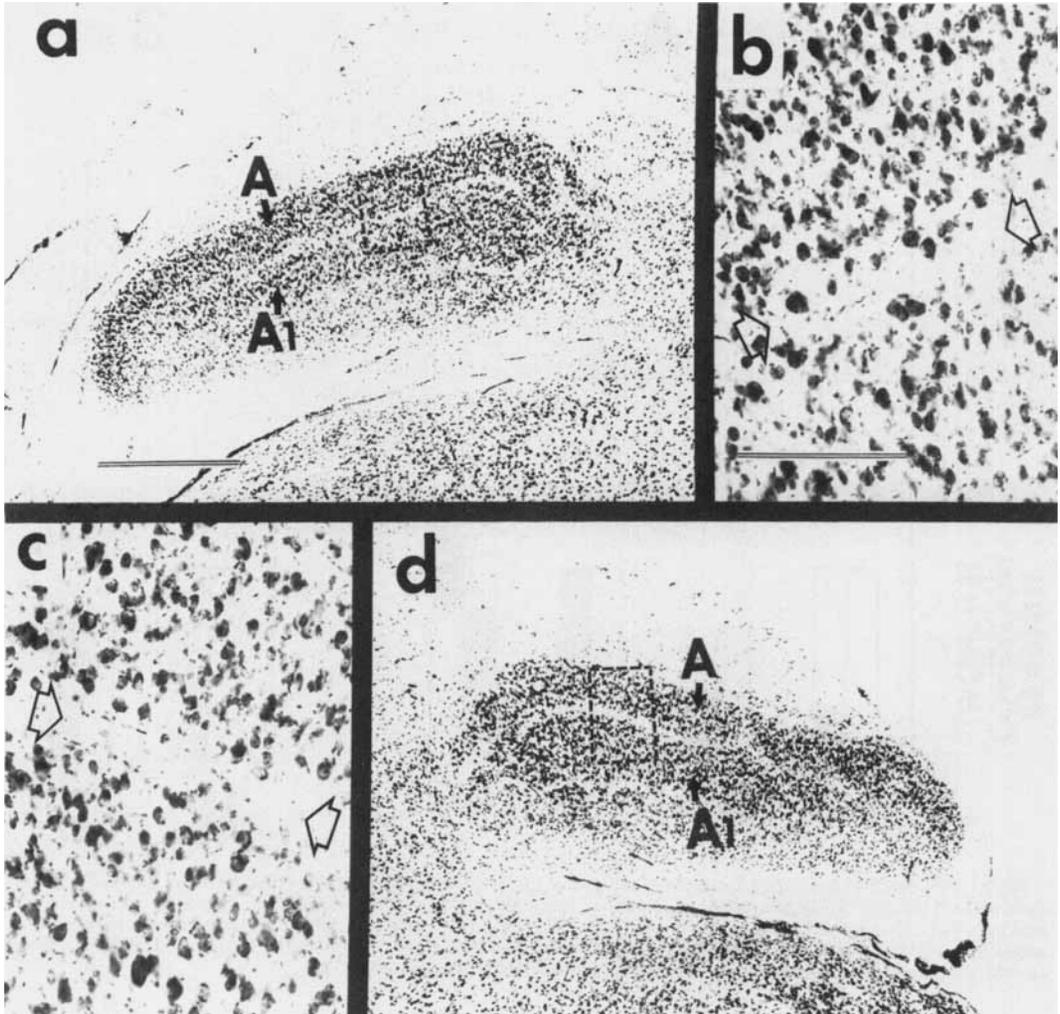


Fig. 3. Photomicrographs of the lateral geniculate nuclei of cat BD9. The cat was reared with binocular suture and then had the right eye opened for several months (see Fig. 1 for rearing conditions). Despite this, no striking interlaminar differences in soma size are evident. a and d. Lower-power view of the left and right nuclei, respectively. Scale line equals 1 mm. Laminae A and A1 are labeled and the dashed rectangles outline the area of higher magnification shown in b (left nucleus) and c (right nucleus). Arrows in b and c point along the interlaminar zones; scale line equals 200 μ m.

Stelzner, '70; Hickey et al., '77). We raised four cats (RMDL, LMDR1, LMDR2, and LMDR3) with one eye sutured from before normal eye-opening until 5–22 months of age, at which time the other eye was sutured and the initially closed eye was opened. They were maintained in this fashion for an additional several months before histological analysis. If geniculate cell sizes were affected by this later asymmetry between the two eyes' visual environments, then the ratio of cell sizes should differ accordingly from that of cats raised with continuous

lid suture. However, casual inspection of the lateral geniculate nuclei in each of these animals indicated a pattern of soma sizes indistinguishable from that seen in continuously monocularly deprived cats. This is illustrated in Figure 5 for cat LMDR2. Figure 6 further shows that a quantitative analysis from each of the cats supports this observation. The three cats raised with continuous monocular suture (Fig. 6B) have geniculate cell size distributions indistinguishable from those raised with the reverse suture. Since adult

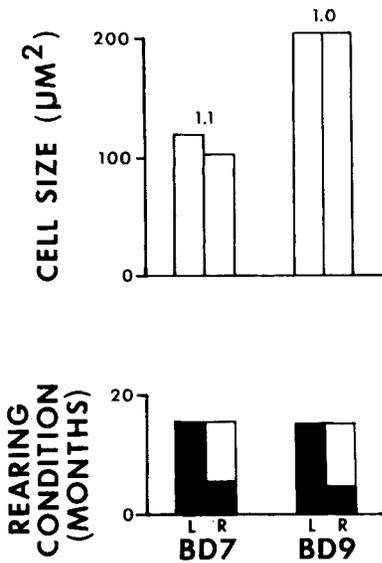


Fig. 4. Mean geniculate soma sizes for cats BD7 and BD9. The lower histograms indicate the rearing conditions as in Figure 1. The upper histograms display data pooled between laminae A and A1 in opposite hemispheres based on input from the left (L) or right (R) eye. The numbers above each pair indicate the ratio (larger/smaller) of soma sizes between laminae related to each eye.

reverse suture did not affect the previously established geniculate cell size distribution, one would expect that the adult binocular environment for cat RMD1 would not affect its cell size distribution (Fig. 6A). This is indeed the case. Figure 6C shows that pooling of the data further supports the conclusion that these adult visual environments cannot affect the previously developed abnormal cell size pattern.

Adult monocular deprivation

Although the above results suggest that in the adult, visual experience cannot affect geniculate cell sizes developed during early visual deprivation, it might still be the case that adult deprivation affects the normally developed cell size distribution. Three cats (ALMD1, ALMD2, ARMD3), obtained as presumably normal adults, were then monocularly deprived by lid suture for 2–3 years. In each of these cats, the cell size distribution was indistinguishable from that of a normal cat. The photomicrographs in Figure 7 illustrate this for cat ARMD3. Figure 8 shows the cell size analysis for each of these cats plus three

normal cats, and no differences are evident. Therefore, the adult environments used here are ineffective in terms of changing previously developed geniculate cell sizes, whether these sizes have resulted from normal or abnormal development.

DISCUSSION

All of our data point strongly to one conclusion. That is, for the environmental manipulations employed in this study, the development of the cat's lateral geniculate nucleus has a definite and proscribed early critical period. This applies specifically to the development of both Y-cells that can be recorded physiologically as well as soma size. In no way were we able to alter the previously developed pattern of geniculate Y-cell proportions or soma size, whether normal or abnormal, by adult visual environments, whether normal or abnormal.

Although our data support the concept of an early critical period for geniculate development, they do not address the question of the dynamics of this period beyond its occurrence somewhere during the first several postnatal months. Dursteler et al. ('76), with a slightly different strategy from ours, have described the dynamics of geniculate cell growth during monocular suture. They conclude that the geniculate critical period is remarkably similar to that described previously for striate cortex (Hubel and Wiesel, '70; Blakemore and Van Sluyters, '74). That is, the period begins during the third or fourth week, peaks early, and is terminated by about the fourth month.

Several reports have described data which contradict ours and challenge the question of a critical period for the lateral geniculate nucleus. First, Chow and Stewart ('72) reported that a reverse-suture experiment (essentially identical to that described here) results in a lateral geniculate nucleus which has larger somata in the laminae related to the first deprived eye and smaller ones in the other laminae. Second, Hoffmann and Cynader ('77) and Hoffmann and Hollander ('78) recorded a limited return of Y-cells in originally deprived laminae of reverse-sutured cats; these same cats displayed no alteration of the previously developed cell size pattern which could be correlated to the Y-cell return. We can offer no simple explanation for our different results for Y-cell sampling in these studies beyond the obvious statement that we have little understanding of the many uncontrolled variables or sampling properties which govern the data. Our conclusion that there exists an early criti-

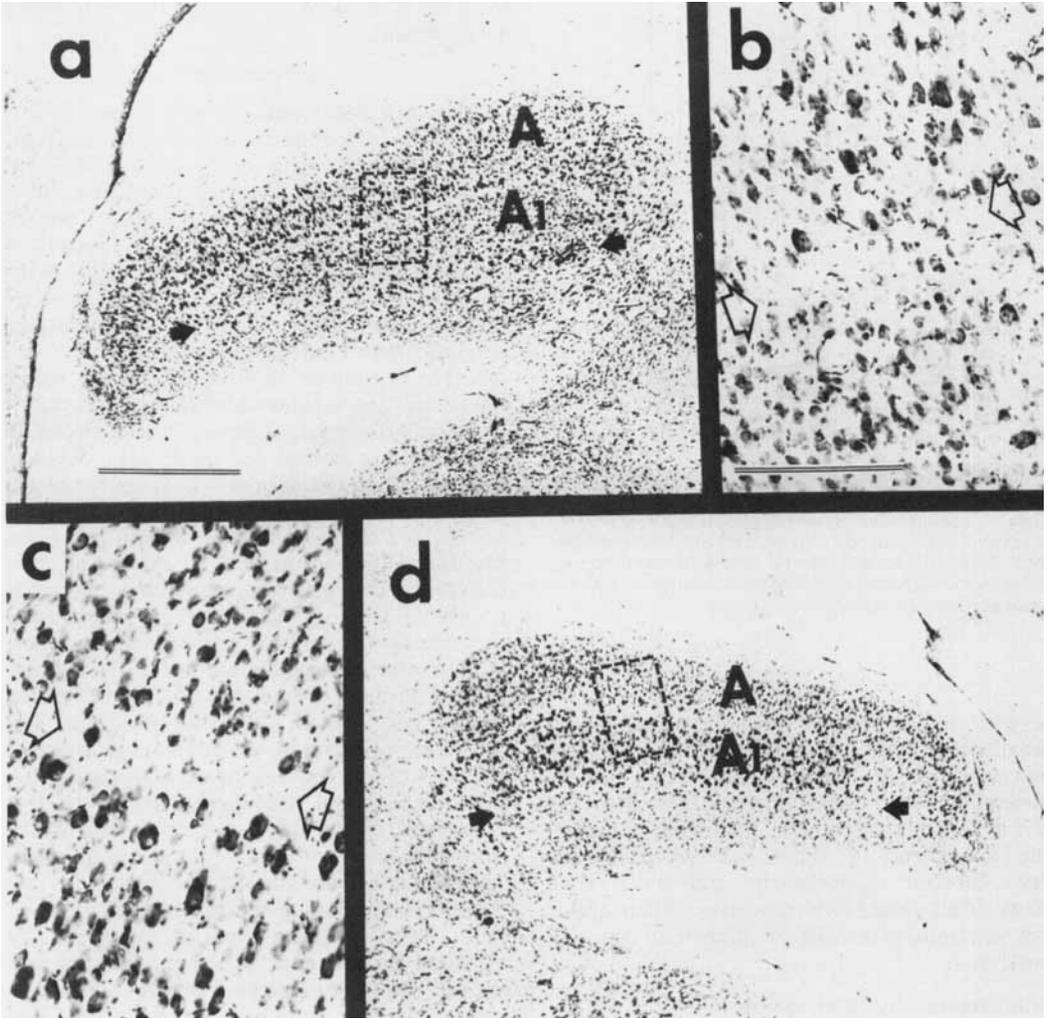


Fig. 5. Photomicrographs of the lateral geniculate nuclei of cat LMDR2. This cat was reared with monocular suture of the left eye followed by reverse suture (see Fig. 2 for rearing conditions). Cells in left lamina A1 and right lamina A are smaller than those in the remaining A laminae, and the row of large C laminae cells in the left nucleus is not apparent in the right nucleus. Conventions and scales as in Figure 3, except that the solid arrows in a and d indicate the C laminae. a and b. Lower- and higher-power views of the left nucleus. c and d. Higher- and lower-power views of the right nucleus.

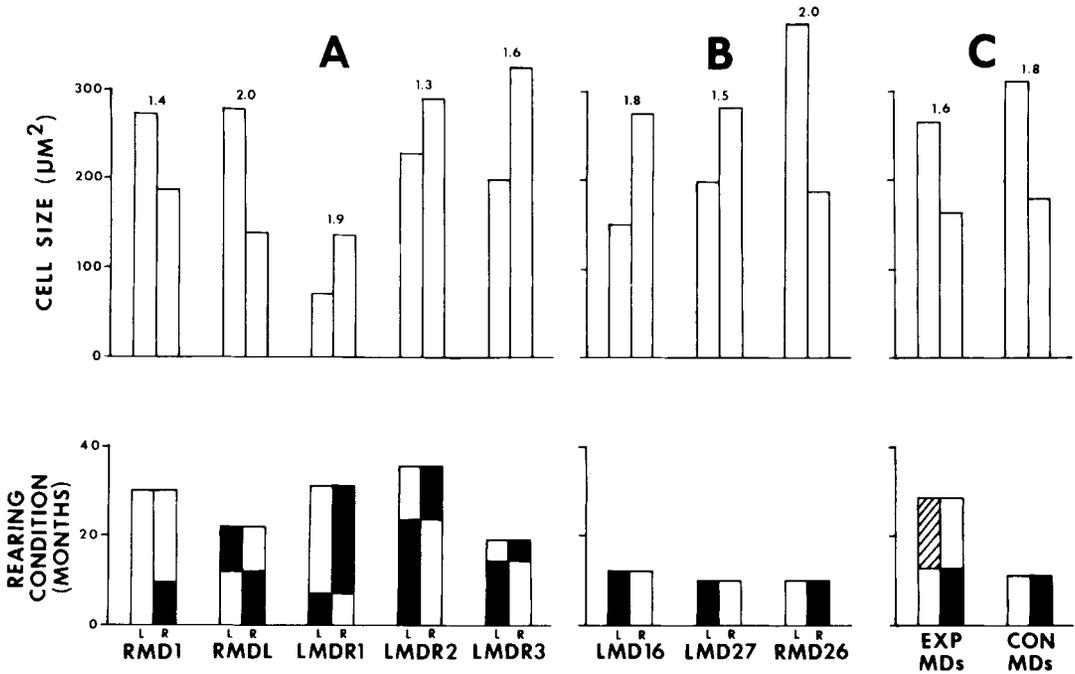


Fig. 6. Mean geniculate soma sizes for cats reared with early monocular suture; conventions as in Figure 4. A. Data for cats with adult experience for the originally deprived eye. B. Data for cats with continuous monocular suture. C. Pooled data; conventions for pooling as in Figure 2. EXP MDs represents the data in A; CON MDs, in B.

cal period for cat geniculate neurons must therefore be qualified.

In addition, we emphasize that our evidence for a critical period is limited to the environmental manipulations we employed. For instance, Cynader and Mitchell ('79) have shown that dark rearing can delay the critical period of cortical development. However, in a limited study of geniculate Y-cell proportions, Kratz et al. ('79) found no evidence of a prolonged critical period in dark-reared cats.

As in the present experiment for geniculate neurons, reverse suture or opening both eyes fails to secure cortical cells for the initially deprived eye (see also Hubel and Weisel, '70; Blakemore and Van Sluyters, '74). In a similar study, however, Kratz et al. ('76) found that enucleation of the nondeprived eye allows the deprived eye of a monocularly sutured cat to activate many cortical cells for the first time. Hoffmann and Cynader ('77) report that adult enucleation of the nondeprived eye of a cat raised with monocular suture restores to normal the geniculate Y-cell recordability in the deprived laminae. Spear and Hickey ('79) likewise showed that similar procedures cause

the previously deprived geniculate neurons to grow to normal size. Curiously, Geisert et al. ('80) find that, in monocularly sutured cats with adult enucleation of the nondeprived eye, deprived geniculate cells grow to nearly normal size, but that there is no restoration of Y-cell numbers for that eye as long as the deprived eye is kept sutured during the postenucleation survival period.

Clearly, there are many discrepant results concerning the concept of an early critical period which cannot yet be explained. It appears that plasticity in central pathways for one eye can occur in adults under certain conditions (e.g., enucleation of the other eye) but not others (e.g., closure of the other eye). There is also no clear relationship between cell size and recorded Y-cell numbers: Kratz et al. ('79) and Geisert et al. ('80) described conditions under which fewer than normal Y-cells could be recorded despite a nearly normal geniculate cell size distribution; Hoffmann and Hollander ('78) described the opposite, whereby the Y-cell proportion was largely restored with no cell size change among the abnormally small geniculate neurons.

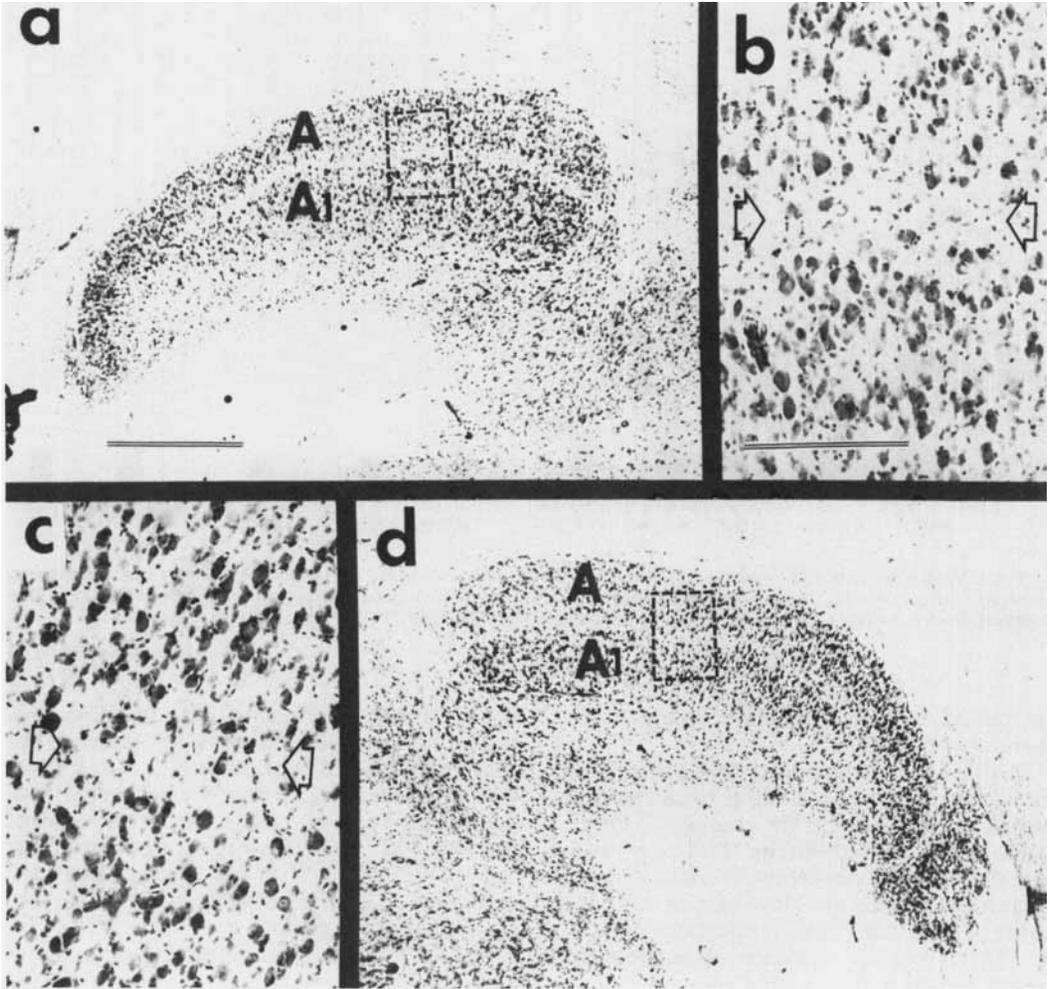


Fig. 7. Photomicrographs of the lateral geniculate nuclei of cat ARMD3. This cat was raised normally but underwent suture of the right eye for several years in adulthood (see Figure 8 for rearing conditions). No striking interlaminar differences in soma size were evident. Conventions and scales as in Figure 3. a and b. Lower- and higher-power views of the left nucleus. c and d. Higher- and lower-power views of the right nucleus.

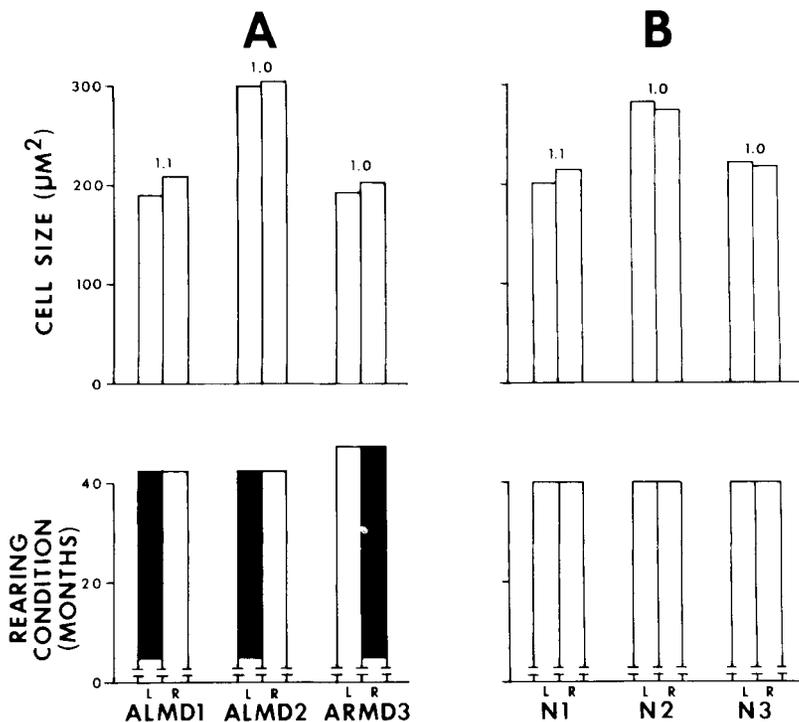


Fig. 8. Mean geniculate soma sizes for normally reared cats; conventions as in Figure 4. A. Cats with extensive periods of monocular suture during adulthood. B. Cats without visual deprivation (normals).

The variability in the literature concerning the permanence of early developed geniculate cell size distributions and Y-cell numbers is puzzling. It is also not evident that these two properties are necessarily correlated with one another. Nevertheless, in our hands and with our rearing conditions, these properties seem insensitive to adult visual environments.

ACKNOWLEDGMENTS

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