

Development of Neuronal Response Properties in the Cat Dorsal Lateral Geniculate Nucleus During Monocular Deprivation

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SUMMARY AND CONCLUSIONS

1. We measured response properties of X- and Y-cells from laminae A and A1 of the dorsal lateral geniculate nucleus of monocularly lid-sutured cats at 8, 12, 16, 24, and 52–60 wk of age. Visual stimuli consisted of small spots of light and vertically oriented sine-wave gratings counterphased at a rate of 2 cycles/s.

2. In cats as young as 8 wk of age, nondeprived and deprived neurons could be clearly identified as X-cells or Y-cells with criteria previously established for adult animals.

3. Nonlinear responses of Y-cells from 8- and 12-wk-old cats were often temporally labile; that is, the amplitude of the nonlinear response of nondeprived and deprived cells increased or decreased suddenly. A similar lability was not noted for the linear response component. This phenomenon rarely occurred in older cats.

4. At 8 wk of age, Y-cell proportions (number of Y-cells/total number of cells) in nondeprived and deprived A-laminae were approximately equal. By 12 wk of age and thereafter, the proportion of Y-cells in deprived laminae was significantly lower than that in nondeprived laminae. At no age was there a systematic difference in response properties (spatial resolution, latency to optic chiasm stimulation, etc.) for Y-cells between deprived and nondeprived laminae.

5. Spatial resolution, defined as the highest spatial frequency to which a cell would respond at a contrast of 0.6, was similar for nondeprived and deprived X-cells until 24 wk of age. In these and older cats, the mean

spatial resolution of deprived X-cells was lower than that of nondeprived X-cells. This difference was noted first for lamina A1 at 24 wk of age and later for lamina A at 52–60 wk of age.

6. The average latency of X-cells to optic chiasm stimulation was slightly greater in deprived laminae than in nondeprived laminae. No such difference was seen for Y-cells.

7. Cells with poor and inconsistent responses were encountered infrequently but were observed far more often in deprived laminae than in nondeprived laminae.

8. Lid suture appears to affect the development of geniculate X- and Y-cells in very different ways. Not only is the final pattern of abnormalities quite different between these cell groups, but the developmental dynamics of these abnormalities also differ.

INTRODUCTION

Early monocular lid suture affects the development of neurons throughout the central visual pathways of the cat (for recent reviews, see Refs. 39, 49). In particular, mean soma size in deprived geniculate laminae is smaller than that in nondeprived or normal laminae (18, 20, 59). Physiological recordings in geniculate laminae A and A1 reveal that the number of recorded Y-cells and the spatial resolution of X-cells are lower in deprived compared to nondeprived laminae (9, 14, 15, 32, 33, 35, 40, 47, 50, 52, 66). In the striate cortex (60, 62), cortical area 18 (51), and the lateral suprasylvian cortex (55), early monocular deprivation dramatically reduces the percentage of neurons that can be influenced

from the deprived eye. A similar reduction in the deprived eye's capacity to influence neurons occurs in the superior colliculus (58).

The onset of these deprivation-induced abnormalities has been extensively investigated only in the striate cortex. After monocular lid suture of the week-old neonate, physiological changes are first observed in the striate cortex by 3–4 wk of age (24). By approximately 4 wk of age, mean cell size in deprived geniculate laminae is lower than that found in nondeprived laminae (19, 27). However, the onset of the physiological changes in geniculate neurons has not yet been determined. Accordingly, we have examined the development of neuronal response properties of geniculate X- and Y-cells during monocular lid suture. Physiological recordings in the A-laminae were made at various ages following early monocular lid suture. Within each age group, the responses of deprived and nondeprived cells were compared to determine the onset of the physiological changes in geniculate X- and Y-cells.

We also dealt with the problem of identifying and classifying geniculate neurons as X- or Y-cells in the young kitten. Studies of the A-laminae in the adult cat have distinguished cells as X- or Y-cells by the linearity of their spatial summation (45, 53, 54) and/or by the use of several other response measures, such as latency to optic chiasm stimulation, tonic or phasic responses, receptive-field center diameter, and responsiveness to fast-moving targets (2, 3, 23, 34). However, the response properties of geniculate neurons are quite immature in young kittens (6, 16, 41, 63). It is thus possible that these neurons in the kitten cannot be separated into the X- or Y-cell classes on the basis of response criteria used for neurons in adult animals. In this study we found that cellular maturation and differentiation in 8-wk-old kittens are sufficient to permit cell identification by the use of criteria normally applied to adult animals.

MATERIALS AND METHODS

Subjects and physiological preparation

We studied response properties of lateral geniculate neurons in monocularly deprived cats of various ages by the use of extracellular-recording

procedures, which have been described in detail elsewhere (23, 24). Although the surgical preparation for extracellular recording was similar for both adult cats and younger kittens, certain modifications were incorporated into these procedures to adjust for the size and frailty of kittens. These modifications are described in detail here, whereas the more general procedures are treated cursorily.

Fifty-three cats, born and reared in the laboratory, were used in this investigation. Each had the lids of either its right or left eye sutured closed just prior to natural eye opening (i.e., 5–9 days postnatal). This monocular deprivation was maintained until the day of physiological recording, at which time the deprived eye was opened under anesthesia. We inspected the kittens daily to ensure that the lids remained closed and that the animals were healthy. At the time of recording, cats ranged in age from 8 wk to over 2 yr. Table 1 shows the ages of cats studied and the number of cats in each age group.

Anesthesia was induced with halothane and oxygen, often mixed with nitrous oxide, and maintained in this fashion for all surgical procedures. Paralysis was maintained with a continuous infusion of gallamine triethiodide. The infusion rate ranged between $10 \text{ mg} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ for 8-wk-old kittens and $5 \text{ mg} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ for adults during surgical procedures, and was doubled during the recording session. The kittens were then artificially ventilated, with end-tidal CO_2 levels fixed near 4%. During recording, halothane was discontinued and the cats were maintained on 70% nitrous oxide and 30% oxygen. We periodically applied a long-acting local anesthetic to all wound edges and ear canals. The heart rate was monitored during many experiments, and core temperature was maintained between 37 and 38°C.

Standard stereotaxic procedures were used for all animals. For younger kittens, the head was held in place after alignment by a bar attached at one end to the stereotaxic frame and cemented to the kitten's skull at the other end.

Electrophysiological procedures

Bipolar stimulating electrodes that straddled the optic chiasm were used to activate geniculate neurons with square-wave pulses of 0.5 mA for 50 μs . Micropipettes filled with 4 M NaCl (usually 8–40 M Ω at 500 Hz) were used to record unit extracellular activity of geniculate cells. Each electrode penetration was terminated when the electrode reached the dorsal portion of lamina C based on the ocular dominance of neural responses. That is, after a sequence of contralaterally dominated cells (lamina A) followed by a similar ipsilaterally dominated sequence (lamina A1), the reappearance of contralaterally dominated cells marked lamina C. This was occasionally verified

histologically. Because we limited our sample to laminac A and A1, we limited our investigation to X- and Y-cells and avoided W-cells located in the C-laminae (e.g., Refs. 4, 64).

Optics and visual stimulation

Atropine and Neo-Synephrine were placed on the corneas to dilate the pupils and to retract the lids and nictitating membranes. Corneal contact lenses with 3-mm-diameter artificial pupils and of appropriate curvature and base diameter (57) were then inserted. Retinoscopy was used to select the correct contact lens so that each eye was focused optimally on the visual stimuli (usually a cathode-ray tube (CRT) face located 57 cm from the eyes). During the recording session, refraction was confirmed by testing the effect of different spectacle lenses on neuronal responses to high spatial frequency stimuli.

We found that, with equivalent contact lenses placed on each cornea (i.e., zero-power lenses with equivalent curvature), the deprived eye consistently required 1–2 diopters less correction for proper focus (cf. Refs. 17, 28, 48, 61, 62). This was especially so for our younger kittens. However, without the lenses, both eyes of each kitten were consistently emmetropic. This suggests that some feature of the deprived eye's cornea (e.g., radius of curvature) compensates for the other unusual optical properties of that eye (e.g., longer axial length, lens position, or lens shape). Details of these data will be published separately. Differences in axial length and contact lens correction probably result in somewhat different image magnification onto the two retinas. However, the 1–2 diopter difference is so slight (roughly 5%) that it cannot account for the much larger acuity differences found between the eyes (see RESULTS).

Visual stimuli consisted of either spots of light from a hand-held projector or vertically oriented, sinusoidally counterphased, sine-wave gratings generated on a CRT (see Refs. 23 and 34 for details). The gratings had a space average luminance ($\frac{1}{2}(L_{\max} + L_{\min})$), where L_{\max} and L_{\min} are, respectively, the maximum and minimum luminance values across the grating) of 33 cd/m². Contrast ($(L_{\max} - L_{\min})/(L_{\max} + L_{\min})$) was continuously variable between 0 and 0.6. Also, the spatial frequency (cycles per degree), temporal frequency (counterphase rate in cycles per second), and spatial phase angle (spatial position) were continuously variable.

Definitions

Some of the terms used in our data analysis are defined here.

Spatial resolution is the highest spatial frequency at 0.6 contrast and 2 Hz to which the neuron can respond. Unless otherwise stated, spatial resolution refers to that of the linear or fun-

damental response component of those cells that also had nonlinear components (see below).

Temporal resolution is the highest temporal frequency at 0.6 contrast and any spatial frequency to which the cell can respond.

Spatial contrast-sensitivity functions are plots of contrast sensitivity (the inverse of the contrast needed to evoke a threshold response) versus spatial frequency for a given temporal frequency (usually 2 Hz).

Fundamental and second harmonic (or doubling) response components are determined from Fourier analysis of the neuronal response. The fundamental component occurs at the same temporal frequency as the stimulus, and the second harmonic component occurs at twice the stimulus frequency. Higher response harmonics were also analyzed but are not considered further in this paper.

A position (or spatial phase) of the stimulus can typically be found that evokes no fundamental response component; this is the null position. A maximum fundamental response is evoked at a spatial phase shift of 90° from the null position, and a sinusoidal variation with spatial phase characterizes this response. The second harmonic, or doubling response component, is typically independent of spatial phase.

A linear response is characterized by a spatially phase-dependent fundamental response. Movshon et al. (38) noted linear responses from some cells of visual cortex that showed little or no spatial phase dependence, but such linear responses do not seem to be a feature of geniculate neurons in the A-laminae. A nonlinear response is characterized by a spatially phase-independent doubling response (cf. Refs. 21, 22).

Finally, a deprived geniculate cell or lamina is one that receives direct retinal afferents from the sutured eye. Conversely, a nondeprived cell or lamina is innervated by the open eye.

Data collection and analysis

We examined as many of the following physiological parameters as possible for each lateral geniculate neuron isolated: *a*) receptive-field size, shape, and position, using flashing spots of light from a hand-held projector; *b*) center-surround type (i.e., on or off); *c*) response to standing contrast (i.e., sustained or transient response); *d*) response to a large, fast-moving (>200°/s) disk brighter or darker than the background; *e*) latency to optic chiasm stimulation; *f*) maintained rate of firing to homogeneous visual displays of luminance 33 or 1 cd/m²; *g*) spatial resolution; *h*) spatial contrast sensitivity; *i*) temporal resolution; *j*) responses to different spatial phases at various spatial frequencies and contrasts; *k*) relative response magnitude at first, second, and higher or-

der harmonics of the stimulus temporal frequency.

The optic disks were projected onto the tangent screen by the method of Fernald and Chase (10). Because the angular distance between the optic disk and area centralis has been determined for cats of all ages (42), a receptive-field's eccentricity from area centralis could be calculated if its distance from the optic disk was measured. Eccentricity determinations were made for several cats with an additional method described by Sanderson and Sherman (44). The resultant eccentricity values obtained with the two methods of measurement were within 1.7° of one another.

Unless otherwise stated, the Mann-Whitney *U* test was used for all statistical comparisons.

RESULTS

Data were collected from 1,091 geniculate neurons of 53 cats raised with monocular lid suture. These neurons included 588 from nondeprived and 503 from deprived laminae A and A1. Table 1 shows the number of nondeprived and deprived cells at each age group and for each response property examined. The receptive fields of all these cells were within 40° of the area centralis and 30° of the horizontal zero parallel.

We have divided the RESULTS into two major sections. First, we examine the development and maturation of neuronal re-

TABLE 1. *Data base for each response property examined*

Age, wk	8 (11)		12 (13)		16 (11)		24 (10)		Adult (8)		Total (53)	
	Ndep	Dep	Ndep	Dep	Ndep	Dep	Ndep	Dep	Ndep	Dep	Ndep	Dep
No. of animals												
Lamina A	8	5	7	8	7	8	6	6	5	6	33	33
Lamina A1	5	7	8	6	6	7	5	7	6	6	30	33
No. of cells	96	80	130	103	131	128	126	100	105	92	588	503
Center-surround type	95	79	130	101	131	128	126	99	105	90	587	497
Receptive-field center size	95	77	130	99	131	128	126	97	105	90	587	491
Fast disk response	94	77	129	99	130	126	125	99	103	89	581	490
Linearity test	92	75	113	89	107	120	116	94	94	85	522	463
Sustained/transient	12	11	66	41	41	23	27	18	32	22	178	115
Latency to optic chiasm stimulation	74	58	106	70	97	85	101	46	96	66	474	325
Spatial resolution (first harmonic)	80	56	91	66	89	103	99	80	75	68	434	373
Spatial resolution (second harmonic)	15	12	21	12	21	15	21	11	29	16	107	66
Temporal resolution	58	44	72	49	62	62	67	46	59	48	318	249
Spatial contrast-sensitivity functions, 0-10°	8	11	6	6	4	11	13	16	16	18	47	62
Depth in geniculate at recording site	88	70	88	88	114	102	96	85	89	80	475	425
Maintained activity	10	11	9	7	20	25	21	20	10	2	70	65
Computer histograms for Fourier analysis	18	11	17	12	7	10	21	16	10	8	73	57
Electrode impedance	83	61	55	35	54	48	98	61	78	76	368	281

Ndep, nondeprived; Dep, deprived; Numbers in parentheses are numbers of animals.

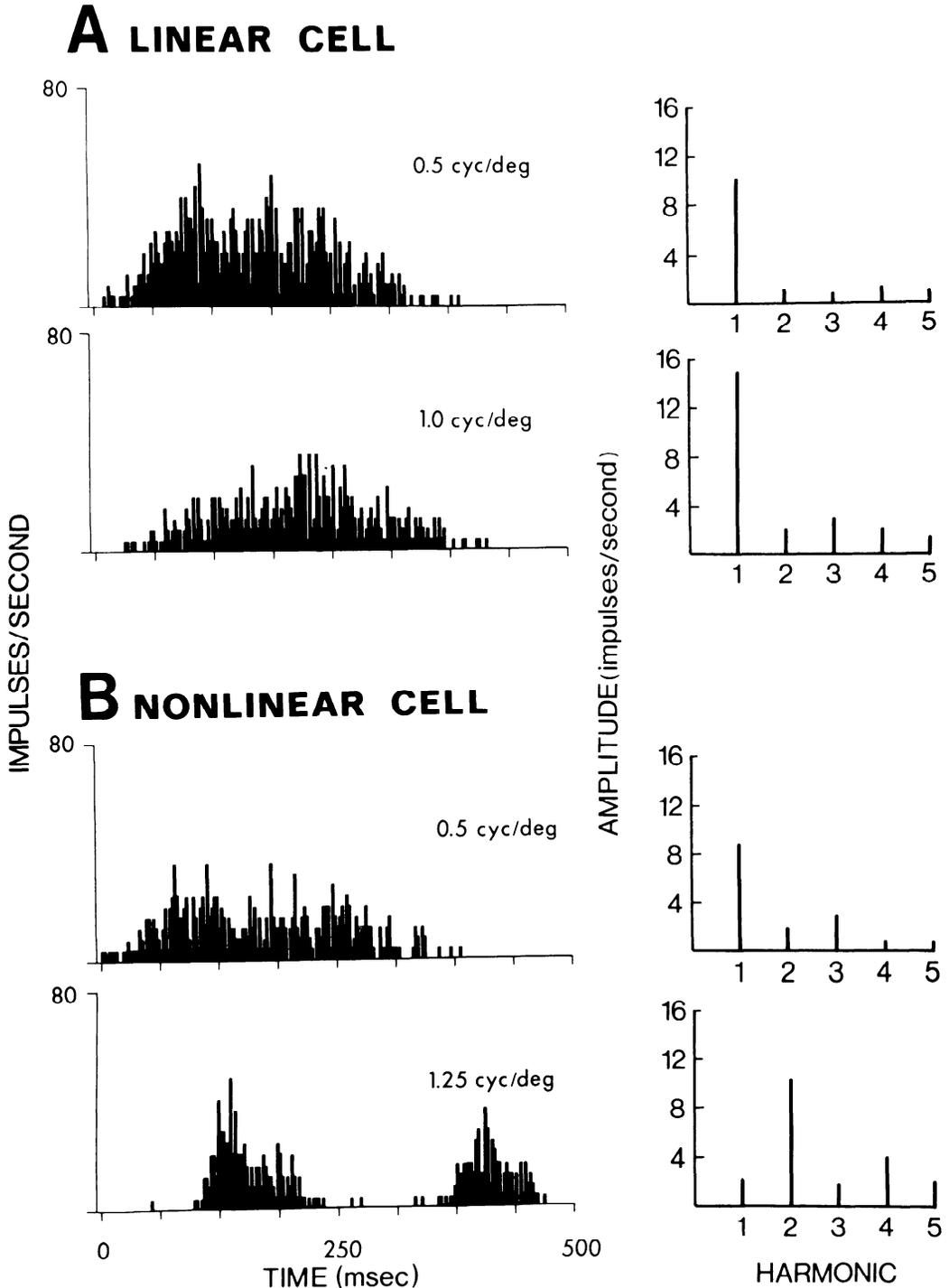


FIG. 1. Peristimulus histograms of averaged neuronal responses for two nondeprived geniculate neurons in 8-wk-old kittens. The left-hand column shows two averaged responses from each cell evoked from two different spatial frequencies, whereas the right-hand column depicts a Fourier analysis of each of these responses into harmonic components of the temporal frequency. Stimuli were stationary sine-wave gratings that were counterphase modulated sinusoidally at 2 Hz. A total of 100 stimulus cycles were averaged. *A*: responses for a linear cell. For the upper responses, the stimulus spatial frequency was 0.5 cycles/deg and the contrast was 0.025; for the lower ones, the

sponse properties from the standpoint of neuronal classification, particularly with respect to X- and Y-cell identification. Second, we compare the development of response properties of nondeprived and deprived X- and Y-cells.

Classification of kitten geniculate neurons

MULTIVARIATE ANALYSIS. Because of the immaturity of receptive-field processes in the lateral geniculate nucleus of the kitten (6, 16, 41, 63), we attempted to identify neurons by the use of as many response measures as feasible. By this approach we could determine whether various response measures tend to cluster together in discrete groupings that might suggest distinguishable neuronal classes (cf. Ref. 2). To achieve cell identification, we adopted the following strategy. We placed cells into one of two groups depending on whether they responded to counterphased, sine-wave gratings linearly or nonlinearly (see *Definitions* in MATERIALS AND METHODS and Ref. 21). During this test, stimulus spatial frequency was adjusted so that the grating was just resolvable; that is, the spatial frequency was 0.25–0.50 cycle/deg lower than the highest spatial frequency to which the cell could respond (regardless of whether a fundamental or doubling response was generated). These two neuronal groups were then compared with respect to four other response measures, including latency to optic chiasm stimulation, spatial resolution, temporal resolution, and receptive-field center diameter. In particular, average values of these four response measures were considered together by the use of a multivariate analogue of the *t* test, called Hotelling's T^2 (65).

Although the dependence of neuronal response on stimulus spatial frequency has been demonstrated in adult visual neurons (21, 34, 53, 54), it has not been shown in younger animals. Figure 1 depicts the average responses of two different 8-wk-old geniculate cells at both low and high spatial frequencies together with a Fourier analysis of

each averaged response. As can be seen in Fig. 1A, linear cells responded in a predominantly linear fashion to stimuli of both low and high spatial frequency. That is, in each case a large-amplitude response was evident only at the fundamental frequency of the stimulus. These cells also exhibited null positions. Figure 1B illustrates the responses of a nonlinear cell. As with Fig. 1A, harmonic amplitude was large only at the fundamental frequency for the lower spatial frequency stimulus, and a null position was evident. However, at the higher spatial frequency, a relatively larger amplitude second harmonic or nonlinear response was revealed by Fourier analysis, and no null position could be found for this response. Not only was this evident in the response histograms, but it was also clearly heard over the audio monitor as a "doubling response" at twice the stimulus temporal frequency.

Figure 2 illustrates the distribution of the second harmonic/first harmonic ratio or "nonlinearity index" (cf. Ref. 21) for cells at each age studied. These response components were measured to gratings counterphased at 2 Hz and just below a cell's spatial resolution. The distributions of this nonlinearity index are discontinuous at each age, as has been previously reported for adults (21). That is, every cell judged as nonlinear by the presence of a doubling response discerned from the audio monitor had a nonlinearity index greater than 1.0 (usually >2.0), and every cell without such doubling had an index of less than 1.0.

The decision to separate geniculate cells initially into two groups based on response linearity is somewhat arbitrary. That is, other cellular response measures, such as latency to optic chiasm stimulation and spatial resolution, also provide information that may be as useful to cell identification as linearity, and these response measures could also have been used to separate cells into two groups.

Once each geniculate neuron had been placed into one of two groups based on this measure of response linearity, we compared

stimulus spatial frequency was 1.0 cycle/deg and the contrast was 0.06. Both responses occurred predominantly at the fundamental frequency. *B*: responses for a nonlinear cell. For the upper responses, the stimulus spatial frequency was 0.5 cycle/deg and the contrast was 0.04; for the lower ones, the frequency was 1.25 cycles/deg and the contrast was 0.34. The upper responses for the nonlinear cell occurred predominantly at the fundamental frequency, whereas the lower response exhibited a large second harmonic component.

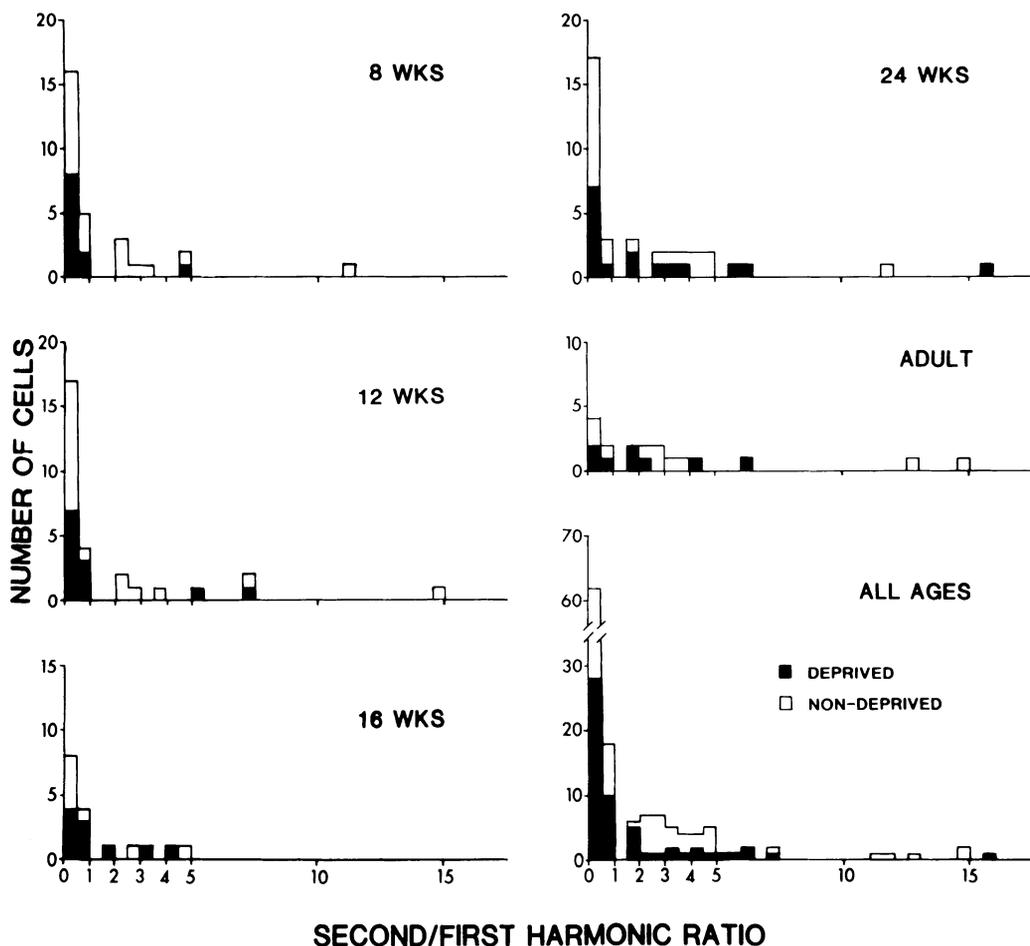


FIG. 2. Cell frequency distributions of second/first harmonic ratios for nondeprived (open) and deprived (filled) geniculate neurons at various ages. Second and first harmonic components were obtained through the use of Fourier analysis of averaged neuronal responses (see Fig. 1). Ages at which data were obtained are indicated for each histogram.

these two groups with respect to their average latency to optic chiasm stimulation, spatial resolution of their fundamental response, temporal resolution, and receptive-field center diameter. Average values of these four response measures were considered together using Hotelling's T^2 (65). In both nondeprived and deprived laminae, linear and nonlinear cells were significantly different in adult cats ($P < 0.00001$) and in 8-wk-old kittens ($P < 0.00001$). In other words, this four-dimensional analysis clearly separates the neurons into two distinct classes, and for the vast majority of neurons, the nonlinearity index adequately identifies these classes (but see below).

X- AND Y-CELL CLASSIFICATION. These results strongly suggest that nondeprived and deprived geniculate neurons in cats 8 wk of age and older can be separated into two cell populations on the basis of the physiological measures described above. Accordingly, we label one of these cell groups X-cells and the other Y-cells. That is, compared to Y-cells, X-cells had more linear responses, longer latencies to optic chiasm stimulation, better spatial resolution, poorer temporal resolution, and smaller receptive-field centers. In practice, cell identification was achieved with the use of a battery of tests that included determining each of the above response properties, and >95% of the geniculate neurons

could be identified as X- or Y-cells in this manner.

Although most geniculate neurons possessed response properties that conformed completely to the characteristics of X- or Y-cells, occasional neurons exhibited one response property with a value that seemed intermediate between those of X- and Y-cells. These cells are identified according to their other more characteristic response properties. For example, a neuron with a latency of 1.6 ms in a 24-wk-old cat was identified as an X- or Y-cell on the basis of its other response properties because 1.6 ms is within the latency range of both X- and Y-cells.

However, one notable exception to this situation occurred. We found that a small percentage of cells responded only at the fundamental frequency of a just-resolvable, counterphased grating stimulus (an X-cell characteristic) but nonetheless possessed other response properties, each of which was characteristic of Y-cells. That is, occasional cells had short latencies to optic chiasm shock (<1.5 ms), low spatial resolutions (<1.0 cycle/deg), high temporal resolutions (>18 cycles/s), and large receptive-field centers (>1.5°), but they nonetheless responded primarily at the fundamental frequency of a counterphased grating stimulus. Because the weight of evidence suggests that these cells are Y-cells, we have identified them as such. We never encountered a neuron that responded nonlinearly and possessed any other properties typical of an X-cell. Other response properties, such as latency and spatial resolution, were less frequently discrepant with the rest of a cell's properties in terms of cell type. Less than 1% of the cells possessed a latency or spatial resolution characteristic of one cell type when its other properties were characteristic of the other cell type. In other words, compared to other response properties, linear responses were far more frequently at odds with the rest of a cell's identification criteria.

Although approximately 8% of our Y-cell population (3% of total population) in cats 16 wk of age and older were linear, the percentage of these linear Y-cells is somewhat greater in younger cats (i.e., 15% of the Y-cells in 8-wk-old cats). This difference is not statistically significant, although it might reflect the relative immaturity of nonlinear re-

ceptive-field mechanisms in younger animals (cf. Ref. 63). Consistent with this is our observation that the second harmonic (nonlinear) component of a Y-cell's response was often temporally labile, especially in the case of 8-wk-old kittens, the youngest animals in this study. That is, second harmonic amplitude often increased or decreased suddenly in the responses of both nondeprived and deprived geniculate cells. This phenomenon was typified by the sudden appearance or disappearance of a cell's doubling response. An analogous phenomenon was illustrated for immature Y-cells in the medial interlaminar nucleus by Wilson et al. (63). Every cell with such a labile nonlinear response component was judged to be a Y-cell by other response criteria. Perhaps most or all of the linear Y-cells described above also had labile nonlinear response components that were not seen during the period of recording.

To avoid unnecessary duplication, parametric data are illustrated below for X- and Y-cells rather than in this section for linear and nonlinear cells. Since nearly all linear or nonlinear cells are X- or Y-cells, respectively, it is not necessary to illustrate each of these features twice. Any of the data illustrated for X- and Y-cells below would appear virtually the same if illustrated for linear and nonlinear cells.

SPATIAL CONTRAST-SENSITIVITY RATIOS. Spatial contrast-sensitivity functions were obtained by the use of previously described procedures (see MATERIALS AND METHODS and Ref. 34). Average spatial functions for nondeprived lateral geniculate X-cells and Y-cells from adult cats are shown in Fig. 3A and from 8-wk-old kittens in Fig. 3B. As can be seen, contrast sensitivity for both cell types at each age attenuated at high spatial frequencies, but a clear difference occurs at low spatial frequencies (34). That is, X-cell contrast sensitivity diminishes with decreasing spatial frequency, and this inverted U-shaped function was not characteristic of Y-cells. Y-cell contrast sensitivity was maximum at the lowest spatial frequency tested (0.125 cycle/deg).

In order to quantify the characteristic difference in the shape of X- and Y-cell spatial contrast-sensitivity functions, we devised the following ratio, called the contrast-sensitivity ratio (CSR): $CSR = (\text{contrast sensitivity at}$

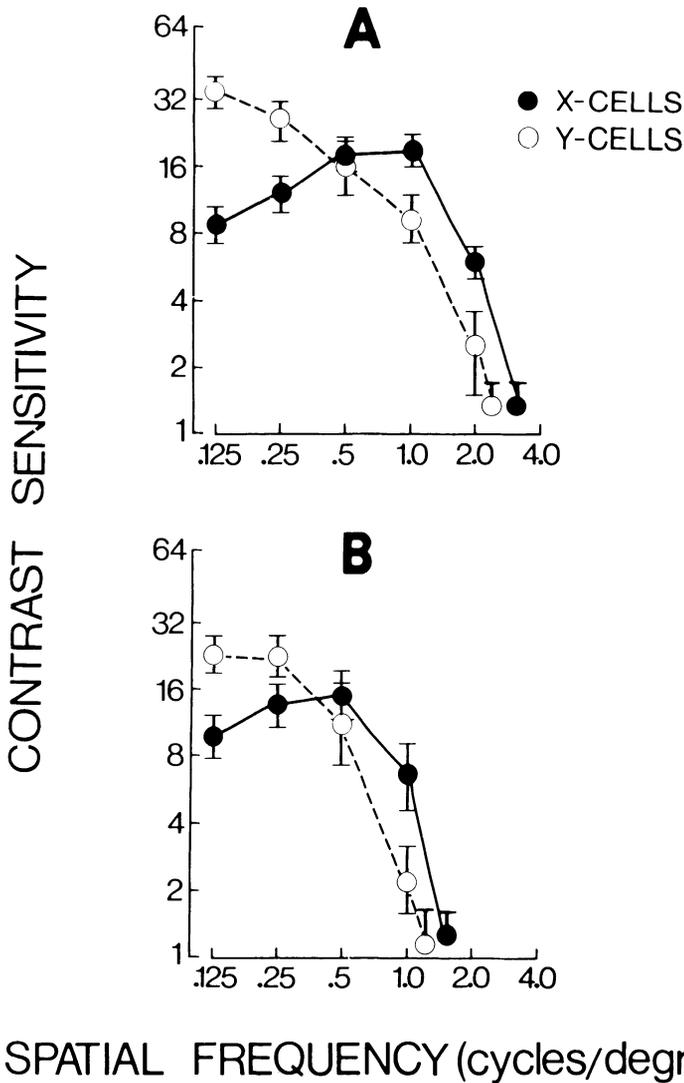


FIG. 3. Average spatial contrast sensitivity functions at 2 Hz for X- and Y-cells in nondeprived geniculate laminae A and A1. Each cell had a receptive field within 15° of the area centralis. Filled circles represent X-cells; open circles, Y-cells. Bars above and below each point represent the standard errors of the mean contrast sensitivity found at each spatial frequency. *A*: average spatial functions for 25 X-cells (mean eccentricity of 4.5°) and 8 Y-cells (mean eccentricity of 9.5°) from cats 24 wk of age and older. *B*: average spatial functions for eight X-cells (mean eccentricity of 8.8°) and four Y-cells (mean eccentricity of 11.2°) from 8-wk-old kittens.

0.125 cycle/deg)/(maximum contrast sensitivity). Typically, each Y-cell CSR was at or nearly equal to 1.0, whereas each X-cell contrast sensitivity ratio was much lower (see Fig. 4). We found that the characteristic difference in the shape of X- and Y-cell spatial contrast-sensitivity functions in 8-wk-old and older cats as revealed by the contrast-sensitivity ratio also serves as a useful criterion for cell identification.

Effects of monocular deprivation on X- and Y-cells

Given that almost all nondeprived and deprived geniculate neurons in cats 8 wk of age and older can be identified clearly as X- or Y-cells, we were able to examine the effects of monocular deprivation separately on these two cell classes. In order to control for interanimal variability, we calculated the

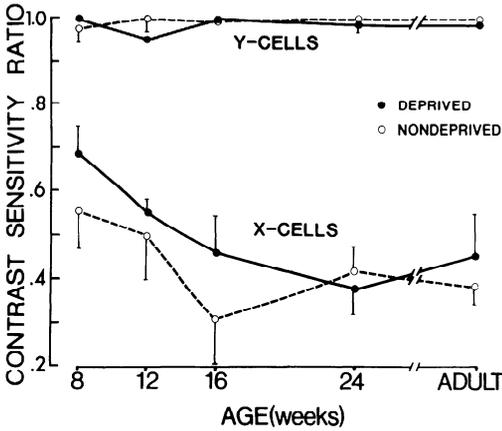


FIG. 4. Mean spatial contrast-sensitivity ratio for nondeprived and deprived X- and Y-cells as a function of age. Data points are averages derived from three to nine cats. The absence of standard error bars in some cases indicates that the magnitude of the standard error is less than the radius of data points.

mean nondeprived and deprived values of the parameter to be studied (e.g., spatial resolution) for each cat, and treated each of these means as a single datum for statistical analysis (cf. Ref. 20). Because equal numbers of cells were not sampled from each cat, this approach eliminates undue emphasis on data from any individual cat that might result from pooling data for all neurons in an age group.

PERCENTAGE OF RECORDED Y-CELLS. Because the proportion of Y-cells recorded in the lateral geniculate nucleus is reduced following early monocular lid suture (9, 13-15, 32, 40, 47, 50, 52, 66; but see Ref. 46), we studied the development of this deprivation effect by comparing the proportions of nondeprived and deprived Y-cells at various ages. By Y-cell proportion we mean the number of Y-cells divided by the total number of cells. As noted above, a deprived and nondeprived Y-cell proportion was determined for each cat, and each of these values was treated as a single datum. We found no obvious difference between laminae A and A1 in the onset or final effect of deprivation on these proportions, and thus data are pooled across laminae A and A1 for both deprived and nondeprived Y-cell proportions.

Figure 5A compares these nondeprived and deprived Y-cell proportions as a function

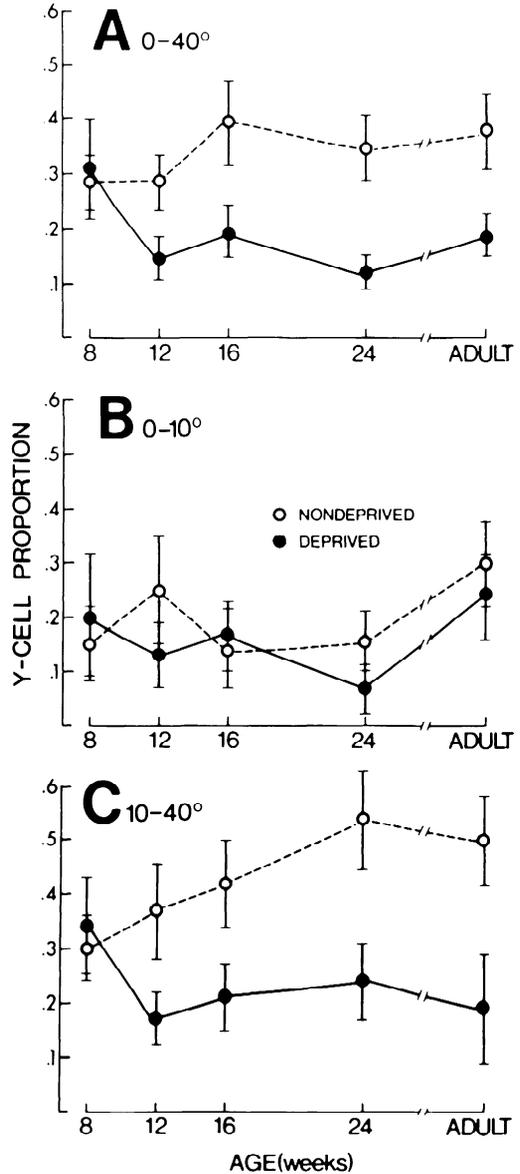


FIG. 5. Average nondeprived and deprived geniculate Y-cell proportions as a function of age. A nondeprived and a deprived Y-cell proportion was determined for each cat as the number of Y-cells divided by the total cell number (nearly all of this total were X- and Y-cells, but 5% were abnormal and unclassified cells). Each cat thus provided a single datum for nondeprived and deprived proportions, and each data point is the average of all of these nondeprived or deprived values at each age. Bars indicate 1 SE of the mean. Open circles denote means for nondeprived cells; filled circles, for deprived cells. A: data from all cells. B: data from cells with receptive fields within 10° of area centralis. C: data from cells with receptive fields between 10° and 40° from area centralis. The number of animals represented by each point in A can be found in Table 1, whereas points in B and C are averages derived from 5 to 11 animals.

of age for our entire neuronal sample. The nondeprived and deprived values are indistinguishable at 8 wk of age ($P > 0.1$) but by 12 wk of age they tend to differ ($P < 0.05$) and by 16 wk of age and thereafter the difference is statistically significant ($P < 0.01$).

Figure 5B, C shows the effect of monocular deprivation on geniculate Y-cell proportions at two different ranges of eccentricity: 0–10° (Fig. 5B) and 10–40° (Fig. 5C). Beyond 40° lies the monocular segment, in which monocular deprivation does not affect the percentage of Y-cells recorded in adults (cf. Refs. 47, 50). No statistical difference between nondeprived and deprived Y-cell proportion is apparent at any age within 10° of area centralis, possibly because of the relative scarcity of Y-cells normally found there (23). However, at 24 wk of age and older, nondeprived Y-cell proportions tend to exceed deprived Y-cell proportions even in this more central representation, but a larger data base would be needed to verify statistically what may be a small change in the absolute percentage of recorded Y-cells. For instance, the same 50% reduction from the normal Y-cell percentage requires roughly 3 times as many data points if the normal percentage is 20% (and reduced to 10%) than if the normal value is 50% (and reduced to 25%). From 10 to 40° eccentricity,

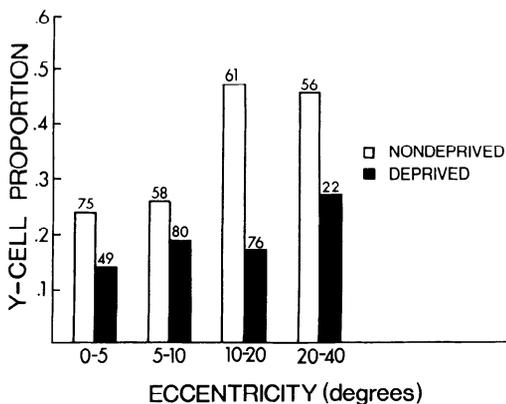


FIG. 6. Average nondeprived and deprived Y-cell proportions as a function of retinal eccentricity. Proportions are of cells sampled from laminae A and A1 of cats 24 wk of age and older. Each proportion value is the number of Y-cells divided by the total number of cells (deprived or nondeprived) at that eccentricity. Nondeprived proportions are indicated by open bars; deprived proportions, by filled bars. The number at the top of each bar indicates the total number of cells sampled.

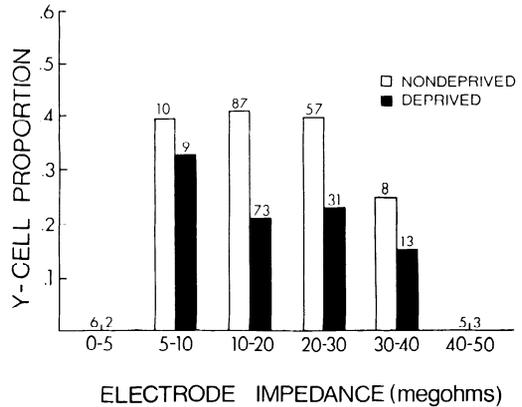


FIG. 7. Average nondeprived and deprived Y-cell proportions as a function of electrode impedance. Conventions are as in Fig. 6.

ity, nondeprived Y-cells are no more numerous than deprived Y-cells at 8 wk of age, tend to become more numerous by 12 wk of age ($0.05 < P < 0.10$), and are clearly more numerous by 16 wk of age ($0.01 < P < 0.05$). These results parallel the findings obtained when data at all eccentricities are considered (see Fig. 5A). In order to illustrate more precisely the effects of visual-field eccentricity on nondeprived and deprived Y-cell proportions of older animals, Fig. 6 illustrates neuronal data pooled across all cats aged 24 wk and older. Because of the data pooling, the reduction in recorded Y-cells evident at all eccentricities, including those most central, may not be statistically valid.

It has been suggested that differences between deprived and nondeprived laminae in recorded Y-cell proportions arise from electrode sampling bias (9, 46; but see Refs. 11, 12, 14, 49). Shapley and So (46) suggested that electrodes with higher impedance and, thus, finer recording tips should be less biased with respect to soma size. Finer tips would consequently record equal proportions of deprived and nondeprived Y-cells if they differ only in soma size. Accordingly, we examined the relationship between Y-cell proportion and electrode impedance of our micropipettes. Figure 7 summarizes these data sampled from cats 24 wk of age and older. No significant correlation was found between Y-cell proportions and electrode impedance either for nondeprived Y-cells ($r = -0.23$; $P > 0.1$) or deprived Y-cells ($r = -0.30$; P

> 0.1), nor did any grouping of impedance ranges suggest that higher impedance electrodes recorded fewer Y-cells in nondeprived or deprived laminae ($P > 0.1$ on a χ^2 test for all groupings). Furthermore, nondeprived Y-cell proportions exceed their deprived counterparts at every impedance range. The greatest difference between deprived and nondeprived laminae occurred with electrodes of 10–30 M Ω , and the smallest with electrodes of 5–10 M Ω . This contradicts the hypothesis of Shapley and So (46). Indeed, our data thus suggest little or no sampling bias with respect to electrode impedance (see also Refs. 12, 13).

SPATIAL RESOLUTION AND CONTRAST SENSITIVITY. X-cells. Figure 8 illustrates the mean spatial resolution of nondeprived and deprived geniculate X-cells as a function of age. As described above, data points represent averages of the means for each cat at each age group. The mean spatial resolution of deprived X-cells is lower than that of their nondeprived counterparts in the adult ($P < 0.01$) for the entire neuronal sample (Fig. 8A), for cells with receptive fields with in 10° of the area centralis (Fig. 8B), and for cells with receptive-field eccentricities of 10– 40° eccentricity (Fig. 8C). However, this effect is seen at 24 wk of age only for the subpopulation of cells within 10° of the area centralis ($P < 0.05$), and at younger ages, no differences in spatial resolution were seen between deprived and nondeprived X-cells.

More extensive tests were conducted on the spatial sensitivity of many of the nondeprived and deprived X-cells within 10° of area centralis by obtaining spatial contrast-sensitivity functions. As illustrated in Fig. 9, a small effect of deprivation is seen initially at 24 wk of age and a clearer effect is evident in adult, deprived X-cells. The sensitivity reduction caused by lid suture is largely limited to higher stimulus spatial frequencies, in confirmation of an earlier report (35).

When an analysis of the effects of lid suture on X-cell spatial resolution is performed separately for laminae A and A1, a curious interlaminar difference emerges for cells with receptive fields within 10° of the area centralis (see Fig. 10). At 24 wk of age, such X-cells from nondeprived and deprived lamina A are indistinguishable with respect to mean

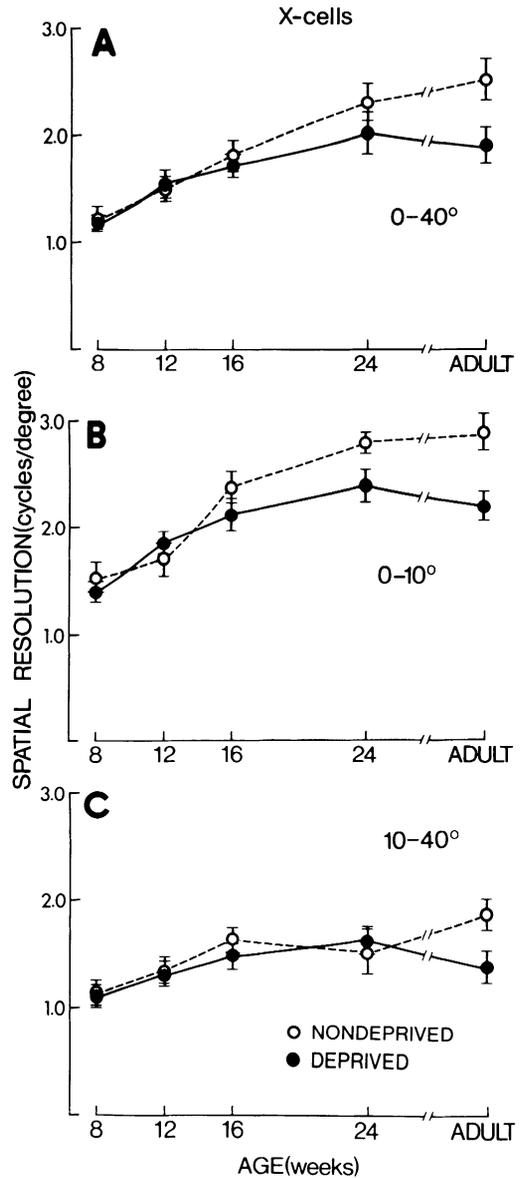


FIG. 8. Mean spatial resolution of X-cells from deprived and nondeprived A-laminae plotted as a function of age. Conventions are as in Fig. 5, and again each cat is treated as a single datum. A: data from all X-cells. B: data from X-cells with receptive fields within 10° of the area centralis. C: data from X-cells with receptive fields between 10 and 40° from the area centralis. The number of animals represented by each point in A can be found in Table 1, whereas points in B and C are averages derived from 5 to 11 animals.

spatial resolution ($P > 0.1$), whereas X-cells from deprived lamina A1 exhibit significantly lower spatial resolution than do X-cells from nondeprived lamina A1 ($P < 0.01$).

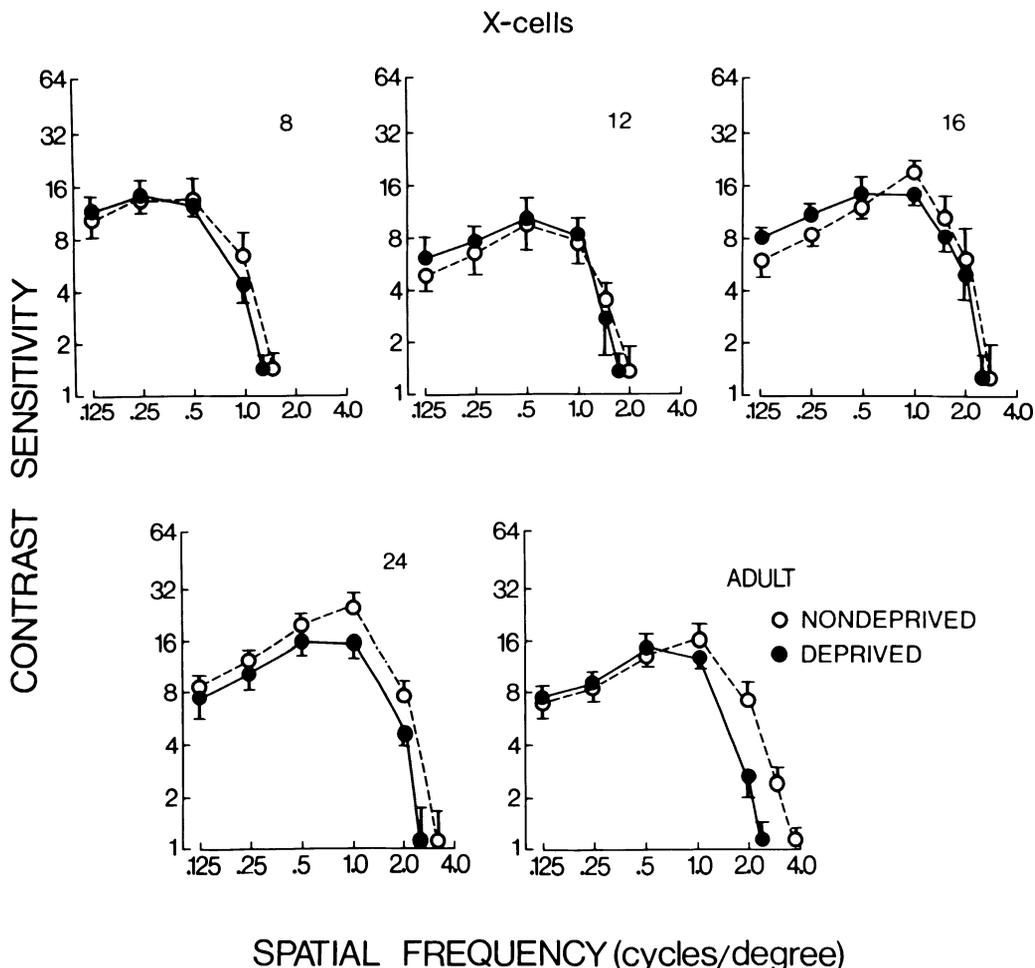


FIG. 9. Average spatial contrast-sensitivity functions at 2 Hz for nondeprived and deprived geniculate X-cells at various ages. Ages at which data were obtained are indicated for each function. All cells had receptive fields within 10° of the area centralis except for the cells from 8-wk-old cats, which had fields within 15° . Functions were determined by averaging from 4 to 16 contrast-sensitivity values at each spatial frequency. Open circles denote means for nondeprived X-cells; filled circles, for deprived X-cells. Bars represent 1 SE.

In adults, however, resolution deficits are seen for each of the deprived X-cell groups ($0\text{--}10^\circ$ eccentricity, $10\text{--}40^\circ$ eccentricity, lamina A, and lamina A1).

Figure 11 further illustrates these interlaminar differences for X-cells with receptive fields within 10° of the area centralis by showing their average spatial functions. At 24 wk of age, contrast sensitivity for deprived X-cells to higher spatial frequencies is greater in lamina A than in lamina A1 (Fig. 11A). However, the effect of deprivation on contrast sensitivity in lamina A is so dramatic

by 13 mo of age that this difference is obliterated or reversed in adults (Fig. 11B). Figure 11C, D again illustrates this same interlaminar difference in another manner. In deprived lamina A, sensitivity to higher spatial frequencies is reduced for X-cells in the adult cats compared to that in 24-wk-old animals (Fig. 11C). However, deprived X-cells in lamina A1 exhibit indistinguishable contrast sensitivity at both ages (Fig. 11D). The possible significance of this curious interlaminar difference will be considered in the DISCUSSION.

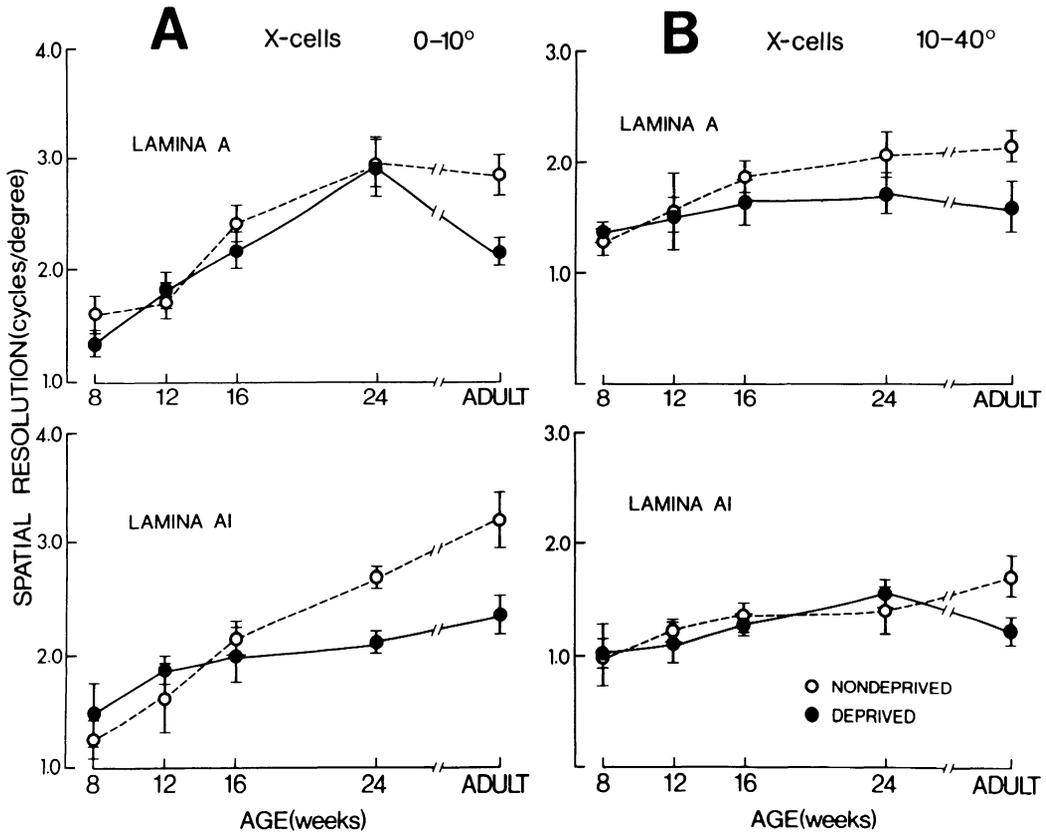


FIG. 10. Mean spatial resolution of nondeprived and deprived geniculate X-cells plotted as a function of age separately for lamina A and A1. Conventions are as in Fig. 8. Data points represent averages of from three to seven cats. *A*: data from neurons with receptive fields within 10° of area centralis. *B*: data from neurons with receptive field eccentricities of 10-40°.

Y-cells. Although Lehmkuhle et al. (35) found no deficit in the spatial resolution of the nonlinear response components of Y-cells following monocular deprivation, Sireteanu and Hoffmann (52) reported that Y-cells in deprived lamina A1 show a reduced spatial resolution of their linear response component. We have examined the spatial resolutions of both the linear and nonlinear Y-cell response components and have compared nondeprived and deprived cells at various ages after monocular lid suture. Figure 12 illustrates these values pooled across all eccentricities as well as laminae A and A1 as a function of age for the nonlinear and linear response components. Too few Y-cells were recorded to illustrate a meaningful breakdown of the data for eccentricity or lamina, but no effect of the deprivation on the spatial

resolution of either the linear or nonlinear response component was evident at any age, eccentricity grouping, or lamina.

Interestingly, for both nondeprived and deprived Y-cells, mean spatial resolution of the fundamental response component does not increase after 8 wk of age (Fig. 12*B*), although mean spatial resolution of the second harmonic response does continue to improve after that age (Fig. 12*A*). This further suggests that the nonlinear response component of Y-cells matures later than does the linear one (see also Ref. 63).

LATENCY TO OPTIC CHIASM STIMULATION. Monocular lid suture also appears to affect the latency to optic chiasm stimulation of X-cells, whereas no effect on Y-cell latencies was observed. This is shown in Fig. 13*A*,

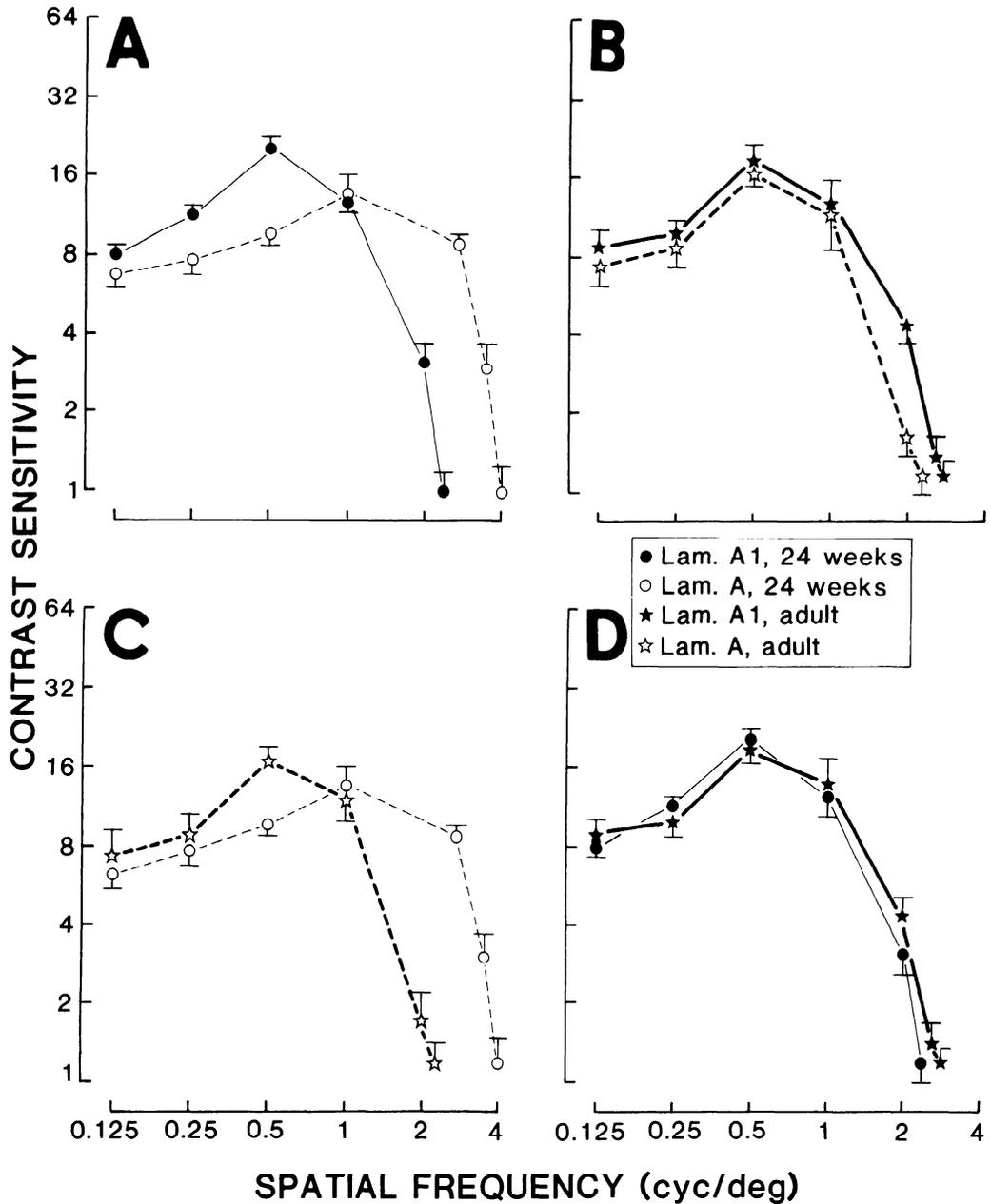


FIG. 11. Average spatial contrast-sensitivity functions at 2 Hz for deprived X-cells in 24-wk-old and adult cats. Each cell had a receptive field within 10° of the area centralis, and functions were derived by averaging contrast-sensitivity values from 4 to 11 neurons at each spatial frequency. Bars indicate 1 SE of each of these mean values. *A* and *B*: spatial functions for 24-wk-old cats (*A*) and adult cats (*B*). *C* and *D*: spatial functions for lamina A (*C*) and lamina A1 (*D*). Lamina A data are indicated by open stars (adult) and open circles (24 wk old); lamina A1 by filled stars (adult) and filled circles (24 wk old).

which depicts average latency for nondeprived and deprived X- and Y-cells as a function of age. Because latency does not vary

with visual-field eccentricity beyond 3° from the area centralis (23), the data are pooled without regard for eccentricity. As can be

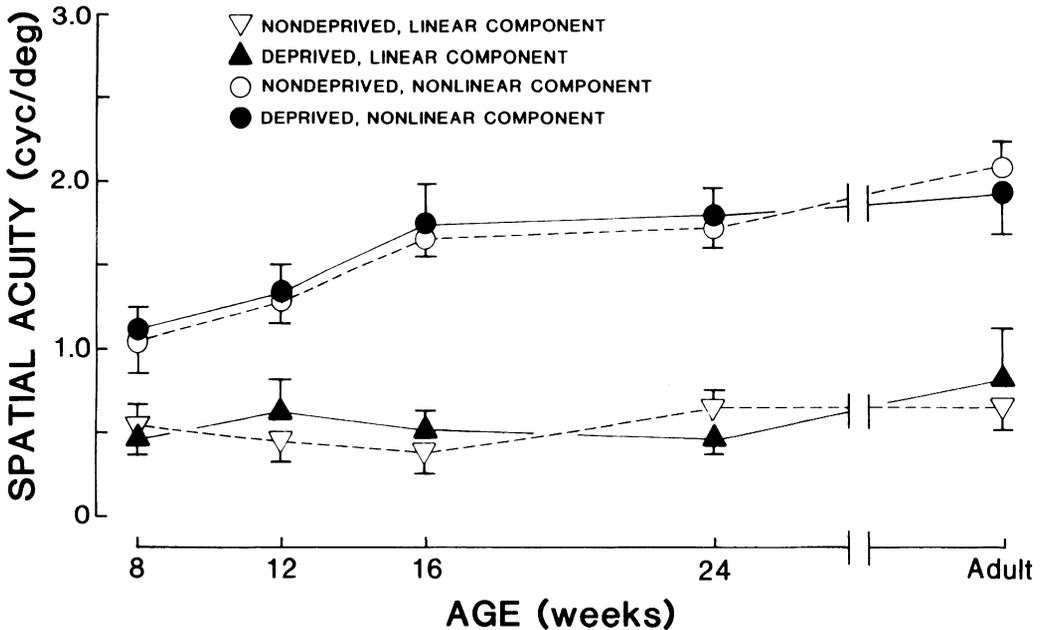


FIG. 12. Mean spatial resolution of nondeprived and deprived geniculate Y-cells plotted as a function of age. The linear and nonlinear response components are shown separately. Each data point is an average from 5 to 11 cats.

seen at each age, the average latency of deprived X-cells slightly exceeds the average of nondeprived X-cells, whereas no such difference is seen for Y-cells.

However, analysis of chiasm latency values is complicated by factors that have little to do with monocular lid suture (e.g., interlaminar differences and interanimal variability in electrode placement). For example, mean X-cell latency is greater in lamina A than in lamina A1. Previously unpublished data from 13 normally reared cats for which data were obtained bilaterally from laminae A and A1 were reexamined. We calculated the mean lamina A and mean lamina A1 X-cell latencies for each hemisphere of each cat and compared the differences between these means for each of the 13 cats. Mean X-cell latency was 2.3 ± 0.2 (mean \pm SD here and below) ms in lamina A and 2.1 ± 0.2 ms in lamina A1. The difference between these means is statistically significant ($P < 0.01$). Interestingly, a similar analysis of Y-cell latency for lamina A (1.4 ± 0.2 ms) and lamina A1 (1.5 ± 0.2 ms) reveals no difference ($P < 0.1$).

Therefore, in order to control for these factors, we adopted the following strategy. For

each monocularly sutured cat recorded in both hemispheres, the mean latency of nondeprived and deprived X-cells was computed separately for laminae A and A1. Again, the mean value from each lamina of each cat is treated as a single datum. We then compared these mean values between deprived and nondeprived lamina A and between deprived and nondeprived lamina A1. Figure 13B shows that in 8- and 12-wk-old kittens the longer latencies for deprived X-cells are not statistically reliable. However, for the older animals, a small but reliable difference emerges such that deprived X-cells exhibit longer latencies than do nondeprived X-cells ($P < 0.01$ for lamina A; $P < 0.05$ for lamina A1). If the expected difference for Y-cells were proportionally extrapolated from that seen for X-cells, the Y-cell difference would be less than the 0.1-ms resolution of our latency measurement, and for this reason, our failure to find an effect of lid suture on Y-cell latencies might reflect technical limitations.

CELLS WITH ABNORMAL RECEPTIVE-FIELD PROPERTIES. Recent evidence suggests that monocular lid suture may cause some Y-cells

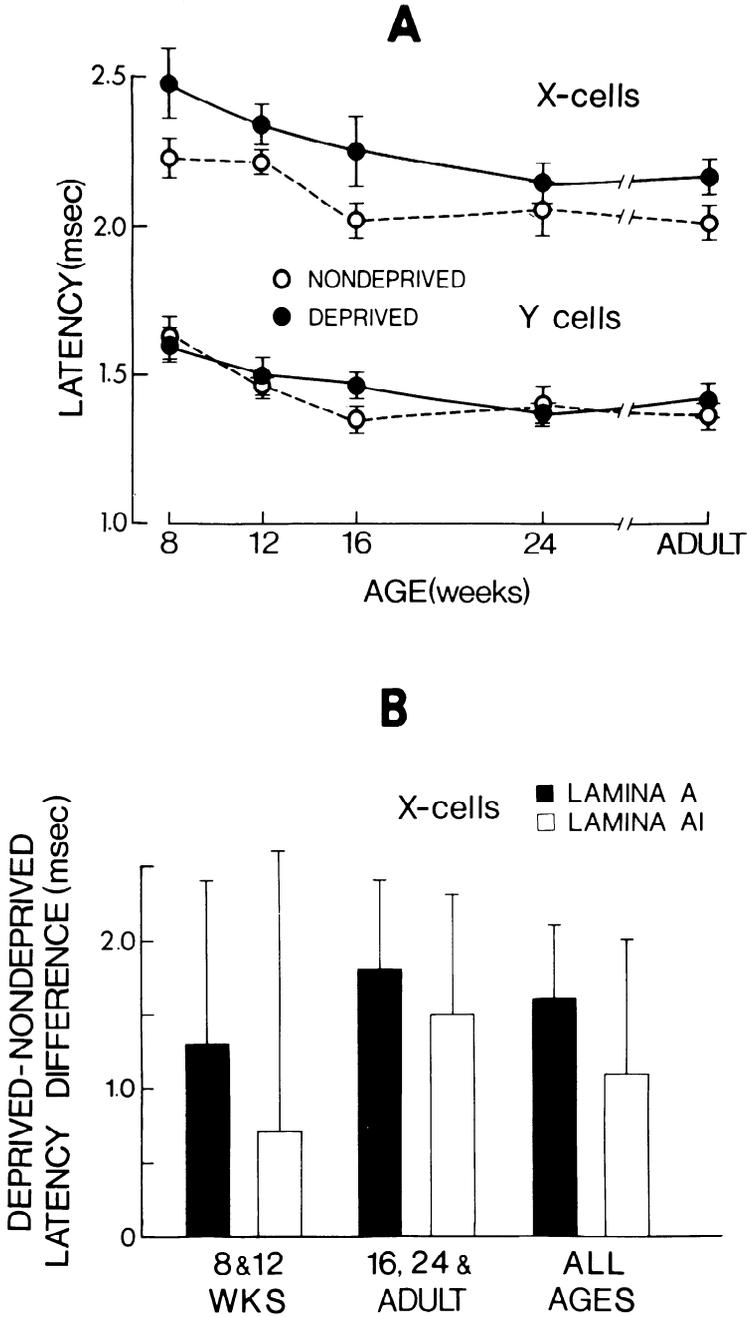


FIG. 13. Response latency of deprived and nondeprived geniculate neurons to optic chiasm stimulation. Most conventions are as in Fig. 8, and the mean value for each cat is treated as a single datum. *A*: average latency of deprived (filled circles) and nondeprived (open circles) X- and Y-cells in laminae A and A1 as a function of age. The number of cats used for this analysis at each age can be derived from Table 1. *B*: latency differences between deprived and nondeprived X-cells for each lamina. Only kittens from which we studied both hemispheres were used in this analysis so that we could compare latencies between deprived and nondeprived lamina A or lamina A1. The average interhemisphere latency difference for lamina A or A1 was computed for each cat, and each of these values was treated as a single datum. Lamina A differences are indicated by filled bars; lamina A1 differences, by open bars. The number of animals from which data were derived are shown above each bar, and the hatch marks indicate the standard error.

to develop abnormal receptive-field properties (14, 32). Similar evidence was obtained in the present study. A small number of cells were found that responded poorly and unreliably to visual or electrical stimuli, but the infrequent responses bore the signature of Y-cells (i.e., nonlinear responses to visual stimuli and short latencies to optic chiasm shock). The encounter rate of such cells was significantly less frequent in nondeprived than in deprived laminae (2/588 versus 13/503; $P < 0.01$ on a χ^2 test). Figure 14 shows spatial contrast-sensitivity functions for three of these abnormally responding cells compared to the spatial function from a deprived Y-cell with normal responses. Sensitivity for the abnormal cells was markedly reduced, but no added attenuation to low spatial frequencies was evident. Finally, occasional unresponsive cells were found in deprived laminae that might represent extreme examples of these abnormal Y-cells.

OTHER RESPONSE PROPERTIES. As reported previously (35), monocular lid suture does

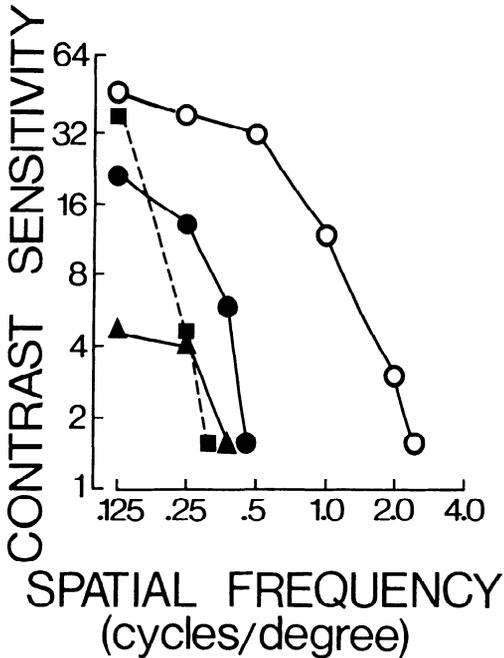


FIG. 14. Spatial contrast-sensitivity functions of deprived A-laminae neurons. The open circles denote a fairly normal Y-cell from a 16-wk-old kitten. The filled symbols denote poorly responsive cells, including two from 16-wk-old animals (filled circles and squares) and one from a 24-wk-old animal (filled triangles).

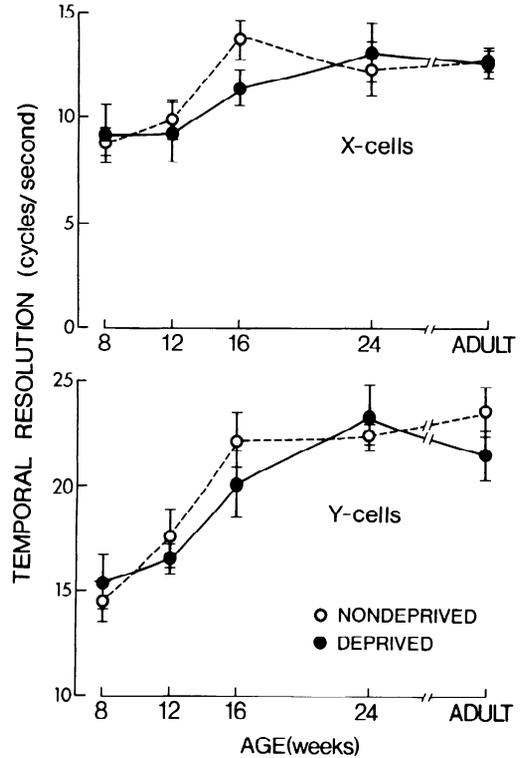


FIG. 15. Average temporal resolution of nondeprived and deprived X-cells (top) and Y-cells (bottom) plotted as a function of age. Conventions are as in Fig. 8. Data points are averages derived from 6 to 13 cats.

not appear to affect the temporal resolution of geniculate X- and Y-cells. Figure 15 confirms this finding for adult cats and extends it to younger animals. Because temporal resolution in the binocular segment of the lateral geniculate nucleus does not vary with retinal eccentricity (34), data were pooled for all eccentricities.

Examination of several other response properties failed to demonstrate any effect of monocular deprivation. For example, receptive-field center diameter was not affected by the deprivation, a finding that corroborates earlier reports (35, 47). In addition, the degree of linearity of spatial summation of X- and Y-cells seems unperturbed by deprivation. This is illustrated in Fig. 2, which depicts the distribution of second/first harmonic ratios for nondeprived and deprived cells at various ages. With rare exceptions, all the cells in Fig. 2 with ratios less than 1.0

are X-cells, whereas the others are Y-cells. No obvious effect of deprivation can be seen on either cell class. Finally, although monocular deprivation alters the spatial resolution of geniculate X-cells, no obvious effect is observed on X- or Y-cell spatial contrast sensitivity ratios (see above), as is shown in Fig. 4.

DISCUSSION

Four principle conclusions emerge from this study. First, in cats as young as 8 wk of age, deprived and nondeprived neurons can be identified as X-cells or Y-cells by the use of criteria previously established for adult animals. Second, the effect of lid suture on the proportion of recorded Y-cells is first observed between 8 and 12 wk of age. Third, the effect of lid suture on X-cell spatial resolution cannot be detected until much later (≥ 24 wk of age), and it appears initially for X-cells in lamina A1 with receptive fields within 10° of the area centralis. Fourth, the mean latency to optic chiasm stimulation is slightly longer for deprived than for nondeprived X-cells. These findings are discussed in more detail below.

Cell classification in kitten's lateral geniculate nucleus

The most accurate and parsimonious identification of geniculate neurons as X- or Y-cells can be achieved by the use of a battery of response measures (43) that includes the linearity of spatial and temporal summation, the latency to optic chiasm stimulation, the spatial resolution of the fundamental response component, and the spatial contrast-sensitivity ratio (defined in RESULTS).

Linearity of spatial summation to a just-resolvable, counterphased grating stimulus does not identify all geniculate neurons in the A-laminae as either X- or Y-cells, although the vast majority are effectively identified by this parameter. In particular, in cats 16 wk of age and older, we found that a small percentage (3%) of all sampled cells responded primarily at the fundamental frequency of a counterphased, grating stimulus, but nonetheless possessed other response characteristics that are all typical of cells that respond at twice the modulation frequency. By certain classification schemes such cells might be identified as X-cells (cf. Refs. 21,

22, 45, 53). However, as Rowe and Stone (43) pointed out, such an "essentialistic" classification is justified only when one can be certain that linearity of spatial summation is of paramount functional importance. Since there is no reason to believe that such linearity is any more important than the battery of other response measures, it seems more appropriate to base the classification on as many functional parameters as possible (43). Furthermore, W-cells in the geniculate C-laminae can be either linear or nonlinear, and these cells are clearly distinct from X- and Y-cells by a number of morphological and physiological criteria (56), so that response linearity alone is not sufficient to classify visual neurons. Use of a single parameter is particularly risky in experimentally modified conditions in which one cannot be certain that the parameter itself has not been specifically modified. Indeed, if only response linearity were used to classify cells, one could never distinguish between an immature (or deprived) Y-cell with poorly developed nonlinear responses and an X-cell (cf. Ref. 63).

Thus, we have classified those neurons that do not exhibit obvious nonlinear spatial or temporal summation (an X-cell property) but that have fast-conducting retinal inputs, large receptive-field centers, poor spatial resolution, and lack low spatial frequency-sensitivity attenuation (Y-cell features) as "linear" Y-cells. Other response properties, such as latency and spatial resolution, were rarely ($\leq 1\%$ of cells) at odds with the rest of a neuron's properties with respect to its cell type. It is possible to account for the properties of these linear Y-cells with the receptive-field model of Hochstein and Shapley (21, 22). That is, these particular Y-cells may simply be lacking all or some nonlinear spatial subunits but possess all other Y-cell receptive-field attributes. If so, then there is evidence that the nonlinear subunits mature later in kittens than do the linear receptive-field mechanisms. Not only are there relatively more linear Y-cells in 8-wk kittens than older animals, but also the nonlinear responses of many Y-cells in younger animals exhibit temporal lability of a form never seen in adult cats (see also Ref. 63). That is, in younger kittens, the second harmonic response component of many Y-cells was seen to ap-

pear and disappear abruptly and unpredictably. This is also consistent with the suggestion of Hochstein and Shapley (21) that the nonlinear subunits of Y-cells are functionally quite distinct from and independent of their linear receptive-field mechanisms. Finally, the nonlinear subunits provide Y-cells with sensitivity to higher spatial frequencies than do the linear receptive-field components. Our observation that the spatial resolution of the nonlinear component continues to improve with age long after that of the linear component achieves maturity is consistent with the later development of Y-cell nonlinear responses.

Because of these considerations, the observations of Norman et al. (41) and Daniels et al. (6) should be reexamined in view of ours. These authors concluded that, from 3 to 6 wk postnatal, geniculate X-cells begin to mature earlier and at a faster rate than do Y-cells. However, the sole identification criterion used was linearity of spatial summation. Our results suggest that a certain fraction of immature Y-cells would exhibit linear summation and might have been interpreted as fairly responsive X-cells. Nonetheless, such cells were relatively rare in our data sample (15% of Y-cells in the youngest kittens), and such linear Y-cells are hardly mature. For these reasons, plus the fact that our data derive from older animals, we cannot dispute the basic conclusions of Norman et al. (41) and Daniels et al. (6). However, the possibility that a larger fraction or even the majority of Y-cells exhibit linear spatial and temporal summation in 3- to 6-wk old kittens should be examined. Perhaps the nonlinear subunits do not begin to mature until the end of the second postnatal month. We also emphasize that even if X-cells begin to mature earlier and more rapidly than do Y-cells, on many response measures (e.g., latency, temporal resolution, etc.) the complete maturation process is gradual for both cell types and final adult levels are achieved at roughly the same age for X- and Y-cells.

Development of deprivation-induced abnormalities

Y-CELL PROPORTIONS. *Onset and time course.* In cats raised to adulthood with monocular suture, the proportion of recorded Y-cells is lower in the deprived than in the non-

deprived A-laminae (9, 14, 15, 32, 40, 47, 50, 52, 66). The present study demonstrates that this difference between nondeprived and deprived Y-cells is seen by about 12 wk of age but not at 8 wk of age. This seems to occur later than the onset of deprivation effects on geniculate soma sizes and on the ocular dominance of cortical neurons.

Both Hickey (19) and Kalil (27) concluded that the development of cell size differences between nondeprived and deprived laminae was essentially complete by 8 wk of age, at which time no equivalent difference in recorded Y-cell proportions can be found. This suggests that the effects on soma size and physiology are separated in time and perhaps even involve different mechanisms. It also suggests that the eventual differences in recorded Y-cell proportions are not due to electrode sampling biases based on soma size (cf. Refs. 11–14). Not only does the 8-wk-old monocularly lid-sutured kitten have equivalent Y-cell proportions recorded in laminae of different soma sizes, but the converse has also been found: Kratz et al. (30) and Geisert et al. (15) reported a loss of recorded Y-cells in the A-laminae of visually deprived cats that had normal soma sizes in these laminae.

It is similarly difficult to relate deprivation-induced changes among geniculate Y-cells with the effects seen in cortex. Cortical cells in normal cats can be driven by either eye, but after early monocular lid suture nearly all of these neurons can be driven only by the nondeprived eye (60, 62). The cortical effects are seen as early as 4 wk of age (24), although the critical period for this may extend as long as 6 mo (26). Clearly, then, cortical changes are evident at least 1 mo prior to any deficit seen among geniculate neurons. This raises several possibilities that can be considered but not yet evaluated. First, the earlier cortical ocular dominance changes might be completely independent of those involving Y-cells. Second, changes in recorded geniculate Y-cells might be a secondary reflection of earlier primary events seen in cortex. This second possibility does not exclude a close relationship between these phenomena. For instance, deprivation might affect the Y-cell pathway first in cortex (e.g., at the geniculocortical synapse). The first change evident might then be a loss of cortical influence from the deprived eye. Later,

retrograde changes might affect the deprived Y-cells in such a way that they can no longer be sampled readily with microelectrodes. Other explanations are also possible, and we cannot yet clearly relate the geniculate and cortical abnormalities that develop during monocular lid suture to one another.

Fate of deprived Y-cells. Although differences in the proportion of recorded Y-cells develop between deprived and nondeprived geniculate laminae (9, 14, 15, 32, 40, 47, 50, 52, 66), the interpretation of this observation has been debated (e.g., Refs. 9, 14, 46). The weight of the evidence strongly suggests that many Y-cells fail to develop normal adult response properties and eventually become unresponsive (for a review of this debate see Ref. 49). Our data from deprived laminae include poorly and inconsistently responsive neurons that still bore the signature of Y-cells plus unresponsive cells, and such abnormal cells were much less often encountered in nondeprived than in deprived laminae. Similar descriptions of abnormal responses among deprived geniculate neurons thought to be Y-cells have been previously reported (14, 32). Indeed, in the first paper on the physiology of geniculate neurons in monocularly lid-sutured cats and before X- and Y-cell classes were appreciated, Wiesel and Hubel (59) noted that 4 of 19 neurons (21%) in the deprived A-laminae exhibited grossly abnormal response properties. Recently, Friedlander et al. (14) reported that such abnormally responding cells, thought to be Y-cells, also displayed dramatically abnormal dendritic morphology.

SPATIAL RESOLUTION OF X-CELLS. *Comparison with other effects of deprivation.* Compared to other effects of monocular deprivation, the effect on X-cell spatial resolution has a rather late onset. In fact, following neonatal monocular lid suture, abnormalities in recorded Y-cell proportions are first observed approximately 3 mo before an effect on X-cell spatial resolution is encountered. This large difference in onset alone suggests that the effect on X-cell spatial resolution does not share common mechanisms or origin with the loss of recorded Y-cells (see also below).

Comparison with other studies. The developmental pattern of X-cell spatial reso-

lution we have described might explain some of the discrepancies in the literature. For instance, Lehmkuhle et al. (35) studied monocularly deprived cats of roughly 24 mo of age and found deficits in spatial resolution of X-cells in both deprived A-laminae. Sireteanu and Hoffmann (52) found deficits for deprived X-cells only in lamina A1, but these authors studied cats monocularly deprived until only 4–6 mo of age. Derrington and Hawken (7) reported no such X-cell deficit, but their two monocularly sutured cats were only 4 and 6 mo old. Our data suggest that no such deficit should be found in younger cats (less than roughly 6 mo of age; e.g., Ref. 7), that it might be limited to deprived X-cells in lamina A1 at intermediate developmental ages (roughly 6 mo of age; e.g., Ref. 52), and that it should be found equally in both A-laminae among fully adult cats (at roughly 24 mo of age; e.g., Ref. 35). However, it should be emphasized that our evidence for an interlaminar effect of lid suture at intermediate ages is based on a single data point at 24 wk of age. Clearly more data are needed to establish this possible interlaminar difference.

Lehmkuhle et al. (35) reported a larger difference in spatial resolution between deprived and nondeprived X-cells for “adult” cats than we report, despite the use of essentially identical methods in the two studies. Although the reason for this difference is not completely clear, a plausible explanation concerns the age of the adult cats. Ours were 13 mo of age, whereas those of Lehmkuhle et al. (35) averaged 24 mo of age. Because the effect of deprivation on X-cell spatial resolution is rather late in onset (Fig. 8), it is possible that the effect increases in magnitude with increasing periods of deprivation.

Two other reports concerning the effects of early monocular suture provide insufficient information to compare with our own data. Maffei and Fiorentini (37) state that deprived geniculate neurons have lower spatial resolution than do nondeprived ones. These authors do not distinguish between X- and Y-cells, and they insufficiently describe the age of their cats only as “at least 3 mo old.” Mower et al. (40) found lower spatial resolution for deprived compared to nondeprived geniculate X-cells in two cats monocularly deprived “throughout early life.”

Nonetheless, one recent report presents data that are difficult to reconcile with the present study and several earlier ones (35, 37, 40, 52). That is, Shapley and So (46) studied geniculate X-cells in cats monocularly deprived from 1 to 3 wk until 6 to 18 mo of age. These authors found equivalent spatial resolution values for these cells in nondeprived lamina A1 and deprived lamina A. These values were quite low, and the main difference between this and other studies lies in the values for nondeprived rather than deprived X-cells.

Although it is possible to offer speculative explanations for some of the confusing and contradictory studies of the effects of lid suture on X-cells, clearly more data are needed to resolve these issues. We feel that the bulk of the evidence, including our own, suggests that monocular deprivation has a surprisingly late developing effect on spatial resolution of geniculate X-cells.

Sites and mechanisms of resolution deficit. We do not have sufficient data to develop a reasonable explanation for the X-cell resolution deficit, but several relevant points will be emphasized. First, the effect does not seem to be an artifact of optics. Not only were the eyes carefully refracted, but differential magnification between the eyes due to lid suture (cf. Refs. 48, 61, 62) was too small to account for the resolution effects on deprived X-cells (see METHODS). Indeed, we occasionally observed spatial resolution values for nonlinear subunits of Y-cells driven by the deprived eye that were higher than those found for the deprived X-cells (see also Ref. 35).

Second, our present data reopen the question of the site of the deficit. Prior studies (5, 29) reported normal spatial resolution for retinal ganglion X-cells in the deprived eye. However, these experiments were performed on cats 7–8 mo of age. Based on our present data, one would like to see these studies repeated on cats at least 1–2 yr of age.

Third, our data show that from 2 to 6 mo of age, spatial resolution of geniculate X-cells roughly doubles in both nondeprived and deprived laminae. Ikeda and Tremain (25) reported a similar phenomenon for X-cells in normal cats. This means that resolution continues to improve dramatically for the deprived X-cells despite a loss of spatial patterns in the visual environment. Much of this

improvement may be optical in origin, because Bonds and Freeman (1) report that the width at 0.1 height of the eye's optical line-spread function decreased by half from 7 wk to adulthood in cats.

Fourth, although we measured spatial resolution only with vertically oriented gratings, the observed differences between nondeprived and deprived X-cells is almost certainly not due to differential receptive-field anisotropy as described for normal ganglion cells by Levick and Thibos (36). These authors found that spatial resolution depended somewhat on grating orientation, the best typically being for grating orientations parallel to the line joining the cell's receptive field with the area centralis. All our data derive from electrode penetrations in which both nondeprived and deprived X-cells were recorded, and the receptive-field locations of nondeprived and deprived neurons are well matched. Consequently, unless deprivation reduces neural responsiveness selectively for vertically oriented gratings, the nondeprived and deprived X-cells should possess similar orientation biases for spatial resolution. The differences in spatial resolution must therefore be due to factors other than a difference in orientation bias.

Finally, Lehmkuhle et al. (35) argued that geniculate X- and Y-cells were affected by monocular deprivation via different developmental mechanisms (see Ref. 49 for a more complete discussion of these mechanisms). Since deprived Y-cells could be recorded in normal numbers only in the monocular segment and when found, possessed normal spatial resolution, a process of binocular competition was implicated for the development of Y-cells. Since deprived X-cells exhibited an equal spatial acuity deficit in the binocular and monocular segments, a binocularly noncompetitive mechanism of development was implicated for these cells. Our evidence that effects on geniculate X- and Y-cells follow separate time courses is consistent with the notion that the mechanisms by which monocular lid suture affect X- and Y-cells are quite distinct from one another.

LATENCY TO OPTIC CHIASM STIMULATION. The effect of lid suture on the response latency to optic chiasm stimulation is quite

small but nonetheless evident. The functional significance and site of this effect are presently unclear. Whether this represents a change in optic tract conduction velocity or a change in synaptic delay due to pre- or postsynaptic factors cannot be derived from our data. Indeed, it is not even clear whether the measured effect results from an increased latency in the deprived pathway or a decreased latency in the nondeprived pathway. This effect of early lid suture warrants further study.

CONCLUSIONS. The physiological effects of monocular lid suture on geniculate X- and Y-cells in cats occur over an extended time course. Differences between deprived and nondeprived laminae are not clearly evident until 12 wk of age for Y-cells and continue to develop until 6–12 mo of age for X-cells. These data suggest that development of the cat's visual system is susceptible to environmental influences for a surprisingly long period that lasts up to 1 yr. Furthermore, the dynamics of the effects on X- and Y-cells are so different that these X- and Y-cell pathways

probably exhibit not only different developmental mechanisms but possibly also different sensitive periods as well. More generally, development of the central visual pathways probably involves a multiplicity of mechanisms and sensitive periods for the various pathways and levels.

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