

Differential Effects of Early Monocular Deprivation on Binocular and Monocular Segments of Cat Striate Cortex

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SUMMARY AND CONCLUSIONS

1. Receptive-field properties were studied for 156 cells in 15 monocularly deprived cats. Particular emphasis was placed on comparisons between receptive fields located in the deprived monocular segment (i.e., far from the vertical meridian) and more centrally located fields.

2. Between 0° and 30° of visual-field eccentricity from the vertical meridian, 36 of 37 cells were influenced, both for the excitatory and inhibitory components, exclusively by the nondeprived eye. Also, several of these cells had abnormal receptive-field properties. At eccentricities greater than 30°, we found 40 cells which responded to stimuli presented to the deprived eye; of these, 4 were influenced binocularly. An additional 43 cells with fields between 30° and 45° eccentricity responded only to stimulation of the nondeprived eye, and 17 cells were studied in the nondeprived monocular segment. About one-third of the cells influenced by the deprived eye had abnormal fields. At least 18 other cells did not respond to any visual stimulus presented to either eye.

3. While the cortical monocular segment related to the nondeprived eye had normal percentages of cell types, the deprived monocular segment had a significant reduction in the ratio of normal complex to normal simple cells. Simple cells in the deprived monocular segment appeared to be normal in every respect we measured.

4. No gross anatomical changes were found which might account for this complex cell loss. That is, we found no differences in cell size or packing density between the deprived and nondeprived monocular segments.

5. The following conclusions were drawn from these results: *a)* in agreement with previous studies, these data suggest that binocular com-

petition does play a role in cortical development in these cats; *b)* monocular deprivation also causes abnormalities in addition to those caused by binocular competition; *c)* complex cells are more susceptible to deprivation effects than are simple cells; *d)* finally, the deprivation also appears to affect the central connections related to the nondeprived eye, as shown by receptive-field abnormalities for some of the cells driven by that eye.

INTRODUCTION

Monocular deprivation of kittens during the first several months of life has profound effects upon the geniculocortical pathways. In the deprived laminae of the lateral geniculate nucleus, cell bodies are abnormally small and few Y-cells can be found (9, 19). In addition, neurons of the binocular portion of striate cortex become dominated by the nondeprived eye (4, 6, 24, 25). However, further studies of the lateral geniculate nucleus indicate that the deficits are mostly limited to its binocular segment¹ since the deprived monocular segment has neurons of nearly normal size and a normal complement of Y-cells (9, 11, 19). This is thought to occur from a developmental mechanism whereby pathways from each eye compete with one another for dominance of central connections. This still general concept of binocular competition (7, 20, 25) suggests the possibility that central connections from the deprived eye can develop only in the monocular segment since, by definition, they cannot suffer there from a competitive disadvantage with respect to connections from the deprived eye.

¹ The binocular segment of the central visual pathways is the portion whose neurons have receptive fields within the binocularly viewed portion of the cat's visual field. The monocular segments contain neurons whose receptive fields are in the peripheral, monocularly viewed crescents of the visual field (see also ref 9, 18, 19).

Electrophysiological studies of the lateral geniculate nucleus in monocularly sutured cats support the notion that binocular competition largely controls development since no abnormalities have yet been described for the deprived monocular segment. However, a similar analysis has not been made at the cortical level. The receptive-field studies of Wiesel and Hubel (24, 25) and others (4, 6) have been confined to the binocular portions of striate cortex. In a recent study of monocularly deprived cats, Sherman et al. (20) found that neurons in the deprived monocular segment of cortex were indeed responsive to stimulation of the deprived eye, but the multiunit recording technique which was used precluded single-cell, receptive-field analysis. These authors were thus unable to ascertain the quality of these responses at the single-unit level. The purpose of the present study was to attempt such an analysis of the binocular and monocular segments with single-unit, receptive-field techniques in cats raised with monocular suture.

Our results demonstrate that many cells in the deprived monocular segment have normal receptive-field properties. This contrasts distinctly with the binocular segment of striate cortex where very few cells are driven by the deprived eye and, of these, virtually none have normal receptive fields. This difference between the monocular and binocular segments provides further evidence that binocular competition plays a part in regulating cortical development. However, since many cells in the deprived monocular segment do not have normal receptive fields, binocular competition cannot dominate the cortical development of these cats in the way that it may control most development of the lateral geniculate nucleus.

METHODS

Subjects

Fifteen cats, born and raised in the laboratory, were studied. Each had one eye closed by eyelid suture before normal eye opening (i.e., 6–10 days of age) and was maintained in this fashion until the terminal recording session. At the time of recording, the cats ranged in age from 6 to 24 mo.

Physiological recording

The preparation, recording techniques, and receptive-field analysis were in all ways identical to those in our previously reported study of normal cat striate cortex (26). The cats were anesthetized, paralyzed, and artificially ventilated. Their pupils were dilated, and their corneas were protected by contact lenses chosen by retinoscopy to ensure conjugacy between the

retinas (central and peripheral) and frontal tangent screen. (Interestingly, the deprived eye was usually 1–2 diopters more myopic than the non-deprived eye, as determined by retinoscopy after placement of equivalent contact lenses over both corneas. Thus, the interocular difference was likely due to different ocular axial lengths, etc.) Rotation of the stereotaxic platform allowed the receptive fields to be brought close to the center of the tangent screen. Insulated tungsten microelectrodes (10–20 M Ω at 500 Hz) were used extracellularly to monitor single-cell activity. Extracellular penetrations were made perpendicular or oblique to the cortical layering, so it is unlikely that we sampled any layer to the exclusion of others. Receptive fields were analyzed first by means of hand-held targets and then, more quantitatively, by means of a computer, which was in synchrony with the visual stimuli and which correlated the stimulus position with the neuronal discharge. The computer averaging with automated stimulus presentation was particularly important for neurons with poor responses. Also, use of the computer permitted study of inhibitory or suppressive portions of the receptive field; for this we often employed the techniques of monocular or binocular conditioning (1, 10). Briefly, these conditioning techniques employ a second (conditioning) visual stimulus moved randomly in the receptive field while the first (test) stimulus is also moved through the field. The conditioning stimulus raises the cell's firing level so that suppressive portions are revealed as drops in this firing level. For averaging purposes, only the test stimulus is in phase with the computer; movements of the conditioning stimulus are random and asynchronous with respect to those of the test stimulus. In monocular conditioning, the test and conditioning stimuli are presented to one eye; with binocular conditioning, each is presented to a separate eye.

Histology

Typically, at least one electrode track in each brain was marked with a small lesion to aid the reconstruction of the electrode paths. This was done following penetrations into the splenial gyrus where peripheral fields are mapped. Following the recording session, the cats were perfused with saline followed by 10% formol-saline, the brains were stereotaxically blocked and cut coronally in 40- μ m slices, and these were stained with cresyl fast violet.

One section from each of two brains was chosen to measure cell sizes and packing densities in the monocular segments. These two sections each had an electrode track passing through the splenial gyrus where cells having receptive fields in the deprived monocular segment had been studied. This ensured that we indeed measured

cells in the monocular segment. Near the electrode track, a convenient 100- μ m band running nearly perpendicular to the cortical layers was chosen. All cells within this band were drawn on graph paper by means of 1,000 \times oil-immersion optics and a camera lucida microscope attachment. Only cells with visible nucleoli were studied, and both cross-sectional areas and packing densities were determined. Identical procedures were used in the same section for the contralateral cortex where the nondeprived monocular segment was situated. Since an electrode track was not available in this area, a band homotypic to that described above but in the contralateral cortex was used. Edema was considered as a possible factor influencing cell sizes near the electrode tracks. However, this possibility was discounted after measurements of cell areas near electrode tracks in normal cats were found to be nearly identical to those in corresponding areas which had no nearby electrode penetrations.

RESULTS

Receptive-field properties were studied for 156 cells in 15 monocularly sutured cats. These properties included cell types (simple, complex, etc.), position in the visual field, ocular dominance,² size, orientation selectivity,³ and speed selectivity. These same properties had previ-

² We used five categories of ocular dominance: class 1 cells are driven exclusively by the contralateral eye; class 2, binocularly but more strongly by the contralateral eye; class 3, nearly equally by either eye; class 4, binocularly but more strongly by the ipsilateral eye; and class 5, exclusively by the ipsilateral eye.

³ We did not routinely test neurons using small, round spots or stationary slits of light at various orientations. Therefore, our use of orientation selectivity does not preclude the possibility that the cells were actually responding to the directional movement of the slit along the axis orthogonal to the slit orientation (cf. ref 15).

ously been studied from striate cortical neurons of normal cats, and definitions for these terms remain the same (26).

Receptive-field classification

Cells were classified as simple, complex, hypercomplex, and nonoriented according to our previously described criteria (21, 26) which represent modifications of earlier criteria (13, 14, 16). Since hypercomplex cells are of two types which resemble simple or complex cells, respectively (5, 17, 26; see also Table 1), we have counted these as simple (six cells) or complex (three cells). Nonoriented cells respond equally well to moving slits of any orientation; these are distinguished from rare complex cells which respond to slits of any orientation, but respond more vigorously to a limited range of orientations (26). Overall, we sampled 63 simple cells, 36 complex cells, 9 nonoriented cells, 1 unclassified cell, 29 cells with abnormal properties (see below), and 18 cells without detectable receptive fields. Table 1 summarizes these data and also, for comparison, shows analogous data collected from normal cats (26).

Although it is tempting to consider the unresponsive cells as an abnormality induced by the lid suture, it is emphasized that such cells are occasionally encountered in normal cats (cf. ref 23, 26). All of these unresponsive cells were found among groups of cells with clearly defined receptive fields. Thus, it seems unlikely that the lack of responsiveness was simply due to inappropriate stimulus presentation. We were able to detect these neurons only by virtue of their spontaneous activity. Since unresponsive neurons with little or no spontaneous firing would have been missed, the 18 cells we did survey may represent a serious underestimate of the number of such cells.

Twenty-nine cells in the deprived cats had properties not encountered in normal cats, and

TABLE 1. Summary of receptive-field types and positions among striate cortical neurons in normal and monocularly sutured cats

Eccentricity	Normal			Nondeprived Eye			Deprived Eye		
	0-30°	30°-45°	45°-90°	0°-30°	30°-45°	45°-90°	0°-30°	30°-45°	45°-90°
Cell type									
Simple	89(7)	8	13(1)	20(4)	17	10	0	3(1)	13(1)
Complex	42(2)	17(2)	21(4)	10(1)	16(1)	7(1)	0	0	2
Nonoriented	1	1	1	1	1	0	0	3	2
Abnormal				5	8	0	0	6	8

Most normal data are from our previous report (26), but data from several normal experiments performed after our earlier study are included. Types I and II hypercomplex cells (5, 17, 26) are tabulated as simple and complex cells, respectively (see text), but the numbers of these hypercomplex cells are given in parentheses. For simplicity, the following data are not tabulated for the deprived cats: a) five binocularly activated neurons (see Fig. 2) which include two nonoriented cells, two abnormal cells, and one complex cell (normal data include monocularly and binocularly driven neurons); b) 18 neurons without detectable receptive fields; and c) one cell driven by the nondeprived eye with conflicting properties that precluded receptive-field classification.

only these have been classified as abnormal. We must qualify this terminology by pointing out that, since the cell sample for normal cat striate cortex is limited, some or all of these "abnormal" cells may be rare types found in normal cortex. Of these 29 abnormal cells, 10 responded to rectangular stimuli moved in any direction, but had either vague, unmappable fields or had unusual properties, such as inhibitory zones in their fields. (The cells classified as nonoriented in this and our previous paper (26) had no such inhibitory receptive-field zones.) Figure 1 illustrates two examples of abnormal cells.

Effects in binocular and monocular segments

Most of the neurons studied (130 of 156) were located in the cortex contralateral to the deprived eye. For these, Fig. 2 shows the position within the visual field, the cell type, and the dominant eye. Each of the 26 cells studied in the hemisphere contralateral to the nondeprived eye was driven exclusively by that eye. Although these cells are not illustrated in Fig. 2, they are considered below. It is clear from Fig. 2 that the deprived eye drives many more cells with receptive fields in the peripheral visual field (i.e., the monocular segment, $> 45^\circ$ eccentricity from the vertical meridian) than it does with fields in the central region (i.e., binocular segment, $< 30^\circ$ eccentricity; the 30° – 45° region of eccentricity is considered below). Since a major portion of this study is concerned with differences between central and peripheral parts of the visual field, our presentation of these data will be in three parts: central (0° – 30°), intermediate (30° – 45°), and peripheral (45° – 90°) parts of the field.

CENTRAL VISUAL FIELD (0° – 30°). We found that in the central 30° of the visual field, nearly every cell (36 of 37; 97%) was driven exclusively by the nondeprived eye, and this is in agreement with previous studies of monocularly deprived cats (4, 6, 24). Only one binocular cell could be influenced, weakly, by the deprived eye, and this cell had an abnormal receptive field. Six cells driven only by the nondeprived eye in the central 30° were also classified as having abnormal fields (see above and Fig. 1B). The remaining 31 cells had receptive fields with normal properties and were classified as simple, complex, or nonoriented (see Table 1).

We noticed two unusual features concerning cells driven by the nondeprived eye. First, we found that 18 of 101 cells, which were driven by the nondeprived eye, responded to moving stimuli with any orientation. The abnormal cell of Fig. 1B is one such cell, and 7 of these 18 were classified as abnormal. In normal cats, we previously found that only 6 of 214 cells responded to any stimulus orientation. This is a significantly

lower ratio than seen here for the nondeprived eye ($P < 0.001$ on a χ^2 test). Second, seven cells driven by the nondeprived eye responded so poorly that the receptive fields were unmappable.

INTERMEDIATE VISUAL FIELD (30° – 45°). An important transition in ocular dominance occurred at about 30° eccentric to the vertical meridian. From 30° to 45° within the cortex contralateral to the deprived eye, we studied 55 cells. Of these, 12 were driven exclusively by the deprived eye. Of these 12, 6 had apparently normal receptive-field properties (3 simple, 3 nonoriented); the remaining 6 cells had abnormal receptive fields. That is, the fields were either extremely large, or the neuronal responses were so poor that precise mapping was impossible. Additionally, there were two nonoriented, one complex, and one abnormal cell which were all binocularly driven. The abnormal and complex cells were driven more strongly by the deprived eye, while the two nonoriented cells were driven more strongly by the nondeprived eye.

The hemisphere contralateral to the deprived eye was emphasized in our recordings because we attempted to reach the deprived monocular segment much more often than the nondeprived monocular segment in the other hemisphere. Within the cortex ipsilateral to the deprived eye, two simple and two complex cells were studied with receptive fields between 30° and 45° , and each of these was driven exclusively by the nondeprived eye.

PERIPHERAL VISUAL FIELD (45° – 90°). From previous work we could be reasonably confident that cells with fields $> 45^\circ$ from the vertical meridian were in the monocular segment (18, 19). We concentrated on the deprived monocular segment, but also made several penetrations into the nondeprived monocular segment. The nondeprived monocular segment was easily found. It contained simple and complex cells (10 and 7, respectively) in apparently normal numbers, and their receptive fields were comparable to those found in monocular segments of normal cats (26). Responses of two of these cells are illustrated in Fig. 3A, B. Thus, the cells in the nondeprived monocular segment seemed essentially the same as those of normal cats (26).

On the other hand, the deprived monocular segment of cortex was abnormal in two respects. First, within this segment we had difficulty locating cells which had receptive fields of any kind. We experienced no such problem either with monocular segment in normally reared cats or with the nondeprived monocular segment in these monocularly sutured cats. We initially thought that this might be attributed to faulty electrodes, damaged cortex, or the electrodes

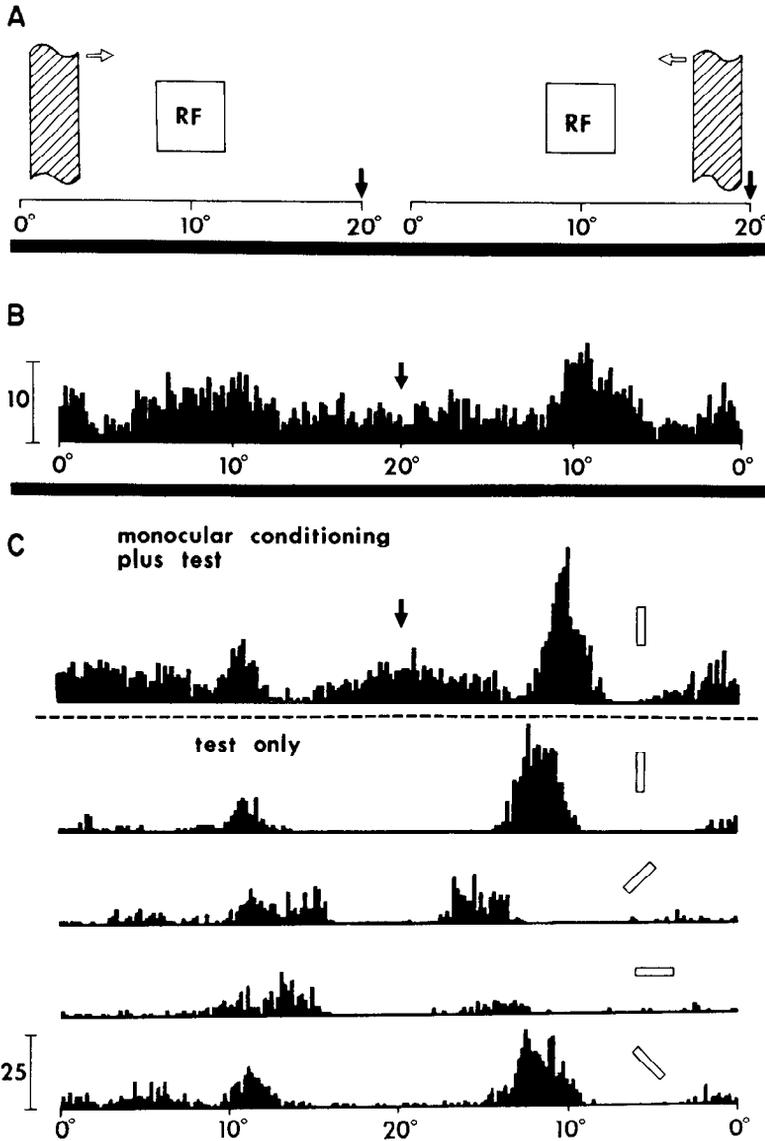


FIG. 1. Average-response histograms for two striate cortical neurons in monocularly deprived cats. These histograms indicate the neuronal firing rate as a function of stimulus position. *A*: stimulus parameters for average-response histograms in this and succeeding figures. An elongated bright rectangle is swept back and forth at constant speed across the receptive field (RF) through a 20° excursion. The rectangle is typically 1° – 2° wide and much longer than the receptive field; it is moved orthogonally to its long axis at speeds and orientations (unless otherwise noted) judged to be optimal for maximum neuronal response. The stimulus cycle begins at 0° with the rectangle moving in one direction until the turn-around point (filled arrow) is reached at 20° , then the rectangle is moved back to 0° to complete the cycle. For each histogram, responses from many such cycles (typically > 100) are summed, and the average spike discharge is displayed for each 0.2° of the stimulus cycle. *B*: average-response histogram for abnormal cell driven by the deprived eye. The neuron was poorly responsive; with hand plotting only an approximate field could be mapped, and no orientation selectivity was evident. The histogram was generated during 600 stimulus cycles and only a weak response is seen in its right half. The scale on the left is calibrated in spikes per second, the turn-around point is indicated by the filled arrow, and distance on the abscissa is shown for the visual field as in *A*. *C*: average-response histograms for an abnormal neuron driven by the nondeprived eye; conventions as in *A* and *B*. Rectangles to the right indicate stimulus orientation since, in this example, different histograms represent differences in responses to this parameter. The top histogram illustrates monocular conditioning (see METHODS) and reveals inhibitory sidebands next to the discharge zone. The lower histograms indicate that this cell responds to all stimulus orientations. Since in normal cats cells with inhibitory sidebands (i.e., simple cells; cf. ref 21, 26) respond to a limited range of stimulus orientations, this cell was classified as abnormal.

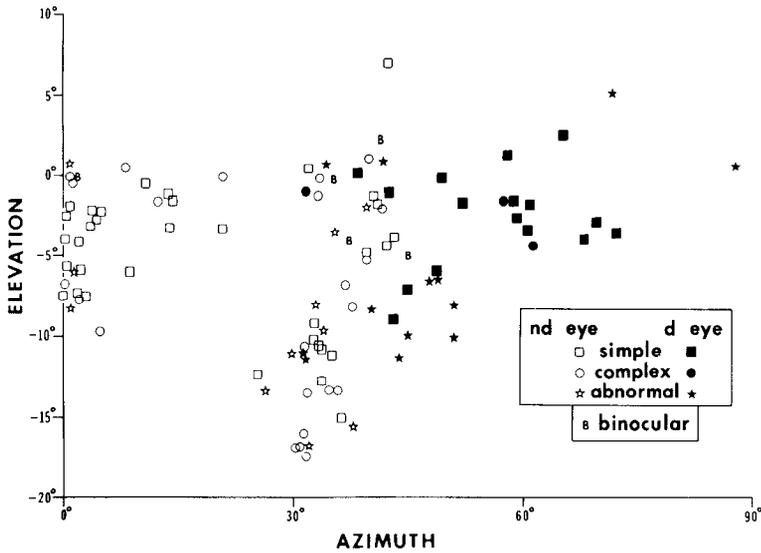


FIG. 2. Representation of the right visual hemifield showing types and receptive-field positions of responsive cells studied in the striate cortex contralateral to the deprived eye. Not illustrated are cells found in cortex ipsilateral to the deprived eye (see text). All fields are shown as if they were located in the right hemifield for right monocularly deprived cats, although some of the fields were, in fact, in the left hemifield for left monocularly deprived cats. Cells driven by the deprived eye (d eye) are represented by filled symbols; the nondeprived eye (nd eye), by open symbols; and five binocularly driven cells, by Bs. Squares represent simple receptive fields; circles, complex fields; and stars, abnormal fields.

missing the splenial gyrus laterally. However, there were several reasons to believe that none of these was responsible. Electrode impedances were frequently checked and found to be unchanged after passing through the area, and also the electrodes were found to be satisfactory for recording single units in the adjacent, binocular portion of the striate cortex. Histological reconstructions indicated that the electrodes passed directly through the correct areas for the monocular segment, and Fig. 4 illustrates such a penetration.

The second unusual feature was that the few cells which did have receptive fields were mostly simple or abnormal cells. Figure 3C shows histograms from one such simple cell; all the receptive-field properties, including the inhibitory sidebands, clearly distinguished it as a normal simple cell (21, 26). In all, 13 simple cells, including one having hypercomplex characteristics, were studied in the deprived monocular segment. These simple cells had receptive-field properties which were normal in every respect we measured. They had small excitatory areas (average, 1.9° wide), fairly narrow orientation selectivities (average, 77° orientation range), of relatively low speed preferences (average, $12^\circ/s$), separated edge discharge zones, and inhibitory side bands (21, 26). Only two complex cells were found in the deprived monocular segment. In normal cats, the percentage of complex cells is higher than that of simple cells in this area (see

Table 1 and ref 26), and this difference between normal and monocularly deprived cats is statistically significant ($P < 0.001$ on a χ^2 test). Two nonoriented and eight abnormal cells were also found in the deprived monocular segment.

The lack of visually responsive cells but normal appearance of simple cells in the deprived monocular segment of cortex can be illustrated in another way. In normal cats and in the cortex contralateral to the nondeprived eye of these monocularly sutured cats, we placed 19 electrode penetrations through the monocular segment and isolated 59 visually responsive cells⁴ (3.1 cells per penetration). We placed 17 electrode penetrations through the deprived monocular segment and isolated only 24 cells (1.4 cells per penetration). These differences are statistically significant ($P < 0.01$ on a Mann-Whitney U test). In all cases, the penetrations were perpendicular to the cortical layering and traversed roughly the same length of gray matter. On the other hand, in the normal and nondeprived monocular segments, we isolated 23 simple cells (1.2 simple cells per penetration), while in the deprived monocular segment, we isolated 13 simple cells (0.8 simple cells per penetration). These differences are not statistically significant ($P > 0.1$ on a Mann-Whitney U test).

⁴ These included seven cells not found in Table 1 because they could not be classified. Such cells were not encountered in the deprived monocular segment.

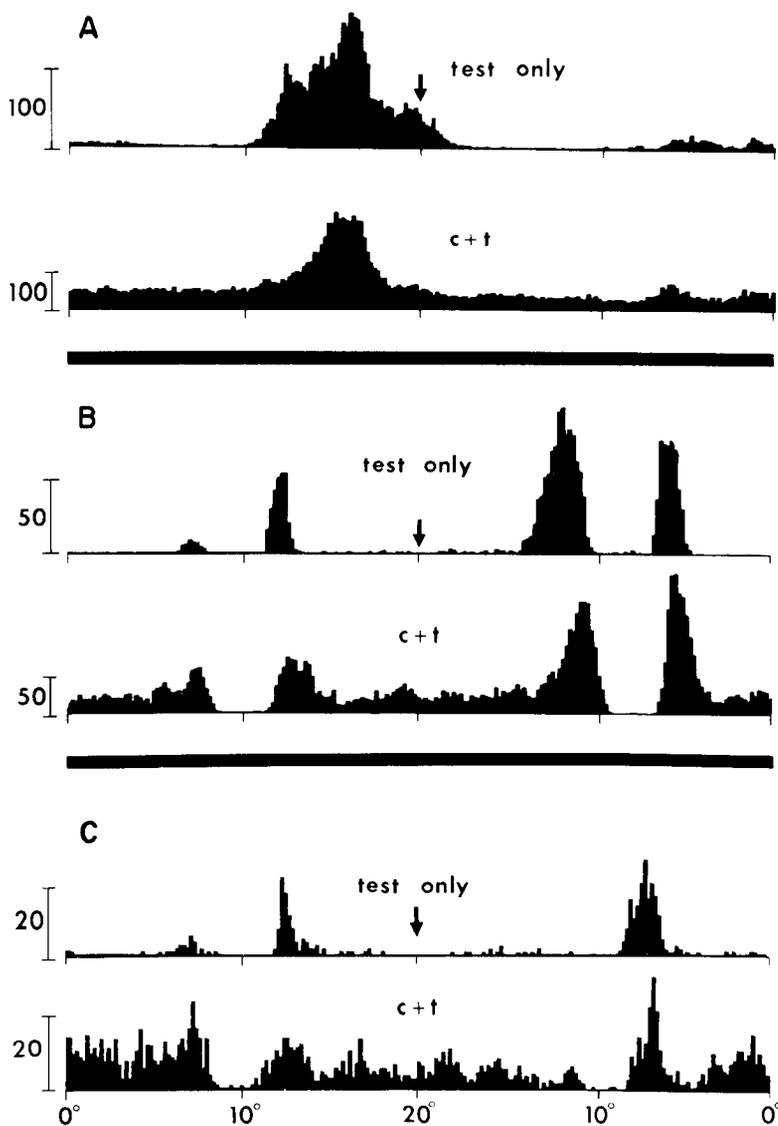


FIG. 3. Representative average-response histograms from three normal cells in the monocular segments of monocularly sutured cats; conventions as in Fig. 1. The top histogram in each pair represents responses to a test stimulus alone; the bottom, to monocular conditioning (see METHODS). *A*: average-response histograms for a normal complex cell in the nondeprived monocular segment. No sideband inhibition is evident (21, 26). *B*: average-response histograms for a normal simple cell in the nondeprived monocular segment. Sideband inhibition is clearly evident (21, 26). *C*: average-response histograms for a normal simple cell in the deprived monocular segment. Sideband inhibition is clearly evident (21, 26).

Responsiveness of cells

As indicated above, many cells driven by the deprived eye were poorly responsive. We attempted to quantify this by comparing the peak responses among these cells, cells driven by the nondeprived eye, and cells in normal cortex. These measures were taken only from cells for which we collected a series of average-response histograms representing a variety of stimulus conditions. By this analysis, peak responses in

55 cells driven by the nondeprived eye were not different from those in 37 cells from normal cats (means \pm SD: 70 ± 57 and 71 ± 64 spikes per second, respectively; $P > 0.10$ on a Mann-Whitney U test). The peak responses for 25 cells driven by the deprived eye were significantly less (39 ± 38 spikes per second) than either of the other groups ($P < 0.005$ on a Mann-Whitney U test for either comparison). When only responses of simple cells were considered, those driven by

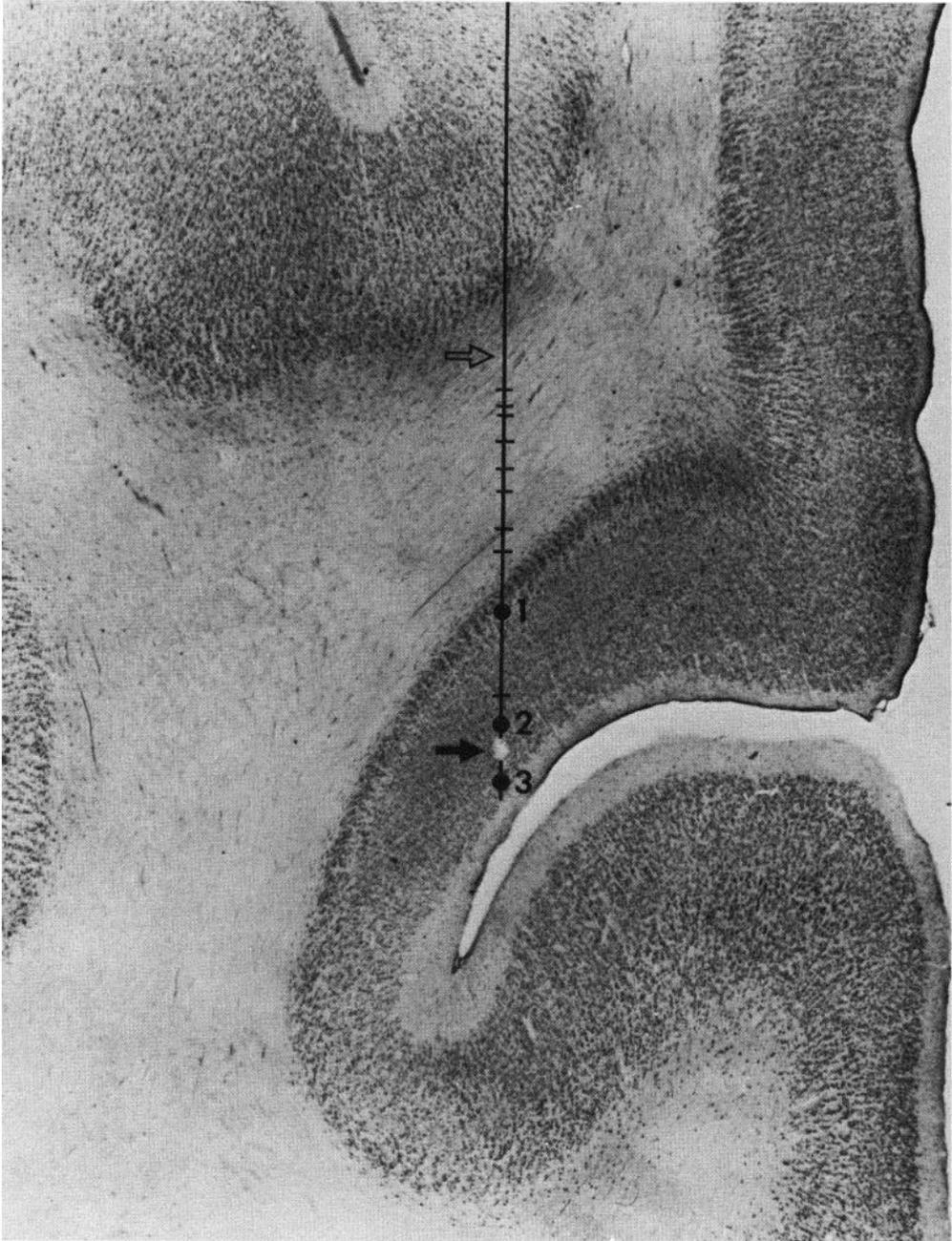


FIG. 4. Photomicrograph centered on the dorsal bank of the splenic gyrus showing an electrode track (vertical line) and marking lesion (filled arrow). The electrode was rapidly moved down to the position of the open arrow before recording was begun. At first, optic radiation fibers were isolated and their locations are indicated by horizontal slashes. The dot labeled 1 represents the location of the first neuron, which had a normal simple field driven by the deprived eye and was located 45° from the vertical meridian. The next cell isolated, 2, was nearly 1 mm deeper and was also driven only by the deprived eye. It responded so poorly that only its field location could be determined at approximately 52° from the vertical meridian. Two more cells (at location 3) were visually unresponsive and may have been outside area 17. The unit isolated between cells 1 and 2 (horizontal slash) was driven by the deprived eye and appeared to be an optic radiation fiber based on its receptive-field properties and location in layer IV.

the deprived eye were still less responsive than normal. Thus the 10 simple cells driven by the deprived eye exhibited a peak mean response of 30 ± 18 spikes per second, the 24 driven by the nondeprived eye had a mean of 60 ± 52 spikes per second, and the 18 in normal cats had a mean of 60 ± 58 spikes per second. Perhaps because of the small sample size, these differences are not significantly different ($P > 0.05$ on a Mann-Whitney U test for all comparisons). Therefore, we cannot conclude that these apparently lower response rates truly represent a significant deficit for the deprived simple cells. With this qualification, we conclude that simple cells driven by the deprived eye are normal, although sufficient data were available from only a small number of cells.

Histology

Cell sizes and packing densities were studied in the cortical monocular segments in an attempt to identify gross morphological correlates for our physiological results. For example, if the cells were smaller or less numerous on the deprived side, the population sampled by the electrode could be biased. Also, since the binocular segments of each cortical hemisphere still receive normal afferents from the nondeprived eye, the cells there may be relatively normal in appearance. A direct interhemispheric comparison of the deprived versus the nondeprived monocular segments would probably provide the most sensitive test for histological effects of deprivation at the cortical level, since these regions can be compared within an animal.

In the cortex of monocularly deprived squirrels, Guillery and Kaas (8) have reported an increased packing density of cells contralateral to the deprived eye both in the binocular and monocular areas. These authors were able to distinguish the monocular segments within striate cortex by the change in thickness of layer IV at the monocular/binocular border. The cat has no such obvious layer IV change in its striate cortex. In order to verify that we were measuring cell sizes and packing densities in the proper area, we relied on electrode tracks which passed through the monocular segment. We determined this by receptive-field positions of cells located by the electrode. In two monocularly deprived cats, approximately 1,500 cells were drawn from all cortical layers of the deprived and nondeprived monocular segments, and the cross-sectional areas of these cells were measured (see METHODS).

The quantitative results of comparing the deprived versus the nondeprived cortical monocular segments verified earlier qualitative observations (24, 25). That is, there were no significant differences in cell packing densities or cell sizes. Figure 5 presents the average cell size and pack-

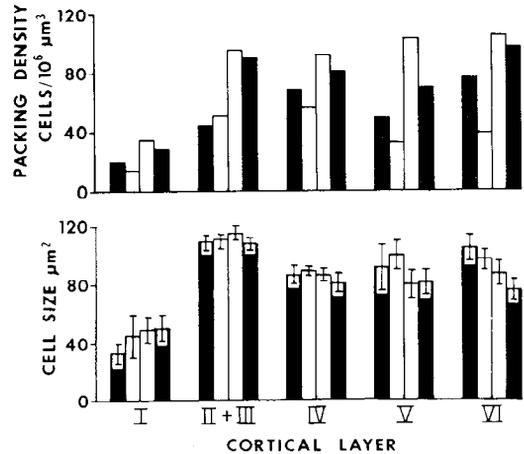


FIG. 5. Comparison of neuronal sizes and packing densities between the nondeprived (open bars) and deprived (filled bars) cortical monocular segments for two monocularly sutured cats. For each cortical layer, the left-hand pair of histograms derive from one of the cats; and the right-hand pair, from the other. There were no significant interhemispheric differences in cell size for any layer ($P > 0.10$ on a t test). For packing density, in one cat no interhemispheric difference was noted ($P > 0.10$ on a χ^2 test) while a weak difference was noted in the second cat ($0.02 < P < 0.05$ on a χ^2 test), such that the deprived segment had a slightly lower packing density than did the nondeprived. The number of cells represented left to right by laminar division are: I—12, 10, 20, 27; II and III—130, 110, 177, 185; IV—98, 142, 124, 146; V—24, 29, 39, 59; VI—29, 48, 57, 60.

ing density for each cortical layer. We stress that accurate localization of the boundaries between layers was very difficult in these areas and, for this reason, layers II and III have been combined. From these histological results we conclude that the cat differs from the squirrel in having no gross morphological effects in the deprived monocular segment of cortex. Nevertheless, our conclusions are much the same as those of Guillery and Kaas (8). They, like us, observed a cortical effect of monocular deprivation in addition to binocular competition. Furthermore, our failure to detect gross morphological changes cannot apply to more subtle abnormalities involving dendrites, synapses, etc., which could well underlie the observed physiological deficits in these cats.

Inhibitory receptive fields

Henry, Bishop, and Coombs (10) suggested that all cortical cells with centrally located receptive fields receive input, either excitatory or inhibitory, from both eyes. As control data for those from monocularly deprived cats, we examined the receptive fields of normal cat striate neurons which had been categorized as class 1 or class 5 ocular dominance (see footnote 2). By the

technique of binocular conditioning (see METHODS and ref 10), we tested these units for inhibitory fields from the eye which had no discernible excitatory input to the cell. Of the 11 tested, 8 had clear inhibitory fields (Fig. 6C) and 3 had very weak inhibitory fields (Fig. 6B).

These data are to be compared with those taken from monocularly deprived cats in which none of the 16 cells categorized as class 1 or class 5 ocular dominance (all driven exclusively by the nondeprived eye) had an inhibitory receptive field from the other (deprived) eye (Fig. 6A).

DISCUSSION

Not only do these data support the concept of binocular competition for cortical development, they also suggest the following three additional effects of early monocular suture on cortical neurons: 1) many neurons in the deprived monocular segment have either no receptive fields or abnormal ones and, thus, deprivation affects cortical development in a region where binocular interactions are not present; 2) many neurons exhibited abnormal receptive fields for the nondeprived eye; 3) complex cells, at least in the monocular segment, appear to be more seriously affected by the deprivation than are simple cells.

Binocular competition and deprivation

The clearest evidence of binocular competition during development consists of a demonstration that, for the deprived eye, the monocular portions of the central visual pathways are less seriously affected by the deprivation than are the binocular portions (20). Such evidence is derived from our data: many cortical neurons had normal receptive fields for the deprived eye in the monocular segment, whereas none was normal in the binocular segment. Note that these effects of binocular competition and deprivation can now be extended to inhibitory regions of the receptive field as well. Furthermore, if monocular deprivation had no effect on geniculocortical development other than its effect on the binocular competitive balance, then the monocular segments should both be equal and normal. Not surprisingly, this was not the case. Many neurons in the deprived monocular segment had abnormal properties and, despite the lack of gross histological changes, we were unable to sample the expected normal number of cells. Thus, an effect of deprivation, which is not related to the binocular competitive balance, must have operated in these cats.

Note that the monocular segment is the only region in which effects of monocular deprivation other than binocular competition can be studied. It is interesting to speculate that the monocular segment in these monocularly sutured cats is fundamentally like the entire cortex of binocu-

larly sutured cats (cf. ref 2, 3, 15), since the balanced, but impoverished environment created by binocular suture prevents the more deleterious effects of binocular competition (25). We are currently investigating this possibility in more detail by studying binocularly sutured cats. Finally, it is possible that the deprivation effects seen in the monocular segment actually occur throughout striate cortex in these monocularly sutured cats and that the properties of binocular segment neurons represent the sum of these effects added to the effects of binocular competition. We emphasize that it is not clear how much of the deprived eye's abnormalities in the binocular segment are due to binocular competition and how much are due to other consequences of deprivation.

Border between monocular and binocular segments

Clearly fields within 30° of the vertical meridian are in the binocular segment and those beyond 45° belong to the monocular segment (18, 19), but the intermediate zone is less clear. Between 30° and 45°, the increase in cells driven by the (contralateral) deprived eye (31%) is large when compared to the central 30°, where only 1 of 37 cells was driven by this eye. The most likely explanation for these results is that the transition between the binocular and monocular segments in cortex is gradual or very irregular. Most cells in this area are destined for binocular input (i.e., for excitatory and/or inhibitory effects), while others may receive a purely monocular input from the contralateral eye. The cells which are influenced only by the contralateral eye can perhaps be functionally considered as being in the monocular segment. For example, like cells with more peripheral fields, these are never influenced by the geniculate A1 or C1 laminae. During development, then, there would be no binocular competition from the nondeprived eye for these monocularly influenced cells found at intermediate (30°–45°) eccentricities. Thus, some could develop normally, as in the more peripheral, deprived monocular segment.

Three additional observations support this notion of gradual or irregular transition between binocular and monocular segment. First, in our study of normal cats (26) we found a fairly uniform ocular dominance pattern for single neurons throughout most of the binocular segment. However, at its peripheral edge (30°–45°) we noted a sudden increase in class 1 cells (i.e., cells driven only by the contralateral eye). Second, a comparison of class 1 cells in this area (30°–45°) between normal (14 of 26, 54%; cf. ref 26) and monocularly deprived cats (13 of 55, 24%) indicates a significant reduction of these cells for the deprived cats ($P < 0.001$ on a χ^2 test). This reduction to approximately half the

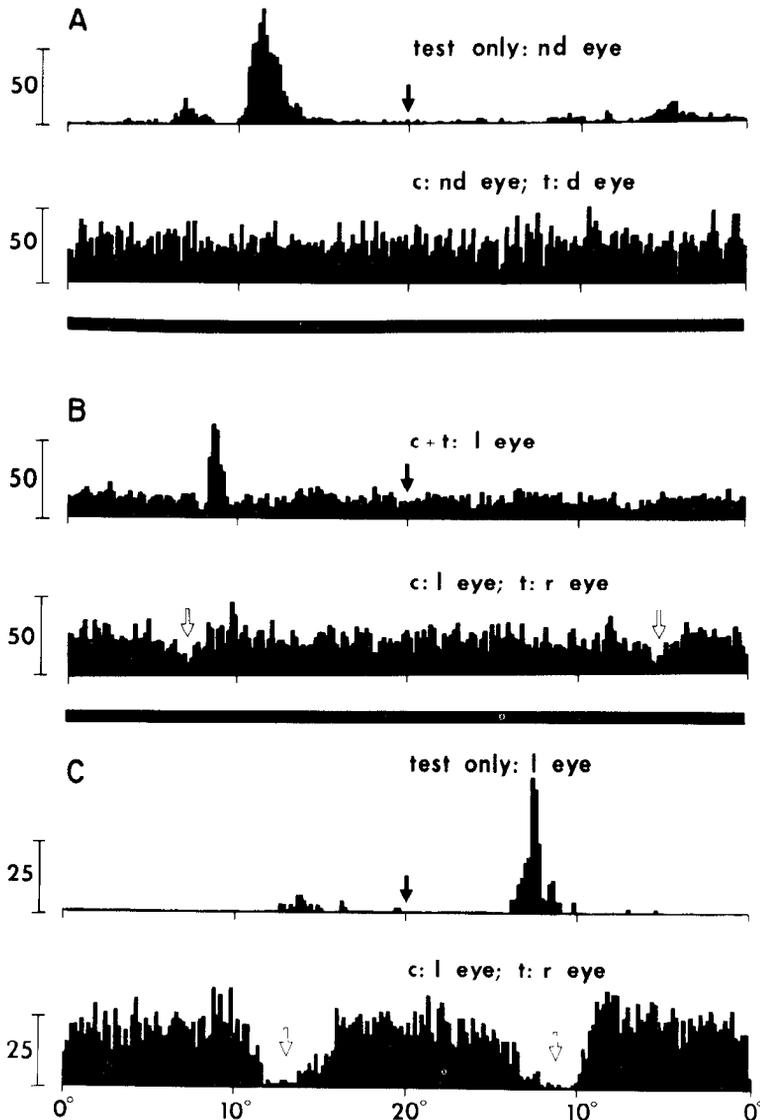


FIG. 6. Representative average-response histograms for three cells driven exclusively by one eye (i.e., class 1 or 5); conventions as in Fig. 1. For each cell, the upper histogram represents stimulation of the dominant eye, and the lower histogram represents binocular conditioning (see METHODS) whereby the nondominant eye is tested for a purely inhibitory field. *A*: average-response histograms for a cell in a monocularly deprived cat driven only by the nondeprived eye (nd eye). When the nondeprived eye is conditioned (c: nd eye) and the deprived eye is tested (t: d eye), there is no indication of an inhibitory receptive-field region. *B*: average-response histograms for a cell in a normal cat driven only by the left eye. The upper histogram represents monocular conditioning of the left eye (see METHODS), and the lower histogram represents conditioning of the left eye while the right is tested. Here, weak inhibitory zones are indicated by the open arrows, and this was the weakest inhibition for the nondominant eye seen in normal cats. *C*: average-response histograms for another cell driven only by the left eye in a normal cat as in *B*. The strong inhibition (open arrows) seen for the nondominant eye is typical for these cells (10).

normal value in this intermediate zone of the deprived cats is roughly the reduction we found in their more peripheral monocular segment. Third, a related result has been reported in the lateral geniculate nucleus of monocularly deprived cats. That is, the survival of large cells in the monocular segment of the deprived lamina

extends beyond the borders of the nondeprived lamina (9).

Receptive fields for nondeprived eye

Two results indicate that the deprivation has had an effect on some of the nondeprived eye's receptive fields. First, we found 16 cells of 101

driven by the nondeprived eye which had abnormal receptive fields (2 of these being binocularly driven). Wiesel and Hubel (25, p. 1032) also reported such cells in monocularly deprived cats. Second, there was an unusually large number of cells driven by the nondeprived eye which responded to stimuli of any orientation. It may be that binocular competition leads, in some cases, to additional synapses for the nondeprived eye, which might give the cell unusual or abnormal receptive-field properties. Consistent with this possibility is the fact that we found no abnormal receptive fields in the monocular segment of the nondeprived eye, although the number of cells studied may be too small to provide statistical significance.

Differential deprivation effects

We found only 3 complex cells compared to 16 simple cells driven by the deprived eye (1 of the complex cells was binocularly driven). This suggests that the deprivation affects complex cells or their inputs more than it does simple cells. Two possibilities clearly stand out. First, given the hierarchical, serial model of Hubel and Wiesel (14), whereby simple cells receive the geniculocortical afferents and complex cells derive their input from simple cells, it is not unexpected that

the effects of deprivation might be more apparent at the second cortical stage of visual processing. The second possibility is related to the parallel processing model of Stone and co-workers (12, 22, 23). This model suggests that the geniculate X-cells provide afferents to simple cells and the Y-cells, to complex cells. Monocular deprivation appears to selectively affect geniculate Y-cells within the binocular segment of deprived laminae, but the monocular segments appear to be unaffected (19). It may be that another consequence of deprivation is to suppress Y-cell terminals in cortex, and this could explain the effects on complex cells in the monocular segment. Y-cells and complex cells, then, are more susceptible to the effects of early visual deprivation. Simple cells, on the other hand, appear to develop normally in the monocular segment, and it may be that the cortical establishment of X-cell terminals more closely follows a pattern dictated by binocular competition.

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