

# Receptive-Field Properties of Neurons in Binocular and Monocular Segments of Striate Cortex in Cats Raised With Binocular Lid Suture

D. W. WATKINS, J. R. WILSON, AND S. MURRAY SHERMAN

*Department of Physiology, University of Virginia School of Medicine,  
Charlottesville, Virginia 22901*

## SUMMARY AND CONCLUSIONS

1. We studied the receptive fields of 171 striate cortical neurons from 17 cats raised with binocular lid suture. Of these, 102 fields were within 10° of the area centralis and the remaining 69 were at least 38° from the vertical meridian.

2. Based on their different response properties, cells were divided into three broad groups: the mappable cells (49%) had clearly defined receptive fields, the unmappable cells (31%) were activated by visual stimuli but had diffuse fields which could not be hand plotted, and the visually inexcitable cells (20%) could not be activated by visual stimuli. Very few ( $\leq 12\%$  of the total sample) normal simple or complex cells could be found.

3. Orientation selectivity was assessed in these cells. Only 12% displayed orientation selectivity within normal bounds, and these were all mappable cells. None of the unmappable cells had discernible orientation selectivity.

4. Ocular dominance was assessed for 62 of the centrally located receptive fields. Among mappable cells, there was an abnormally low proportion of binocular fields, while no such abnormality was seen for unmappable cells.

5. For 47 of the neurons, average response histograms were compiled for moving stimuli of various parameters in an effort to evoke the maximum discharge or peak response. This peak response was normal for mappable cells but reduced for unmappable cells.

6. We devised a technique for studying potential inhibitory receptive-field zones in these neurons, validated the method in normal striate cortex, and used it to test 20 mappable cells in the lid-sutured cats. None showed the pattern of strong inhibitory side bands seen in normal simple cells, although six showed weak or abnormal inhibitory zones. Interestingly, six of the

seven visually inexcitable cells tested by this method had purely inhibitory receptive fields.

7. The effects of binocular suture were essentially identical for the binocular and monocular segments since the cell types and their response properties did not differ between these two areas of cortex. Furthermore, the cortical monocular segments of these cats seemed qualitatively different from the deprived cortical monocular segment after monocular suture. This extends an analogous difference for these cats reported for the monocular segments of the lateral geniculate nucleus. We thus conclude that monocularly and binocularly sutured cats develop by qualitatively different mechanisms. For the former, competition between central synapses related to each eye is a prominent feature of geniculocortical development, whereas, for the latter, such specific forms of geniculocortical development may not obtain.

## INTRODUCTION

Wiesel and Hubel (39) reported that many cortical cells in cats raised with binocular lid suture have fairly normal and specific receptive-field properties. They thus suggested that these properties can develop, to a large extent, in the absence of visual experience (see also ref 14). Several recent studies (4, 5, 15, 22, 26) have reexamined this hypothesis. For instance, Pettigrew (22), in a study of normal and binocularly sutured kittens up to 6 wk of age, suggested that selectivity for retinal disparity and, to a large extent, stimulus orientation, depends on appropriate visual experience. Blakemore and Van Sluyters (4) reported that orientation-selective neurons are infrequent in kitten striate cortex, and that, with binocular suture, the number of such neurons remains essentially constant at least up to 10 wk of age. It is possible that the absence of visual experience

Received for publication May 31, 1977.

simply delays development of specific receptive-field properties, as Grobstein and Chow (9) have suggested, and that the results reported by Pettigrew (22) or Blakemore and Van Sluyters (4) represent a stage in a development process that eventually leads to more or less normal cortex. Thus, the first objective of this study was to examine striate cortical neurons quantitatively in adult cats binocularly deprived from birth, and the results of these experiments are similar to those reported previously (4, 22).

Our second objective was to study cortical neuronal responses in both the binocular and monocular segments<sup>1</sup> of these binocularly deprived cats and compare this with our previously published, analogous data from normal and monocularly deprived cats (34, 40, 41). We found that, in binocularly deprived cats, there were qualitatively no differences in the pattern of abnormalities occurring in the binocular and monocular segments of striate cortex.

## METHODS

### Subjects

Seventeen cats, born and raised in the laboratory, were studied. Each had both eyes closed by lid suture at the time of normal eye opening (i.e., 6–10 days of age) and were maintained in this fashion until the terminal recording session. Extensive observations ensured that no lid holes exposing the pupils were present in any of these cats previous to the terminal experiments. At the time of recording, the cats ranged in age from 10 to 24 mo.

### Preparation

The preparation, recording techniques, and receptive-field analysis were identical to those of our previous studies (35, 40) of normal cat striate cortex and are briefly described here. Initial anesthesia was induced with halothane and maintained during the surgical preparation for recording. During the subsequent recording session, a 70/30 nitrous oxide/oxygen mixture was used to maintain anesthesia. The cats were paralyzed, artificially respirated, and placed in a stereotaxic apparatus facing a frontal tangent screen 114 cm from the eyes. End-tidal CO<sub>2</sub> was monitored and kept near 4%. Body temperature was monitored and maintained near 38°C by means of a heating pad. In some prepara-

tions, electrocardiograms were monitored. The corneas were covered with contact lenses, and retinoscopy was used to determine which spectacle lenses (if any) were chosen to make the retinas conjugate with the frontal tangent screen. The position of the optic disk and, by inference, the area centralis (2, 25) was monitored by the technique of Fernald and Chase (8). The activity of striate cortical neurons was extracellularly recorded with 3 M KCl-filled glass micropipettes or insulated, tungsten microelectrodes (either type, 5–20 MΩ at 500 Hz) inserted through a hydraulically sealed craniotomy.

### Receptive-field analysis

Hand-held targets were used to plot receptive fields. For more quantitative analysis, a computer was used to prepare a series of average-response histograms relating the neuron's discharge rate to stimulus position (1, 23). For these histograms, the stimuli consisted of slits of light (1.0–1.5 log units above background; background = 0.6 cd/m<sup>2</sup>) moving across the receptive field. The width, orientation, position, and speed of the slits were systematically varied to determine which parameters evoked the best response in each cell. In order to study inhibitory (or more accurately, suppressive; see ref 1, 35) portions of the receptive field in neurons with little or no spontaneous activity, we created an artificial, background activity by iontophoresis of potassium ions from the recording pipette. Inhibition was inferred from regions in which the stimulus reduced firing levels below this background level. Since this technique has not previously been applied to the analysis of visual receptive fields, we felt that its validation in a sample of normal striate neurons was indicated; the results of these validating experiments are provided in the APPENDIX, together with methodological details. The visual-conditioning techniques used by Bishop et al. (1) and Sherman et al. (35) to elucidate these inhibitory areas proved unsuitable for the striate cortex of these visually deprived cats in which many cells respond poorly to visual stimuli.

## RESULTS

### Receptive-field types

We studied receptive fields of single units in 51 penetrations through striate cortex of 17 adult, binocularly deprived cats. Since the cell types, proportions, and properties sampled by the metal electrodes and pipettes were indistinguishable, these data are pooled. Furthermore, although slight interanimal variability in cell populations was evident, this was not significant (19), and no cat contributed more than 20 cells to the

<sup>1</sup> The binocular segment of the central visual pathways (including striate cortex) is the portion whose neurons have receptive fields within the binocularly viewed portion of the cat's visual field. The monocular segments contain neurons whose receptive fields are in the peripheral, monocularly viewed crescents of the visual field (see also ref 11, 34, 40).

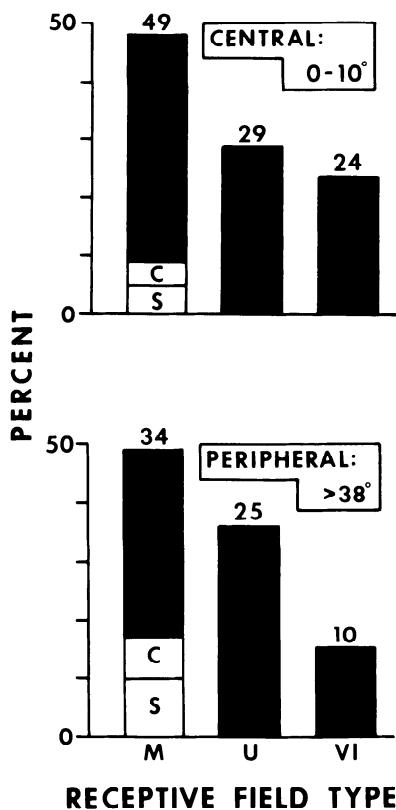


FIG. 1. Relative proportion of various receptive-field types found for cells in striate cortex of binocularly sutured cats. Both the central and peripheral visual-field representations are indicated as  $0-10^\circ$  and  $>38^\circ$ , respectively. Proportions of mappable (M), unmappable (U), and visually inexcitable (VI) fields are shown (see text), and within the mappable group the simple (S) and complex (C) fields are separately indicated. At the top of each column is shown the number of cells in each group.

sample. Thus, the data from all cats were also pooled. We attempted to classify every well-isolated cell in terms of its visual responsiveness. Eight units were classified as fibers from the lateral geniculate nucleus on the basis of waveform and receptive-field characteristics and are not further considered. Visually inexcitable units constituted 20% (34/171) of our sample. The term visually inexcitable seems more appropriate than visually unresponsive because, as we shall show, some visually inexcitable cells responded with purely suppressive or inhibitory receptive fields. Neurons were considered visually inexcitable if we could not evoke a discharge in 20–60 min of testing with a standard battery of stimuli which always included stationary, flashed stimuli (i.e., small spots or slits of light and diffuse flashes) and moving stimuli

(i.e., spots, slits of light, dark bars, and single edges). With moving-line stimuli, orientations all around the clock and a wide range of stimulus speeds were tested. Such cells were noticed by their spontaneous activity or, occasionally, by their discharge in response to application of potassium ions through the recording pipette (see APPENDIX). Visually excitable single units comprised 80% (137/171) of our sample. These single units were further subdivided on the basis of our ability to hand plot their receptive fields. Reliable hand plotting of receptive fields requires relatively consistent and audibly distinguishable responses. With standard handplotting techniques (40) it was possible to map the receptive fields of 49% (83/171) of our sample. The remainder (31%; 54/171) were visually activated, but had vaguely defined receptive-field borders. These visually activated single units whose receptive-field borders we could not delimit will be referred to as unmappable cells; those with definable receptive-field borders, as mappable cells. We believe this distinction is warranted because, as we shall show, these groups also differ in terms of orientation specificity, ocular dominance, and responsiveness. The mappable cells also included a subpopulation of simple and complex cells, which are described more fully in the following section. For the unmappable cells, often large flashed spots, large rapidly moving targets, or full-field diffuse flashes activated these cells, while attempts to plot their receptive fields with more confined stimuli failed. The approximate visual-field location plus the ocular dominance of these cells could usually be ascertained, and visually inexcitable cells were assigned the receptive-field location of the nearest identified receptive field of the same electrode track.

In short, we have assigned cells to three categories: mappable, unmappable, or visually inexcitable. Our sample of 171 cortical cells includes 102 units located within  $10^\circ$  of area centralis and 69 units located  $38^\circ$  or more from area centralis.<sup>2</sup> The gap in data for fields between  $10^\circ$  and  $38^\circ$  eccentricity is simply a consequence of our experimental design. That is, we concentrated on central fields and fields in the monocular segment; electrodes were not placed through the medial portion of the suprasplenial sulcus, where most of the intervening

<sup>2</sup> All but four of the cells had receptive fields beyond  $45^\circ$  eccentricity. These four were all mappable cells without orientation selectivity or bias. Since the monocular segment may not include fields of  $<45^\circ$  eccentricity (see ref 41), these cells are not included among the population of monocular segment cells in Fig. 9, but are included in Figs. 1 and 2.

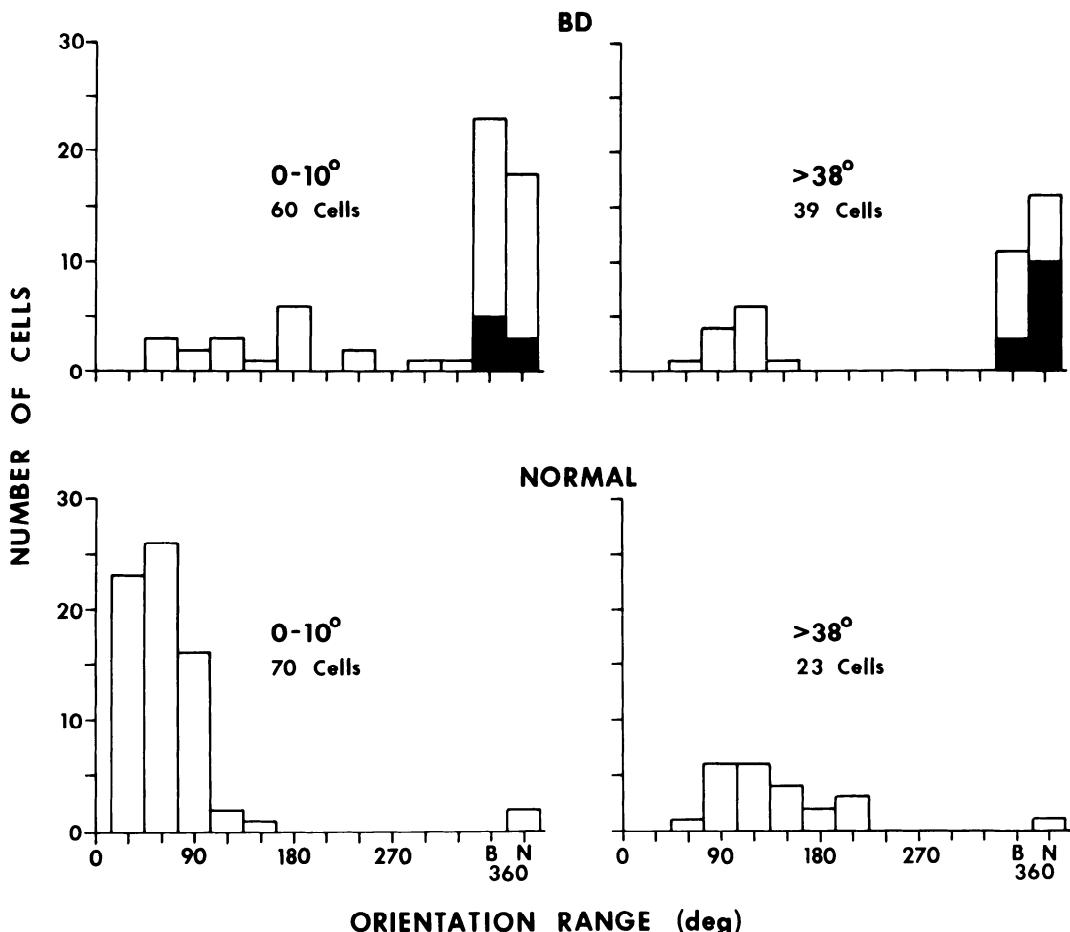


FIG. 2. Frequency histograms of cells as a function of the range of stimulus orientations to which they are responsive. The top row represents data from the present study of binocularly sutured (BD) cats and the bottom row, from previously published studies of normal cats (40). The left column includes central fields ( $0-10^\circ$ ); and the right column, peripheral fields ( $>38^\circ$ ). Open bars represent mappable cells and black bars, unmappable cells. Orientation ranges of  $0-150^\circ$  indicate cells with orientation selectivity, of  $180-330^\circ$  indicate cells with direction selectivity, and of  $360^\circ$  indicate cells with orientation bias (B) or nonoriented cells (N).

fields would be found. In 10 cats, only central fields were studied, and in the remaining 7 both central and peripheral fields were studied. The distribution of cortical cells into the above three categories is shown separately for the centrally and peripherally located receptive fields in Fig. 1. All three categories of cells were found both centrally and peripherally in essentially equal proportions ( $P > 0.2$  on a  $\chi^2$  test).

#### *Orientation and direction selectivity*

Selectivities for orientation and direction of stimulus movement were determined in accordance with the schemes of Pettigrew (22) and Blakemore and Van Sluyters (4) as follows. Nonoriented cells responded to moving stimuli

but with no clear preference for any particular orientation or direction of movement. Moving spots of light were usually as effective as elongated targets. Such cells differed from lateral geniculate fibers by having larger, often binocular, receptive fields and waveforms typical of cells. Directionally selective cells showed a clear preferred direction with little or no response in the reverse direction; once again, target shape had little influence on the response. These are the cells in Fig. 2 with orientation ranges between  $180^\circ$  and  $360^\circ$ . Cells showing an orientation bias generally responded better to moving-line stimuli than to moving spots; and, while responding to all orientations and directions, they responded more vigorously or consistently to stimuli of a particular orientation.

or direction. Orientation-selective cells displayed a preference for elongated stimuli over spots, a narrower range of effective orientations for moving-line stimuli when compared to the range of effective directions for moving spots, and usually a preference for moving targets over stationary targets.

The orientation and direction selectivity of striate cortical neurons in these cats was studied with two techniques. First, for each of 99 visually excitable neurons the total range of effective stimulus orientations was deter-

mined with hand-plotting techniques. These 99 cells included 52 mappable plus 8 unmappable from the central representation ( $<10^\circ$  eccentricity) and 26 mappable plus 13 unmappable from the peripheral representation ( $>38^\circ$  eccentricity). The results are shown in Fig. 2 together with data from normal cat striate cortex from comparable regions of the visual fields. Three points are apparent on inspection of these data: 1) Of the neurons tested, 69% (68/99) responded to stimuli all around the clock, either equally well to all orientations and

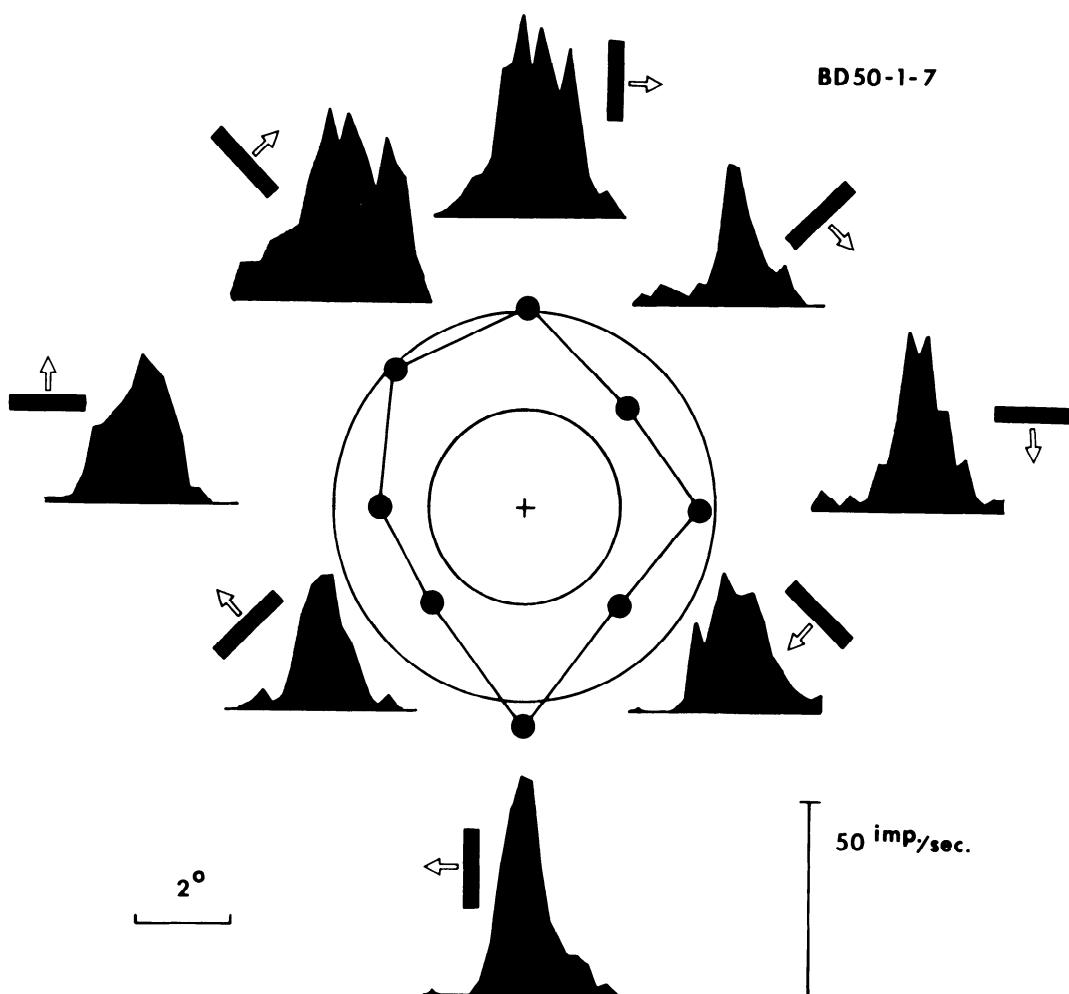


FIG. 3. Polar plot from a deprived cat of a striate neuron's peak response as a function of stimulus orientation and direction. The stimulus was a  $0.5^\circ$ -wide bar moved at  $20^\circ/\text{sec}$ . Also shown are the relevant portions of the average response histograms used to determine the peak response based on an average of the highest five bins in the histogram. The orientation and direction of the stimuli are indicated, respectively, by bars and arrows next to each histogram. Hand-plotted measures of orientation and direction selectivity indicated that the cell responded around the clock with a preference for vertically oriented stimuli (i.e., it was classified as orientation bias); the quantitative measures confirm these observations. The  $2^\circ$  marker scales histograms horizontally to provide information regarding the spatial extent of the receptive field; the 50 impulses/s scales both histograms and polar plot.

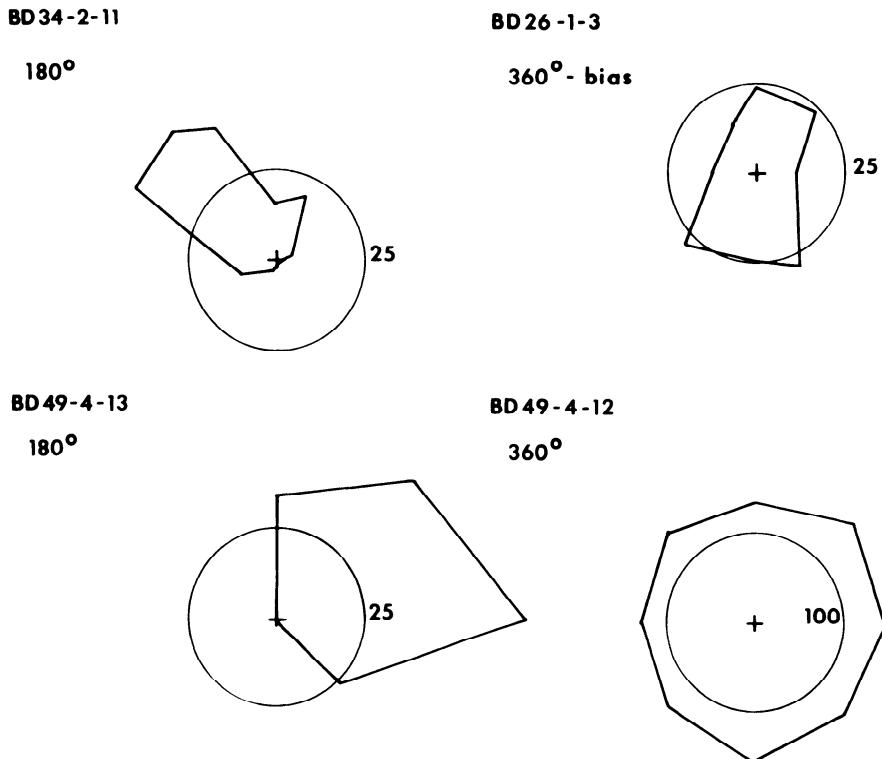


FIG. 4. Polar plots of four different striate neurons' peak responses as a function of stimulus orientation and direction; conventions as in Fig. 3. These plots typify the most common response-orientation curves found for striate neurons in deprived cats. The number near each circle scales the response in spikes per second. The hand-determined orientation range is shown below each unit identification number (above and left of each plot).

directions (nonoriented) or somewhat better to a limited range of orientations and directions (orientation bias). This includes, from the central representation, 15 mappable plus 3 unmappable fields which were nonoriented and 18 mappable plus 5 unmappable fields with orientation bias; from the peripheral representation, 6 mappable plus 10 unmappable fields which were nonoriented and 8 mappable plus 3 unmappable fields with orientation bias. Since from equivalent visual field representations nonoriented fields constituted only 3% (3/93) of our normal sample and no orientation-bias fields were normally found in these regions, there is a remarkable failure to develop orientation and direction selectivity following binocular deprivation ( $P < 0.001$  on a  $\chi^2$  test, even if fields with orientation bias are considered selective). 2) This lack of orientation selectivity is present in both the central and peripheral visual fields to the same degree ( $P > 0.2$  on a  $\chi^2$  test). 3) All neurons showing orientation and direction selectivity within the normal range had mappable receptive fields, while all unmappable cells tested re-

sponded to all stimulus orientations and directions.

It is interesting to note that 66% of the above 99 cells showed some orientation or direction preference (i.e., including the cells with orientation bias), even though 68% responded clearly to all orientations of stimuli. Successively recorded cells of the same electrode track tended to have similar stimulus requirements. Binocular deprivation appears to affect the number of orientation-selective cells and the degree of their selectivity, but perhaps not the basic columnar organization for orientation.

A second, more quantitative test of orientation and direction selectivity was applied in the deprived cats to 23 visually excitable cells (central fields: 12 mappable, 4 unmappable; peripheral fields: 4 mappable, 3 unmappable). For these cells average-response histograms were prepared using a narrow (usually 0.4–0.6°), moving slit for each of a number of orientations and directions spaced all around the clock. Figure 3 shows such average-response histograms for one cell with a polar plot of the peak response as a function of

stimulus orientation and direction. Figure 4 illustrates polar plots of the peak neuronal response as a function of these stimulus parameters for four typical cells representing differing degrees of orientation and direction selectivity. In every instance, these more quantitative measures of stimulus specificity confirmed our hand-plotted assessments.

Blakemore and Van Sluyters (4) have suggested that, based on the degree of their orientation selectivity, striate neurons can be subdivided into the four categories defined above (i.e., nonoriented, direction selective, orientation bias, and orientation selective). They did not describe an unmappable category and, while it might be reasonable to assume that most of our unmappable fields would be classified as nonoriented and the rest as orientation bias by them, we point out that Singer and Tretter (37) probably would have classified our unmappable fields as visually inexcitable (see DISCUSSION). The data of Blakemore and Van Sluyters (4) were apparently limited to cells with fairly centrally located receptive fields. To compare our results best with those of Blakemore and Van Sluyters (4) we used their scheme to categorize the 60 centrally located, binocularly deprived striate neurons for which orientation selectivity was measured. Among these, we found 18 nonoriented cells (30%), 10 directionally selective cells (17%), 23 orientation-bias cells (38%), and 9 orientation-selective cells (15%). The orientation-selective cells include our sample of normal simple and complex cells (see below). The average receptive-field width of these orientation-selective cells (mean = 1.1°) is smaller than those of non-oriented cells (mean = 2.03°) but close to that found for normal simple cells (mean = 0.84°; from ref 35). Finally, when subdivided in this way, we find the relative proportion of cell types in the adult binocularly deprived cat compares closely with that found by Blakemore and Van Sluyters (4) for the binocularly deprived kitten. That is, the relative ratios they report among responsive cells are roughly 49% non-oriented, 30% orientation bias, 7% direction selective, and 14% orientation selective. There consequently appears to be little change in the proportions of these cell types as binocular deprivation is extended from 10 wk (4) to 10 mo or more as in the present study.

Few cells could be classified as simple or complex on the basis of previously described criteria (13, 15, 35). Of the 83 mappable cells, 21 had orientation selectivity within the normal range (i.e., compared to our control data from ref 40) and, thus, the upper limit for the proportion of simple and complex cells is 12% (21/171; 12 simple and 9 complex). Unfortunately, only 10

of these (6 simple and 4 complex) were isolated long enough to test completely for normal receptive-field properties. We are less certain about the remaining six simple and five complex cells which were lost prematurely, but we shall continue to refer to them as normal cells. This consequently yields a conservative estimate for the degree of abnormality in these cats. Again, no statistical difference between central and peripheral fields was noted ( $P > 0.2$  on a  $\chi^2$  test) since of 102 cells with central fields, 9 were normal (5 simple and 4 complex); and of 69 peripheral fields, 12 were normal (7 simple and 5 complex).

#### *Ocular dominance*

We tested 62 centrally located (<10° eccentricity), visually excitable cortical cells for ocular dominance. Figure 5 compares the ocular dominance of this sample of striate neurons from the deprived cats with equivalent data from normal adult striate cortex (40) and reveals no statistically significant differences ( $P > 0.2$  on a  $\chi^2$  test). However, considering the mappable striate neurons from the deprived cats ( $N = 49$ ) separately, we find that the ocular dominance does perhaps differ from normal ( $P < 0.05$  on a  $\chi^2$  test). The mappable cells tend to be monocularly activated and dominated by the contralateral eye. Our sample of striate neurons from the lid-sutured cats includes 13 unmappable single units which we were able to test for ocular dominance. These tended to be binocularly activated (11/13; 85%), and this pattern is not significantly different from normal ( $P > 0.2$  on a  $\chi^2$  test) but differs significantly from the mappable cells ( $P < 0.01$  on a  $\chi^2$  test). Thus, there appears to be a reduction in binocular activation among the mappable cells but not among the unmappable cells (see ref 4, 19, 20 for analogous conclusions).

Because units sharing the same ocular dominance are found clustered together (13, 15), a sampling bias may be introduced when each unit's ocular dominance is considered as an independent measure of ocular dominance. To avoid this bias, each electrode penetration was given an ocular dominance, which was determined by the first mappable unit tested. In 20 electrode penetrations in striate cortex of deprived cats, 40% (8/20) of the first mappable cells were binocularly activated; in 21 tracks in normal striate cortex, 76% (16/21) of the first recorded cells were binocularly activated, again suggesting fewer binocularly driven cells among the mappable group ( $P < 0.05$  on a  $\chi^2$  test).

#### *Visual responsiveness*

For 47 visually excitable striate neurons in the lid-sutured cats, average-response histo-

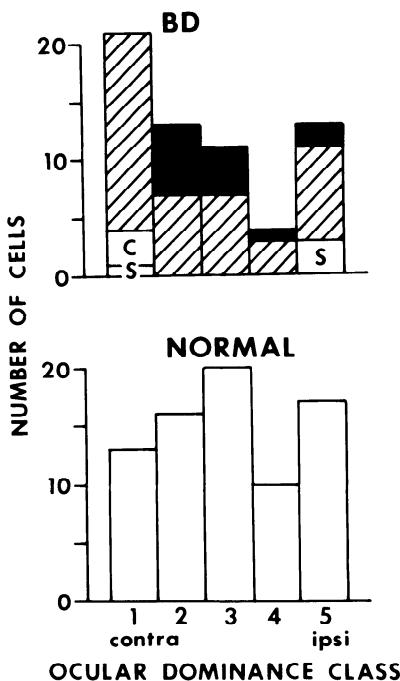


FIG. 5. Ocular-dominance distributions of samples of centrally located (less than 10° from area centralis), single units in the adult binocularly deprived (upper histogram) and normal adult striate cortex (lower histogram; data from ref 40). Ocular dominance was scored on a five-category scale as follows: 1) activated by stimulation of the contralateral eye only, 2) binocularly activated with stronger responses to stimulation of the contralateral eye, 3) binocularly activated about equally by stimulation of either eye, 4) binocularly activated with stronger responses to stimulation of the ipsilateral eye, 5) activated by stimulation of the ipsilateral eye alone. In the upper histogram, the ocular dominance distributions of mappable (hatched) and unmappable (black) cells are shown separately; not hatched among mappable cells but shown separately are the simple (S) and complex (C) cells. Note the reduction in the proportion of binocularly activated mappable cells compared either to the unmappable or normal cells.

grams were compiled using a slit of light varied in orientation, speed, and width in an effort to obtain the maximum visually evoked discharge rate. The five highest bins within each histogram were averaged to calculate the histogram's peak response rate, and the highest such response rate found among a cell's histograms was the cell's peak response. The same procedure was used to determine the peak response of 59 cells in normal striate cortex (40). Since the peak response did not differ significantly with different electrode types or visual-field locations, the data of Fig. 6 are pooled. While it is clearly not possible to be certain

of selecting the stimulus parameters appropriate to maximal activation, under reasonably matched experimental conditions two points emerge. First, the qualitative impression that unmappable cells are less responsive than normal is confirmed quantitatively ( $P < 0.001$  on a Mann-Whitney  $U$  test). Second, and perhaps more interestingly, the visual responsiveness of mappable cells in these deprived cats does not differ significantly ( $P > 0.2$  on a Mann-Whitney  $U$  test) from the responsiveness of normal striate cortical neurons (see Fig. 6).

#### Inhibitory receptive-field regions

Normal simple cells have receptive fields consisting of an excitatory zone with adjoining inhibitory or suppressive side bands (35). These side bands are seen as a stimulus-evoked reduction in maintained firing rate. Since these cells usually have low rates of spontaneous activity, it is difficult to assess suppressive side bands in this fashion without artificially elevating the

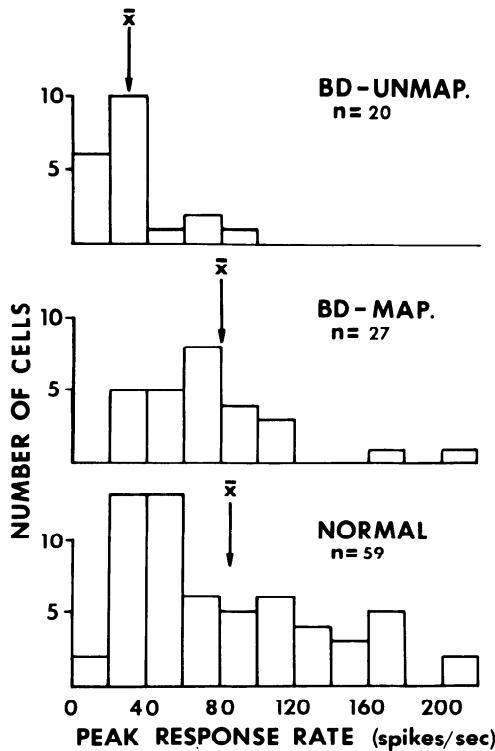


FIG. 6. Peak response rates to optimal visual stimuli of cells in striate cortex of binocularly sutured and normal cats (see text). The mean of each sample is indicated by an  $\bar{x}$  with a downward-pointing arrow. Shown separately for the deprived cats are the unmappable cells (top histogram) and the mappable cells (middle histogram). Note that visual responsiveness is reduced for unmappable cells, but normal for mappable cells.

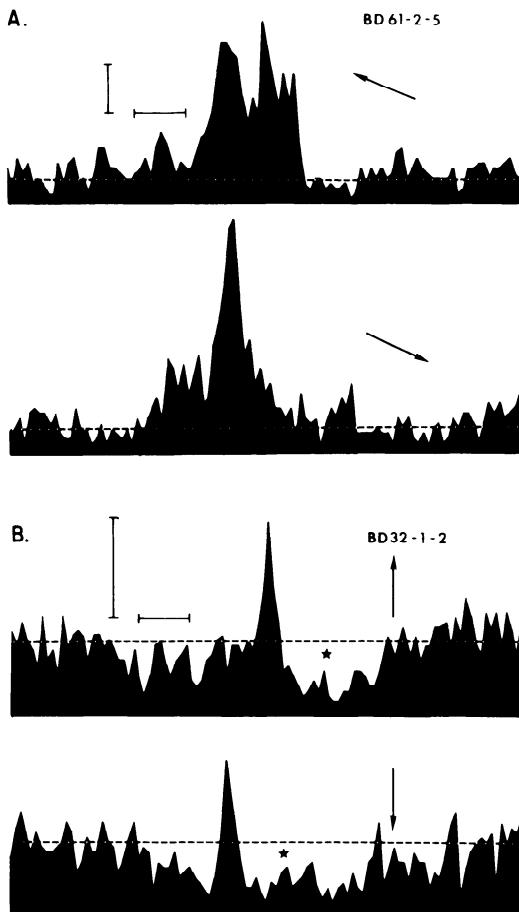


FIG. 7. Response histograms for two mappable cortical cells of the lid-sutured cats. Narrow slits were swept to and fro across the receptive field in the preferred stimulus orientation in the presence of a background discharge induced by K<sup>+</sup> iontophoresis (see APPENDIX). The mean background discharge rate in the absence of stimulation is indicated by the dashed line for each histogram. The horizontal and vertical scales for each histogram represent 2° of visual space and 50 spikes/s, respectively. A: cell with no detectable inhibitory zones. Each histogram represents a separate direction of stimulus motion (to or fro) as indicated by the arrows, and nowhere is the response clearly suppressed below the dashed line. B: cell with weak inhibitory zone indicated by stars; conventions as in A.

background firing rate. We thus applied a procedure to elevate these firing rates in 20 visually excitable cortical cells in the binocularly sutured cats (see APPENDIX for details and methodology). Of these cells, 14 showed no clear evidence of inhibitory receptive-field regions. The remaining six cells showed unusual types of inhibitory regions: that is, either very weak inhibitory areas or inhibition for only one direc-

tion of stimulus movement. In any case, the powerful, flanking inhibitory side bands typical of normal simple cells were missing from each of these 20 neurons. Figure 7 illustrates average response histograms from two of these cells.

On the other hand, most of the visually inexcitable cells seem to have strong, purely suppressive receptive fields. Of the seven such cells tested for this, six clearly responded with reduced firing to visual stimuli of all orientations and directions tested, and Fig. 8 shows average response histograms from a typical example. Although the sample is small, it seems clear that many cells in these cats which are visually inexcitable are, nonetheless, responsive to visual stimuli.

## DISCUSSION

These results indicate that continuous binocular lid suture throughout the first 10–24 mo of a cat's life results in very few normal simple and complex cells in the striate cortex. Instead, most cells could be placed into one of two other categories. The first, representing mappable cells, is characterized by abnormal receptive-field organization, but also by fairly limited field dimensions and normal response levels to visual stimulation. The second, represented by unmappable and visually inexcitable cells, had diffuse or undetectable receptive fields and weak or undetectable excitability to visual stimulation. We found no detectable difference in this pattern between central and peripheral receptive fields.

### Comparisons with other studies

Despite the numerous studies reporting the effects of binocular deprivation on developing kitten cortex, there exists some confusion about the effects of this deprivation on cortical neurons, perhaps due to slightly different rearing conditions and/or different classification schemes for cortical neurons. Careful inspection of the data, however, reveals few real discrepancies, and we shall cite two typical examples.

First, many studies indicate that binocular deprivation results in reduced responsiveness for cortical neurons, but percentages differ. For instance, we report that 80% of the cells are visually excitable. While this is in reasonable agreement with the findings of Wiesel and Hubel (39) (73% excitable), Pettigrew (22) (59% excitable), and Blakemore and Van Sluyters (4) (70–90% excitable), it seems at variance with the findings of Singer and Tretter (37) (33% excitable). However, these last authors defined as visually excitable only those "... which could be clearly demonstrated with hand-held stimuli and were vigorous enough to permit a receptive-

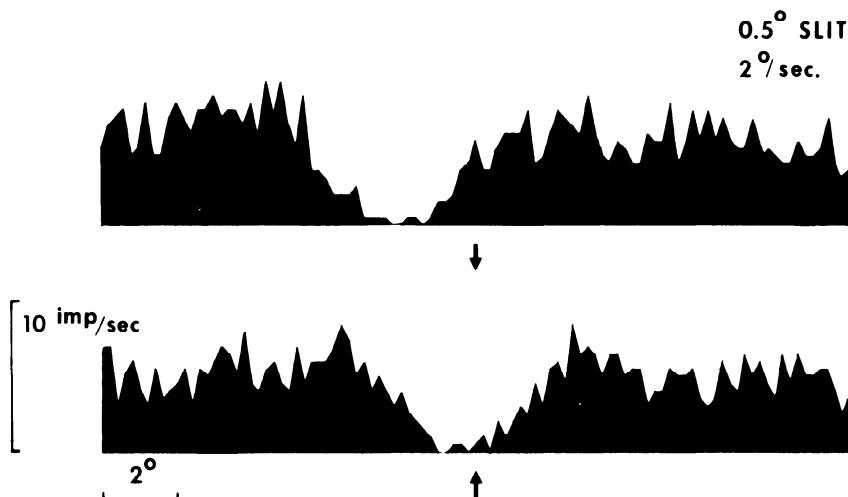


FIG. 8. Activity profiles for a visually inexcitable single unit in striate cortex of a deprived cat in response to a narrow slit ( $0.5^\circ$ ) swept slowly ( $2^\circ/\text{sec}$ ) and orthogonally across the receptive field in two directions (as indicated by arrows beneath the activity profiles). The horizontal and vertical scales represent  $2^\circ$  of visual angle and 10 impulses/s., respectively. An induced background discharge is created by  $\text{K}^+$  iontophoresis (see APPENDIX). Note the suppression of the cell's discharge in the absence of an excitatory response. This suppression was seen for all orientations tested.

field mapping'' (p. 616 of ref 37). Since we were able to hand map only 49% of our sample, this discrepancy seems more apparent than real, and they presumably classified as visually inexcitable many cells we describe as unmappable. Second, an analogous point can be made about cells with orientation selectivity. All reports indicate a reduction of these cortical cells following binocular deprivation, but not all percentages are similar. For instance, we found that 12% of our cortical neuronal sample were orientation selective, and this is not substantially different from data reported by Pettigrew (22) (6% orientation selective), Blakemore and Van Sluyters (4) (0–14% orientation selective), and Kratz and Spear (19) (21% orientation selective). Imbert and Buisseret (17) found no orientation-selective cells in their experiments, but they studied dark-reared cats, while the remainder of cited data are from cats reared with binocular lid suture. In contrast, Singer and Tretter (37) reported that 55% of their sample were orientation selective. Again, perhaps their criterion for orientation selectivity differed from ours, and this suggestion is supported by Fig. 1 of their paper. Here are illustrated two cells classified as orientation selective which, in fact, respond to all stimulus orientations, although they respond preferentially to a limited orientation range. These cells would be classified by us and Blakemore and Van Sluyters (4) as having an orientation bias. If such a difference in classification is present, then no discrepancy between

reports exists since our total of orientation-selective plus bias cells is roughly 48% (i.e., of those tested, 73% of the mappable fields and 38% of the unmappable fields displayed at least orientation bias and, given the percentage of these field types in our overall population, we estimate that 48% of the cells display at least orientation bias). Because all normal simple and complex cells have true orientation selectivity, we emphasize that the appearance of only about 10–20% orientation selective cells after binocular suture represents a fundamental lack of this receptive-field characteristic.

#### Receptive-field organization

In normal cat striate cortex, nearly all receptive fields can be classified as simple or complex (7, 13, 15, 24, 40). Among other features, the simple fields are characterized by inhibitory or suppressive side bands flanking the discharge center, whereas complex fields exhibit no such inhibition (35). Despite the fact that simple fields normally constitute roughly two-thirds of the population, at least for fields located within about  $10^\circ$  of the area centralis, none of the visually excitable cortical cells in the binocularly deprived cats displayed strong inhibitory side bands. Since these side bands are thought to play a role in orientation selectivity (3, 6, 12, 38), their absence is consistent with the reduced orientation selectivity found in the deprived cats.

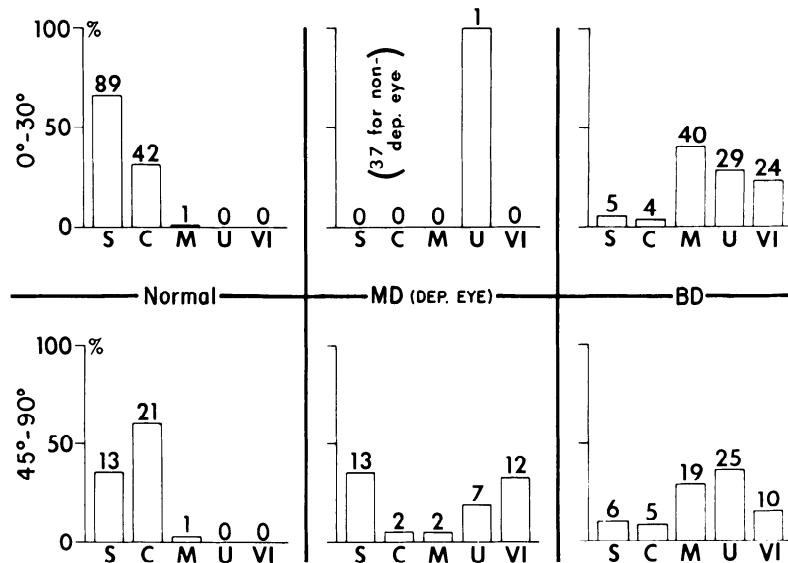


FIG. 9. Summary diagram showing frequency histograms of cell types in striate cortex for normal cats (left column; data from ref 40), monocularly deprived cats (middle column; data from ref 41), plus binocularly deprived cats (right column; data from present paper), and for binocular segment (top row; 0°-30° eccentricity of receptive fields) plus monocular segment (bottom row; 45°-90° eccentricity). The distribution of receptive-field eccentricities was similar among the three groups of cats. Cell types include simple (S), complex (C), mappable (M), unmappable (U), and visually inexcitable (VI). The number above each bar represents the sample size for each cell type in histograms. Data from the monocularly deprived cats include only cells driven by the deprived eye; as indicated in the binocular segment for comparison, 37 cells were driven exclusively by the nondeprived eye, and only one, by the deprived eye. In normal cats nearly all cells were classified as simple or complex, and the latter shifted from the minority to the majority of sampled cells as the electrode moved from the binocular to monocular segment. For monocularly sutured cats, the binocular segment had practically no cells driven by the deprived eye, whereas the monocular segment had many such cells; however, nearly all of the normal receptive-field types were classified as simple, and these included roughly the expected normal proportion. For binocularly sutured cats, there was no obvious difference in the pattern of cells between binocular and monocular segments, and few normal simple or complex cells were found anywhere. Note that the pattern of cell types found in the deprived monocular segments was quite different between monocularly and binocularly deprived cats.

### Comparison with neonate kittens

A loss of orientation selectivity among cortical cells in the adult cat binocularly sutured from birth could reflect: 1) a degradative process from the neonatal, visually inexperienced condition; and/or 2) an arrest of development. By neonate we mean a kitten younger than the beginning of the critical period (i.e., up to the 4th wk of life; cf. ref 16). Unfortunately, the presently available reports conflict concerning the status of orientation selectivity in the neonate kitten's striate cortex and we, consequently, cannot yet choose between these alternatives. Hubel and Wiesel (14) and Sherk and Stryker (26) report an almost normal adult degree of orientation selectivity in the neonate kitten, and this suggests the first alternative. On the other hand, Blakemore and Van Sluyters (4) and Pettigrew (22) report a degree of orientation selectivity in the neonate kitten quite similar

to that reported here for deprived cats, and this suggests the second alternative. Finally, the data of Buisseret and Imbert (5) support an intermediate level of orientation selectivity for the neonate kitten. At present, we can only conclude that the development and/or maintenance of orientation selectivity depends on appropriate visual experience.

### Comparison with monocularly sutured cats

Considerable evidence has now been accumulated that a form of competitive interaction between synapses related to each eye (i.e., binocular competition; see ref 33) controls much development in the geniculocortical pathways. This evidence derives mostly from studies of monocularly sutured cats in which deficits have been described for the lateral geniculate nucleus (10, 11, 34, 36), striate cortex (33, 41), and visual-orienting behavior (27, 28, 33). Generally, these deficits for the deprived eye

are maximal in the binocular segments (where pathways from the two eyes can interact and compete) and minimal in the monocular segments (where the deprived eye's pathways by definition cannot be at a disadvantage to those of the open eye).

If the same developmental mechanisms, including binocular competition, apply during binocular suture, then the deprived monocular segments in the lateral geniculate nucleus and striate cortex should be indistinguishable whether one or both eyes were sutured. This follows, because it would seem that neurons in these areas are equally deprived and equally free of binocular competitive interactions whether one or both eyes are sutured and, thus, they should develop in a similar fashion. Evidence from the lateral geniculate nucleus fails to support this prediction because in monocularly sutured cats, Y-cells driven by the deprived eye can be recorded in normal numbers only in the monocular segment, whereas in binocularly sutured cats, the monocular segments are as deficient in Y-cell numbers as are the binocular segments (34, 36). To the extent that the deprived monocular segments develop qualitatively differently after monocular and binocular suture, we must consider that different developmental mechanisms occur in the two forms of deprivation.

Analogous evidence of differences between monocular segments was found from the present study of striate cortex and is illustrated by Fig. 9 (data representing normal and monocularly deprived cats from ref 40, 41). After monocular suture, virtually no cells could be driven by the deprived eye in the binocular segment, but many could in the monocular segment. Of these in the monocular segment, there were the expected number of normal simple cells, abnormally few complex cells, and many cells with abnormal receptive fields (41). By contrast, the binocularly sutured cats exhibited no obvious difference between binocular and monocular segments ( $P > 0.2$  on a  $\chi^2$  test) since the cell distributions were the same, and few normal receptive fields were found anywhere. More important, the pattern of cell types seen in the monocular segments of monocularly deprived and binocularly deprived cats was quite different from one another ( $P < 0.001$  on a  $\chi^2$  test). In this regard, these cortical data are analogous to those from the lateral geniculate nucleus (34) and suggest the same conclusions. That is, the deprived monocular segments in monocularly and binocularly sutured cats appear to develop quite differently from one another.

As mentioned above, this tentative conclusion that the monocular segments differ with the different deprivation conditions at first seems

puzzling because it would seem that neurons here are exposed to the same environmental manipulations in all cats. This difference implies that different developmental mechanisms apply, at least for the monocular segments and probably throughout the geniculocortical pathways. We reiterate a previous suggestion based on behavioral data (32); that is, it may be that at least some pattern vision is needed to initiate the geniculocortical development seen in normal and monocularly sutured cats. This development is characterized by strong binocular competition within the binocular segment and relatively normal maturation in the deprived monocular segment which is spared the deleterious consequences of the competitive interactions (33). With no pattern vision, as during binocular lid suture, perhaps this specific development is never initiated and, in many ways, the geniculocortical pathways remain neonatal. Thus, the monocular segments do not mature as they do during monocular suture, and there may be no competitive interactions in the binocular segment. In fact, there is no evidence for significant binocular competition during binocular suture (however, see ref 19; it could be argued that the abnormally few binocular fields found among mappable cells in the present study reflect some binocular competition, although other explanations exist). Behavioral data support this notion of qualitatively different developmental mechanisms during monocular versus binocular suture. Normal and monocularly sutured cats clearly develop cortical pathways for visual orientation, since cortical lesions affect their orienting behavior (29, 30), but binocularly sutured cats do not seem to develop such pathways since cortical lesions do not affect their orienting behavior (31).<sup>3</sup> While there now exist considerable data to suggest that geniculocortical development occurs with different mechanisms during monocular and binocular suture, we are at a loss to suggest specifically why these mechanisms should be different (see also ref 32).

#### APPENDIX

Because we wished to study the inhibitory regions in the receptive fields of striate neurons in the binocularly sutured cats and because the activated discharge technique of Bishop's group (1)<sup>4</sup> proved

<sup>3</sup> However, it should be noted that cortical lesions do affect visual discrimination behavior after binocular lid suture (21).

<sup>4</sup> The activated discharge technique (also monocular or binocular conditioning) is used in the following manner. A second (conditioning) visual stimulus is moved randomly in the receptive field while the first (test) stimulus is also moved through the field. The

K9-1-2

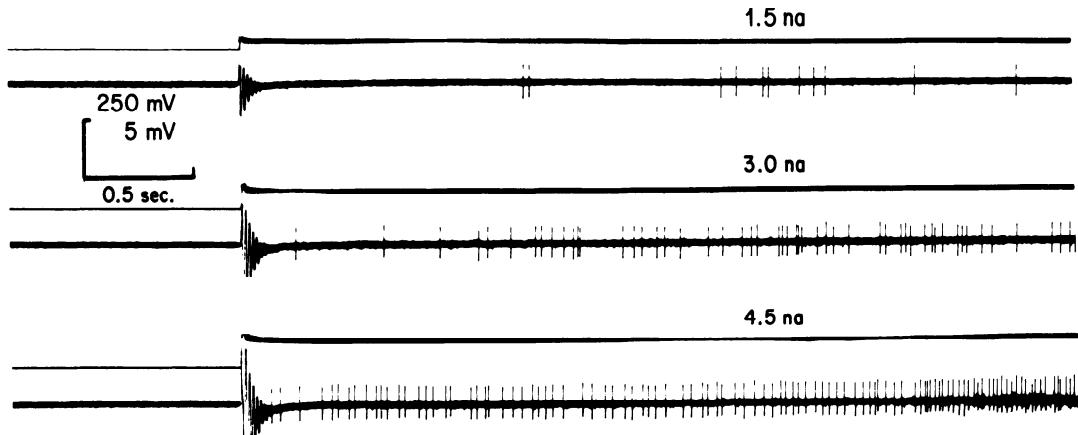


FIG. 10. Effect of  $K^+$  iontophoresis on the discharge of a single unit in cat striate cortex. The upper trace in each of the three records is a DC recording of the potential at the electrode; the lower trace is a standard (10-Hz to 10-kHz bandpass) single-unit recording. The artifact at the beginning of each lower trace is due to the mechanical switch closure used to inject current, and it thus marks the beginning of current injection. The upward deflection in the upper trace indicates the onset of a positive current. Three current levels are shown: 1.5, 3.0, and 4.5 nA. Greater currents produce higher discharge rates which begin at shorter latencies.

inadequate for the many weakly excitable cortical cells found in the deprived cats, we developed an alternative means for demonstrating inhibitory regions in the receptive field. The essence of the technique is the creation of a steady discharge rate by iontophoresis of potassium ions ( $K^+$ ) from the recording pipette. This steady discharge rate then serves as a background against which suppressive effects can be studied. Because such a procedure had unknown effects on the receptive-field organization, we felt that its validation on normal cat cortical cells, where the receptive-field organization of cells has been extensively studied, was necessary before applying the technique to the binocularly sutured cats. The following briefly describes these validating experiments performed on striate cortical cells in normal adult cats.

We mapped and classified receptive fields according to the criteria established by Hubel and Wiesel (13), Pettigrew et al. (23), and Sherman et al. (35). We tested many neurons, including a large number not studied for receptive-field properties, for their responses to iontophoresis of  $K^+$  from the recording electrode. Every well-isolated single cell responded to some level of positive current ( $K^+$  iontophoresis) with an increased discharge rate. The effect was always reversible and dose dependent. The amplitude of and latency to this increase in discharge rate

generally depended on the level of current applied; more current produced higher discharge rates, which were evident at shorter latencies. Figure 10 illustrates an example of these effects for one cortical cell.

Not only did  $K^+$  iontophoresis increase spontaneous activity, but it also increased the excitability of the cell to visual stimuli. On a few occasions, cells with relatively sluggish responses were transformed into briskly responding cells following the application of small positive currents. We also saw opposite effects with passage of negative current ( $Cl^-$  iontophoresis). In this case, cells with spontaneous activity had the level of such activity reduced or abolished, and occasionally receptive fields became difficult to map due to the cell's diminished responses. We made no systematic attempt to determine whether these effects of  $K^+$  and  $Cl^-$  iontophoresis are ion specific or whether they result from the electrotonic effects of current injection. However, in a few experiments with NaCl-filled micropipettes we were unable to obtain increased discharge rates with the injection of positive current at levels comparable to those used with KCl electrodes. The remainder of this APPENDIX deals solely with the effects of  $K^+$  iontophoresis.

Individual single neurons differed in the amount of current required to produce a particular discharge rate. For most cells, there was some low level of current (usually less than 5 nA) that failed to produce a detectable increase in spontaneous activity. There was, as well, some relatively high level of current at which most cells' discharge frequencies tended to accelerate and finally cease in a manner reminiscent of injury discharges. However, at cessation of even these high currents (occasionally up to 50 nA), the cell's action potential recovered in a few seconds. We always found an intermediate current level (generally 1–10 nA), which produced a discharge rate suitable for our study of suppressive side bands.

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, and movements of the test and conditioning stimuli are random and asynchronous with respect to one another. In monocular conditioning, the test and conditioning stimuli are presented to one eye; with binocular conditioning, each is presented to a separate eye.

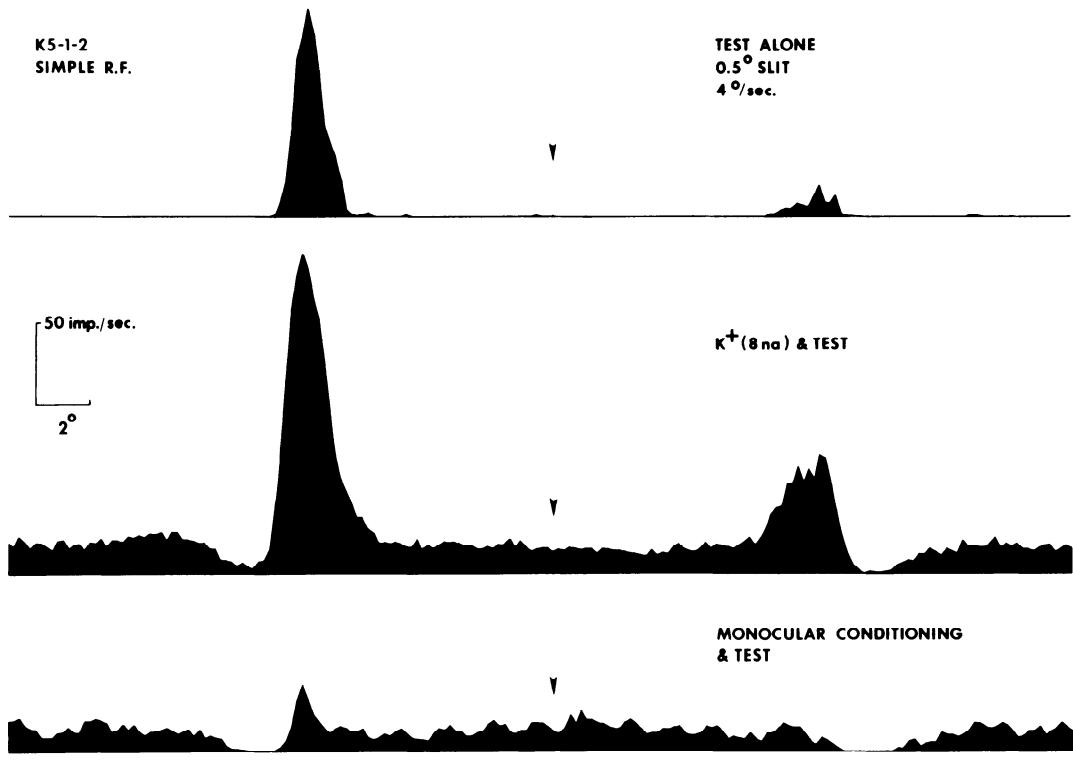


FIG. 11. Average response histograms from a simple cell in cat striate cortex. The test stimulus was, in each case, a slit of light ( $0.5^\circ$  wide) in the preferred orientation moved back and forth across the receptive field at  $4^\circ/\text{sec}$ . The vertical arrowheads above each histogram indicate the stimulus turnaround point. Arrows below histograms indicate the direction of stimulus movement. The unit's responses to the test stimulus alone are shown in the top histogram. The middle histogram shows responses to the test stimulus in combination with  $\text{K}^+$  iontophoresis. The bottom histogram shows responses to the test stimulus with monocular conditioning.

With such  $\text{K}^+$  iontophoresis we have examined the organization of excitatory and suppressive zones of 13 simple receptive fields, all located within about  $5^\circ$  of the area centralis. In five of these we also studied the receptive fields by the monocular-conditioning technique (1) so that results from the two techniques could be directly compared (see Fig. 11). The number and spatial location of excitatory and inhibitory zones were the same, regardless of which method was used, although the relative strength of the excitatory and suppressive influences seemed to depend slightly on the method employed. In general, monocular conditioning produced weaker excitation and stronger suppression. There are at least three possible explanations for this difference. 1) Suppression could occur as a result of intracortical inhibition, disinhibition of the lateral geniculate afferents, or both of the above (cf. ref 18). With monocular conditioning, the elevated spontaneous activity could be suppressed at many levels between retina and cortex. Assuming  $\text{K}^+$  iontophoresis excites essentially only cortical neurons (excitation of geniculate terminals is also possible), then the test stimulus can suppress the background firing level only in cortex. These factors, then,

would tend to create stronger suppressive influences for monocular conditioning than for  $\text{K}^+$  iontophoresis. 2) With monocular conditioning, the conditioning stimulus at times physically obscures the test stimulus, thus weakening the excitatory influence of the test stimulus; this does not occur with  $\text{K}^+$  iontophoresis, which thus would provide for more excitation than monocular conditioning. 3) In monocular conditioning, the background rate is achieved due to activity in retinal and geniculate neurons. Further excitation of these neurons by the test stimulus could be limited either by adaptation or neuronal refractory periods. With  $\text{K}^+$  iontophoresis, however, retinal and geniculate cells are primarily excited only by the test stimulus, and thus greater excitation could result with the test stimulus using the iontophoretic rather than the monocular conditioning technique.

The occurrence and spatial extent of suppressive side bands in the 13 simple cells studied with  $\text{K}^+$  iontophoresis were in good agreement with previously published data (1). All of the 13 simple cells had clear suppressive side bands in their receptive fields. Of these, 11 had one discharge peak to the test slit (unimodal in the terminology of ref 23), and 9 of these 11 had suppressive side bands flank-

ing both sides of the discharge zone. In these nine receptive fields, the larger side band averaged 2.5° (range: 1.1°–3.3°) across, while the smaller one averaged 1.1° (range: 0.4°–1.9°) across. One simple cell was also tested with the slit oriented perpendicular to the preferred orientation, and this produced a purely suppressive zone 3.3° across and centered on the discharge zone. Two of the unimodal simple cells each had only one suppressive side band flanking the discharge zone, and an example is shown in Fig. 11. Bishop et al. (1) reported that all of their sample of 18 simple cells had suppressive side bands flanking both sides of the discharge center. Our use of somewhat wider test stimuli (0.5° compared to their 0.29°) and wider histogram bins (0.2° compared to their 0.07°) may have caused us to miss the smallest suppressive zones, which are reported to be as small as 0.2° (cf. ref 1). However, Innocenti and Fiore (18) have recently reported striate neurons with suppressive side bands flanking the discharge zone on only one side.

In conclusion, we suggest that the present technique of K<sup>+</sup> iontophoresis for revealing suppressive zones of visual receptive fields offers certain advantages over previous techniques of monocular or binocular conditioning (1): 1) K<sup>+</sup> iontophoresis eliminates the need for a second visual conditioning stimulus, which must be kept moving asynchronously with the test stimulus. 2) With monocular conditioning a complication results from the physical interaction of the visual stimuli, which means that the test stimulus is not always of equal contrast. This sometimes causes certain (usually excitatory) portions of

the receptive field to be obscured. For example, in Fig. 11 the discharge peak seen in the right half of the histogram for the test stimulus alone is preserved with K<sup>+</sup> iontophoresis but obscured with monocular conditioning. 3) To test receptive fields for each eye with binocular conditioning requires that the cell be excited strongly from each eye. Even monocular conditioning requires a fairly responsive field for one eye and, in many experimental preparations (e.g., visually deprived cats), this may not occur. K<sup>+</sup> iontophoresis can be done on a neuron which lacks a strong excitatory component in the receptive field. 4) K<sup>+</sup> iontophoresis is not influenced by adaptation or potentially limited firing rates of retinal or lateral geniculate neurons. 5) Finally, because K<sup>+</sup> iontophoresis produces a relatively constant background discharge rate, whereas monocular or binocular conditioning typically produces repeated bursts of neuronal firing, satisfactory average response histograms can be achieved in a shorter time with the iontophoretic method. We have found the method to be applicable to single units of all receptive-field types found in striate cortex and suggest that it might find more general use in other parts of the brain.

#### ACKNOWLEDGMENTS

This research was supported by Grants EY 01565 and EY 01492 and Research Career Development Award EY 00020 to S. M. Sherman from the Public Health Service.

#### REFERENCES

- BISHOP, P. O., COOMBS, J. S., AND HENRY, G. H. Receptive fields of simple cells in the cat striate cortex. *J. Physiol., London* 231: 31–60, 1973.
- BISHOP, P. O., KOZAK, W., AND VAKKUR, G. J. Some quantitative aspects of the cat's eye: axis and plane of reference, visual field coordinates and optics. *J. Physiol., London* 163: 466–502, 1962.
- BLAKEMORE, C. AND TOBIN, E. A. Lateral inhibition between orientation detectors in the cat's visual cortex. *Exptl. Brain Res.* 14: 439–440, 1972.
- BLAKEMORE, C. AND VAN SLUYTERS, R. C. Innate and environmental factors in the development of the kitten's visual cortex. *J. Physiol., London* 248: 663–716, 1975.
- BUISSET, P. AND IMBERT, M. Visual cortical cells: their developmental properties in normal and dark reared kittens. *J. Physiol., London* 255: 511–525, 1976.
- CREUTZFELDT, O. D., KUHNT, U., AND BENEVENTO, L. A. An intracellular analysis of visual cortical neurones to moving stimuli: response in a co-operative neuronal network. *Exptl. Brain Res.* 21: 251–274, 1974.
- DREHER, B. Hypercomplex cells in the cat's striate cortex. *Invest. Ophthalmol.* 11: 355–356, 1972.
- FERNALD, R. AND CHASE, R. An improved method for plotting retinal landmarks and focusing the eyes. *Vision Res.* 11: 95–96, 1971.
- GROBSTEIN, P. AND CHOW, K. L. Receptive field development and individual experience. *Science* 190: 352–358, 1975.
- GUILLERY, R. W. Binocular competition in the control of geniculate cell growth. *J. Comp. Neurol.* 144: 117–130, 1972.
- GUILLERY, R. W. AND STELZNER, D. J. The differential effects of unilateral lid closure upon the monocular and binocular segments of the dorsal lateral geniculate nucleus of the cat. *J. Comp. Neurol.* 139: 413–422, 1970.
- HENRY, G. H., DREHER, B., AND BISHOP, P. O. Orientation specificity of cells in cat striate cortex. *J. Neurophysiol.* 37: 1394–1409, 1974.
- HUBEL, D. H. AND WIESEL, T. N. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol., London* 160: 106–154, 1962.
- HUBEL, D. H. AND WIESEL, T. N. Receptive fields of cells in striate cortex of very young, visually inexperienced kittens. *J. Neurophysiol.* 26: 994–1002, 1963.
- HUBEL, D. H. AND WIESEL, T. N. Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of cat. *J. Neurophysiol.* 28: 229–289, 1965.
- HUBEL, D. H. AND WIESEL, T. N. The period of susceptibility to the physiological effects of unilateral eye closure in kittens. *J. Physiol., London* 206: 419–436, 1970.
- IMBERT, M. AND BUISSERET, P. Receptive field

- characteristics and plastic properties of visual cortical cells in kittens reared with or without visual experience. *Exptl. Brain Res.* 22: 25-36, 1975.
18. INNOCENTI, G. M. AND FIORE, L. Post-synaptic inhibitory components of the responses to moving stimuli in area 17. *Brain Res.* 80: 122-126, 1974.
  19. KRATZ, K. E. AND SPEAR, P. D. Effects of visual deprivation and alterations in binocular competition on responses of striate cortex neurons in the cat. *J. Comp. Neurol.* 170: 141-152, 1976.
  20. LEVENTHAL, A. G. AND HIRSCH, H. V. B. Effects of early experience upon orientation sensitivity and binocularity of neurons in visual cortex of cats. *Proc. Natl. Acad. Sci. U.S.* 74: 1272-1276, 1977.
  21. LOOP, M. S. AND SHERMAN, S. M. The effect of cortical lesions upon visual discriminations in binocularly deprived cats. *J. Comp. Neurol.* 174: 89-94, 1977.
  22. PETTIGREW, J. D. The effect of visual experience on the development of stimulus specificity by kitten cortical neurones. *J. Physiol., London* 237: 49-74, 1974.
  23. PETTIGREW, J. D., NIKARA, T., AND BISHOP, P. O. Responses to moving slits by single units in cat striate cortex. *Exptl. Brain Res.* 6: 373-390, 1968.
  24. ROSE, D. The hypercomplex cell classification in the cat's striate cortex. *J. Physiol., London* 242: 123-125P, 1974.
  25. SANDERSON, K. J. AND SHERMAN, S. M. Naso-temporal overlap in visual field projected to lateral geniculate nucleus in the cat. *J. Neurophysiol.* 34: 453-466, 1971.
  26. SHERK, H. AND STRYKER, M. P. Quantitative study of cortical orientation selectivity in visually inexperienced kitten. *J. Neurophysiol.* 39: 63-70, 1976.
  27. SHERMAN, S. M. Visual field defects in monocularly deprived cats. *Brain Res.* 49: 25-45, 1973.
  28. SHERMAN, S. M. Permanence of visual perimetry deficits in monocularly and binocularly deprived cats. *Brain Res.* 73: 491-501, 1974.
  29. SHERMAN, S. M. Monocularly deprived cats: improvement of the deprived eye's vision by visual decortication. *Science* 186: 267-269, 1974.
  30. SHERMAN, S. M. The effect of superior colliculus lesions upon the visual fields of cats with cortical ablations. *J. Comp. Neurol.* 172: 211-230, 1977.
  31. SHERMAN, S. M. The effect of cortical and tectal lesions on the visual fields of binocularly deprived cats. *J. Comp. Neurol.* 172: 231-246, 1977.
  32. SHERMAN, S. M. AND GUILLERY, R. W. Behavioral studies of binocular competition in cats. *Vision Res.* 16: 1479-1481, 1976.
  33. SHERMAN, S. M., GUILLERY, R. W., KAAS, J. H., AND SANDERSON, K. J. Behavioral, electrophysiological and morphological studies of binocular competition in the development of the geniculocortical pathways of cats. *J. Comp. Neurol.* 158: 1-18, 1974.
  34. SHERMAN, S. M., HOFFMANN, K.-P., AND STONE, J. Loss of a specific cell type from dorsal lateral geniculate nucleus in visually deprived cats. *J. Neurophysiol.* 35: 532-541, 1972.
  35. SHERMAN, S. M., WATKINS, D. W., AND WILSON, J. R. Further differences in receptive field properties of simple and complex cells in cat striate cortex. *Vision Res.* 16: 919-927, 1976.
  36. SHERMAN, S. M., WILSON, J. R., AND GUILLERY, R. W. Evidence that binocular competition affects the postnatal development of Y-cells in the cat's lateral geniculate nucleus. *Brain Res.* 100: 441-444, 1975.
  37. SINGER, W. AND TRETTER, F. Receptive-field properties and neuronal connectivity in striate and parastriate cortex of contour-deprived cats. *J. Neurophysiol.* 39: 613-630, 1976.
  38. WATKINS, D. W. AND BERKLEY, M. A. The orientation selectivity of single neurons in cat striate cortex. *Exptl. Brain Res.* 10: 433-466, 1974.
  39. WIESEL, T. N. AND HUBEL, D. H. Comparison of the effects of unilateral and bilateral eye closure on cortical unit responses in kittens. *J. Neurophysiol.* 28: 1029-1040, 1965.
  40. WILSON, J. R. AND SHERMAN, S. M. Receptive-field characteristics of neurons in cat striate cortex: changes with visual field eccentricity. *J. Neurophysiol.* 39: 512-533, 1976.
  41. WILSON, J. R. AND SHERMAN, S. M. Differential effects of early monocular deprivation on binocular and monocular segments of cat striate cortex. *J. Neurophysiol.* 40: 892-903, 1977.