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CONDITIONS FOR DOMINANCE OF ONE EYE DURING COMPETITIVE DEVELOPMENT OF CENTRAL CONNECTIONS IN VISUALLY DEPRIVED CATS

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SUMMARY

Three groups of visually deprived cats were studied for evidence that one eye gained a competitive advantage over the other during development of central connections. We attempted to detect such an advantage by measuring lateral geniculate cell sizes, by recording the proportion of lateral geniculate Y-cells and the ocular dominance of cortical neurons, and/or by testing visual orienting behavior. Three cats were raised with one eye covered by the lids, and the other, by the nictitating membrane. Lids reduce illumination by 3–4 log units, nictitating membranes, by about one log unit, and both eliminate spatial patterns. Neither eye in these cats appeared to develop with a competitive advantage over the other. Four cats raised with monocular nictitating membrane closure developed with a clear advantage to the open eye, and in all ways data from these cats were indistinguishable from those previously reported for monocularly lid sutured cats. Finally, 4 cats reared with binocular lid closure, but with additional, temporally modulated stimulation through the right lids, showed no evidence of a competitive advantage to either eye. We conclude that interocular differences in light intensity or temporal patterns do not confer a significant competitive advantage to either eye during development of central connections.

INTRODUCTION

Cats raised with monocular eyelid closure develop obvious abnormalities in their central visual pathways. For example, in laminae of the lateral geniculate nucleus receiving afferents from the sutured eye, the cells are abnormally small[4,17]. Also, few Y-cells can be recorded with microelectrodes in these laminae, although the X-cell population seems unaffected[14]. Striate cortical cells, instead of showing their normal pattern of binocular receptive fields, tend to be influenced exclusively by the non-

deprived eye in these cats[18]. In the geniculocortical pathways, these deficits are largely limited to the binocular segment*. That is, the deprived monocular segment of the lateral geniculate nucleus has cells of nearly normal size[4,5] as well as the normal ratio of Y-cells[14,16], and the deprived eye influences many neurons in the deprived monocular segment of striate cortex[13,21]. This binocular/monocular segment difference in deprived cats has a behavioral correlate: with the deprived eye, these cats can orient to visual stimulation in the monocular, but not the binocular, segment of visual field[11,12].

These data support the notion that binocular competition among central synapses related to the two eyes plays a major role in visual development[4,13,19]. Where binocular interactions can occur (i.e. in the binocular segment), synapses related to the open eye have a competitive advantage and develop dominance at the expense of the 'deprived' synapses. Where these interactions cannot occur (i.e. in the monocular segments), the 'deprived' synapses suffer no such competitive disadvantage, and in many cases they develop relatively normally.

While considerable evidence supports the existence of this binocular competition (cf. refs. 3, 13), little is known concerning the details of this process. This paper represents an attempt to define some aspects of the early environment that permit one eye to gain a competitive developmental advantage over the other. For instance, the open eye has such an advantage over the closed eye, but the differences in the environment between eyes include different light intensities, differences in image quality (i.e. spatial patterns on the retina), local differences in the time-varying patterns of retinal stimulation as a spatial pattern is moved across the non-deprived retina, etc. In the present study, cats were raised with a variety of interocular differences, including those for spatial patterns, temporal patterns, and light intensity. They were then tested as adults for evidence of binocular competition. Our results suggest that interocular differences in spatial patterns, but not temporal patterns or light intensity, provide important advantages to one eye over the other in the competitive development of central connections (cf. ref. 1).

MATERIALS AND METHODS

Subjects and treatments

Eleven cats, born and reared in the laboratory, received one of the following 3 treatments (see Fig. 1). (1) Four kittens (RN1, RN2, LN1, RN3) each had the nictitating membrane sutured across one cornea at 5–10 days of age, and complete coverage of the cornea was carefully monitored until the cats were studied as adults. This essentially eliminated pattern vision to one retina and reduced the light intensity by only about 1 log unit (see below). (2) Three kittens (RL/LN1, RL/LN2, LL/RN2) at 8–10 days of age had the lids of one eye closed and the nictitating membrane of the

* The binocular portion 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 refs. 4, 14).

other eye sutured across the cornea as above. Again, these closures were carefully monitored until the cats were studied as adults. Since the lids also eliminate pattern vision and attenuate light by about 3–4 log units, the lid sutured eye received over 2 log units less illumination than did the eye occluded by the nictitating membrane (see below and also refs. 2, 8, 17). (3) The final 4 kittens (B1, B2, B3, B4) had the lids of both eyes sutured at 5–10 days of age. From postnatal weeks 3–22, each received 0.5 h/day (B1, B2, B3) or 2 h/day (B4), 4–6 days per week, of extra stimulation to the right eye through the closed lids via a fiber optic system. They thus received 44–188 h of extra stimulation to one eye. During this stimulation period, each kitten was restrained in a sling and headholder, and it was closely monitored. The stimulation consisted of light which was 3 log units above background intensity and was square-wave modulated from 1 to 60 Hz in a pseudo-random fashion. This last treatment was designed to stimulate retinal ganglion cells in the right eye which might respond poorly or not at all to the small time-varying changes of illumination normally experienced in a lid sutured eye. Also, the difference in intensity striking the two corneas under these conditions roughly equalled that for a monocularly sutured cat.

We estimated the amount of light attenuated by the lids and nictitating membranes by means of photometry. The techniques are described in detail elsewhere[8] and will be briefly outlined here. Readings from a photometer were made before and after a freshly excised lid or nictitating membrane was placed over the photometer's probe. Light sources at various wavelengths were used, and the attenuation values were fairly constant throughout the cat's visible spectrum. For 9 adult cats (including several in this experiment at the time of their sacrifice), the eyelids consistently attenuated 3–4 log units of light, and the nictitating membranes, 1–1.5 log units. For individual cats, the lids attenuated $>$ 2 log units more light than did the nictitating membrane (see also refs. 2, 17). Since the critical period for deprivation occurs during the 2nd and 3rd postnatal month[7], we also carried out these measurements on 5 kittens ranging in age from 5 to 14 weeks (cf. ref. 8). The lid and nictitating membrane densities were somewhat reduced in these kittens compared to adults, but still the nictitating membranes transmitted about 2 log units more light than did the eyelids.

Data collection

Anatomical, electrophysiological and/or behavioral techniques were used in these cats to assess whether or not one eye developed central connection at the expense of the other. For each of the experimental groups and for most individual cats, at least two different methods of assessment were employed (see Fig. 1).

Anatomical methods

For each cat except RN2 and LN1, the cross-sectional areas of 100 cells in the dorsal lateral geniculate nucleus were measured, and our previously described techniques were used[15]. The cats were perfused with saline followed by 10% formol–saline. The brains were stereotaxically blocked, removed, embedded in celloidin or egg yolk (the latter for frozen sectioning), and cut coronally into 40 μm sections. The sections were stained with cresylecht violet. Twenty-five cells per cat were measured from each

of 4 zones: laminae A and A_1 from matched portions of the binocular segment in each hemisphere. Interhemispheric differences in size for cells of lamina A or A_1 would be taken as evidence for a competitive advantage of one eye over the other. The cell outlines were drawn at 1000 × with a microscope drawing tube attachment, and cross-sectional areas were measured with a planimeter. Only neurons with visible nucleoli were selected, and care was taken to sample an unbiased representation of available cells (see ref. 15).

Electrophysiological techniques

We used varnished, tungsten microelectrodes (10–20 mΩ at 500 Hz) to record extracellular activity from the lateral geniculate nucleus (RN1, RN2, LN1, RN3, B1) or striate cortex (B2, B4). Our recording techniques and methods of receptive field analysis have been described in detail previously[6,20]. The cats were anesthetized, paralyzed, and artifically ventilated, with end-tidal CO_2 kept near 4%. Their retinae were made conjugate with a frontal tangent screen (for receptive field plots) by means of contact lenses chosen by retinoscopy. Stimulating electrodes were placed in the optic chiasm for the lateral geniculate experiments. Lateral geniculate neurons were classified as X-cells or Y-cells on the basis of their receptive field properties and response latency to optic chiasm stimulation[6]. For cortical cells, we concentrated on ocular dominance and placed each cell into one of 3 categories: (1) driven exclusively or nearly so by the right eye; (2) driven binocularly; (3) driven exclusively or nearly so by the left eye. Either a difference in the ratio of geniculate Y-cells driven by each eye, or a tendency for the cortical cells to be dominated by one eye, would be taken as evidence of a competitive advantage to one eye during development.

Behavior

We measured the extent of the binocular and monocular fields using a test for visually guided orienting behavior that has previously been described in detail[11,12]. Briefly, monocular fields were measured with one eye occluded by an opaque contact lens. The cat fixated on the visual and auditory cues of one object while a second visual stimulus was introduced into a limited portion of the visual field. Every 15° sector of the horizontal extent of visual field was repeatedly tested, and the cat's orientation or lack of orientation to the second stimulus determined the extent of functional visual field. Each 15° sector was tested at least 50 times, and a response level (% orientations) to each was determined. As a control, these response levels were compared to a baseline of 'spontaneous' orientations in the absence of the second stimulus. These spontaneous response levels were 3–14% in this study, and were measured from > 100 such control trials for each cat during monocular and binocular viewing. After determining this spontaneous level for every cat during each viewing condition, the response levels for a given sector of the visual field were normalized by the formula: (% orientation to stimulus — % spontaneous orientations) divided by (100% — % spontaneous orientations). In other words, since the cat appears to spontaneously search for an absent novel stimulus at a measurable rate, we consider as functional visual field only regions in which the stimulus evoked response level is

higher than this spontaneous orienting level. A difference between the eyes either in responsiveness or the extent of functional visual field would be taken as evidence of a competitive advantage of one eye over the other during development.

RESULTS

Although there were a variety of experimental conditions in this study, with two exceptions noted below, the results consistently support the conclusion that light intensity and temporal patterns of stimulation are less important for binocular competition than are spatial patterns. These results are organized below in terms of the anatomical, electrophysiological and behavioral methods used to assess binocular competition.

Anatomy

Fig. 2 illustrates the geniculate cell size measurements for 9 of the cats in this study (cf. Fig. 1). Also shown are similar measurements from 4 monocularly lid sutured cats which received no further special treatment (Sherman and Wilson, unpublished; Fig. 2A). Geniculate cell sizes in cats raised with monocular nictitating membrane closure (Fig. 2B) closely match those in cats raised with monocular lid closure (Fig. 2A), and the proportions of deprived to non-deprived cell sizes are fairly close in both deprivation conditions (62.4% for lid suture and 69.9% for nictitating membrane suture). In two of the cats raised with one lid and one nictitating membrane closed (RL/LN1 and LL/RN1 in Fig. 2C), there was no evidence that cells related to

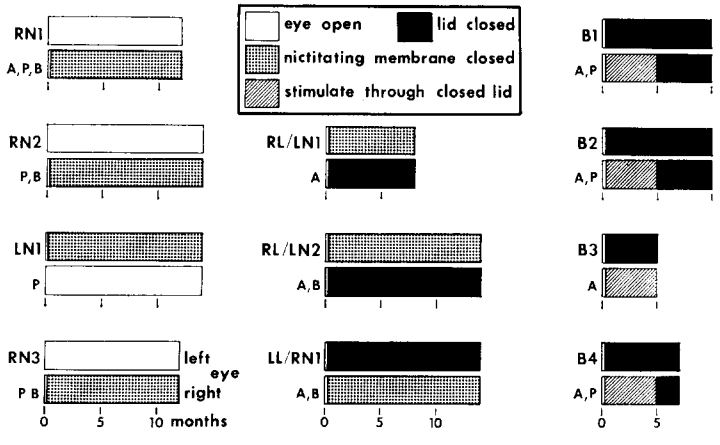

Fig. 1. Charts showing the experimental design for the 11 cats of this study. For each cat, a chart shows the deprivation conditions up to the time of the terminal experiments in adulthood. Also indicated for each cat are the types of experiments carried out: anatomical (A; lateral geniculate cell size measurements), physiological (P; lateral geniculate Y-cell ratios or cortical ocular dominance patterns), and/or behavioral (B; visual orienting). On the left are shown the 4 cats raised with one eye open and the other eye covered by the nictitating membrane. In the center are shown 3 cats raised with one eye covered by the eyelids and the other, by the nictitating membrane. On the right are shown 4 cats raised with binocular lid closure but with extra photic stimulation delivered through the right eyelids. The key, which indicates the various ocular conditions in this figure, also applies to Figs. 2–5.

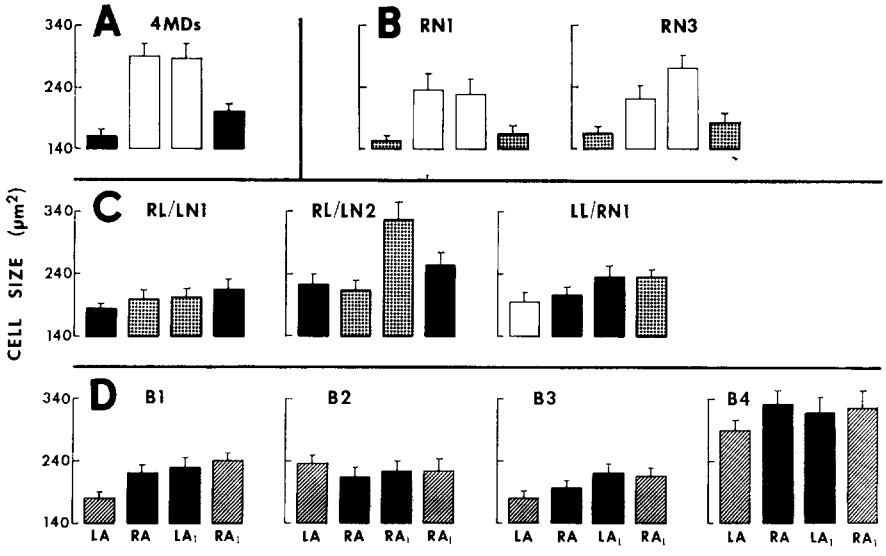

Fig. 2. Measurements of cell size from laminae A and A_1 of the lateral geniculate nucleus. Each graph shows the mean plus one standard error for cell areas in matched portions of left lamina A (LA), right lamina A (RA), left lamina A_1 (LA_1), and right lamina A_1 (RA_1). The bars are shaded in accordance with the key in Fig. 1. Each bar represents a sample of 25 neurons except the bars in A, each of which represents 200 neurons. A: cell sizes from monocularly lid sutured cats (data from Sherman and Wilson, unpublished). B: cell sizes from cats RN1 and RN3. C: cell sizes from cats RL/LN1, RL/LN2, and LL/RN1. D: cell sizes from cats B1, B2, B3, and B4.

one eye grew larger than those related to the other eye. In the third cat of this group (RL/LN2) there was no interhemispheric difference for cells in lamina A, but inexplicably the lamina A_1 cells related to the nictitating membrane sutured eye were somewhat larger than those related to the lid sutured eye ($0.05>P>0.02$ on a t-test). Unfortunately no prior electrophysiological or behavioral data were available for this cat. We cannot explain this difference for the A_1 laminae in only one cat, but taken as a whole, the data in Fig. 2C support the conclusion that the growth of geniculate cells related to either eye is equally affected. Finally, Fig. 2D shows that the 4 cats raised with binocular lid suture but extra photic stimulation through the right eyelids demonstrate no interhemispheric asymmetry in geniculate cell growth.

Electrophysiology

Lateral geniculate nucleus. Fig. 3 summarizes the data from single cell analysis of geniculate X- and Y-cells. On the left are shown previously published data[14] indicating the percentage of Y-cells located electrophysiologically in monocularly lid sutured cats. Rearing with monocular lid suture greatly reduces the ratio of Y-cells innervated from the sutured eye, presumably because of imbalanced binocular competition during development[14,16]. Cat B1, raised with binocular lid suture and extra photic stimulation through the right lid, had a fairly equal percentage of geniculate Y-cells driven for each eye, so there was no evidence of a competitive advantage for the right eye. The remaining 4 cats all had nictitating membrane closures over one eye. Of these,

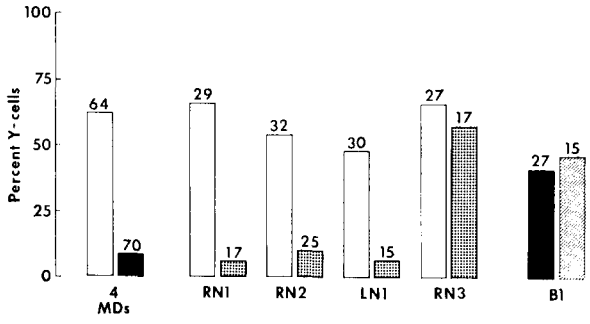

Fig. 3. Percentage of Y-cells recorded in laminae A and A_1 of the lateral geniculate nucleus; only X- and Y-cells are considered in this figure, and only cells from laminae A and A_1 were sampled. The shading for each bar is derived from the key in Fig. 1 (e.g. for RN1, the open bar represents cells driven by the open eye and the dot-filled bar represents cells driven by the eye covered with the nictitating membrane, etc.). The number above each bar indicates the total number of cells from which each percentage is derived. Percentages are shown from 4 monocularly lid sutured cats (data from ref. 14), from cats RN1, RN2, LN1, RN3, and from cat B1.

the pattern of recordable Y-cells for cats RN1, RN2, and LN1 closely matches the pattern seen for monocularly lid sutured cats. From these data, it would appear that nictitating membrane closure has as large an effect on the competitive development of Y-cells as does lid closure. On the other hand, the ratio of geniculate Y-cells was roughly equal for both eyes of cat RN3. The anatomical and behavioral data from this cat (Figs. 2B, 5D) were indistinguishable from those seen in monocularly lid sutured cats (Figs. 2A, 5B), and we cannot explain the high proportion of geniculate Y-cells found for its deprived eye.

Striate cortex. The ocular dominance of single striate cortex neurons was determined for cats B2 and B4 by recording from the right hemispheres. Fig. 4A summarizes these data, and they are consistent with the geniculate Y-cell proportions above for another cat of this series (B1). Analogous data are shown in Fig. 4 for binocularly sutured cats (Watkins, Wilson and Sherman, unpublished data; see also ref. 19). The

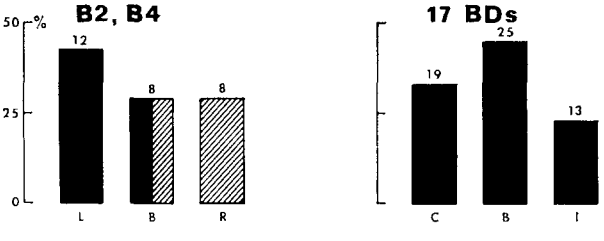

Fig. 4. Ocular dominance distributions for neurons in striate cortex of cats B2 and B4; for comparison are shown similar distributions from 17 cats reared with binocular lid suture and no further special treatment (Watkins, Wilson, and Sherman, unpublished). All receptive fields were within 20° of the visual axis, and samples from cats B2 and B4 were taken from the right cortex. Cells were placed into one of three categories (see text): (1) driven exclusively or nearly so by the left (L) or contralateral (C) eye; (2) driven binocularly (B); and (3) driven exclusively or nearly so by the right (R) or ipsilateral (I) eye. The numbers above each bar represent the number of cells in each group, and the shading of the bars corresponds to the key in Fig. 1. The ocular dominance distributions of cats B2 and B4 (left half) are indistinguishable from that of the binocular lid sutured cats (right half; $P > 0.10$ on a χ^2-test).

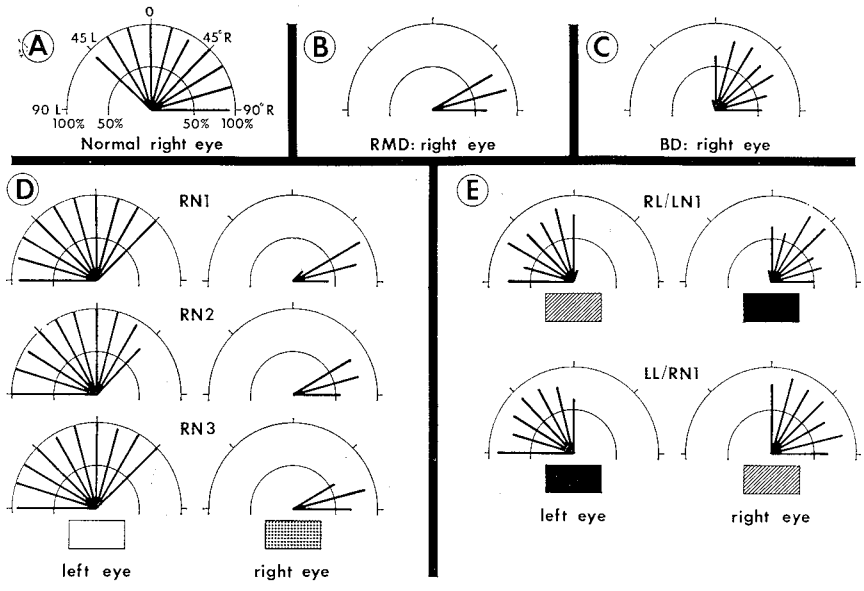

Fig. 5. Visual fields mapped during monocular testing of various cats. The visual fields are represented by polar plots which show the normalized response level in every horizontal 15° sector of visual field (see text). The outer semicircle represents the 100% response level; and the inner circle, the 50% level. A, B, and C are drawn from previously published data[11,12], and the keys in D and E are the same as in Fig. 1. A: monocular (right eye) field for a normally reared cat or for the open eye of a monocularly lid sutured cat. Normal monocular vision thus extends from 90° ipsilateral to 45° contralateral to the open eye. B: field for the right eye of a right-monocularly lid sutured cat. Functional vision here appears to be essentially limited to the monocular segment. C: field for the right eye of a binocularly lid sutured cat. Here vision appears limited to the ipsilateral 90° of visual field. D: fields for cats RN1, RN2, and RN3. These fields are in all ways identical to fields for monocularly lid sutured cats[11,12]. E: fields for cats RL/LN1 and LL/RN1. In each cat the fields and response levels appeared equal for either eye, and in all ways these fields were indistinguishable from those of binocularly lid sutured cats[11,12].

ocular dominance patterns of cats B2 and B4 seem to correspond to cats reared with the eyelids of both eyes sutured and no further special treatment, but due to technical difficulties only a small cell sample was available from B2 and B4. With this reservation, it appears that, for binocularly lid sutured cats, extra photic stimulation to the right eye did not provide a competitive advantage to that eye over the left eye.

Behavior. Fig. 5 summarizes the results of the visual field testing, and Fig. 5A–C show previously published data for typical monocular fields for a normal or non-deprived eye, the deprived eye of a monocularly lid sutured cat, and a binocularly lid sutured cat[11,12]. As Fig. 5D illustrates, the monocular visual orienting behavior of cats raised with monocular nictitating membrane closure is indistinguishable from that of cats raised with monocular lid suture. Consistent with this, Fig. 5E shows that the fields of cats raised with one eye closed by lid suture and the other closed by nictitating membrane suture are indistinguishable from those of cats raised with binocular lid closure; we also detected no interocular difference in the accuracy or vigor of the responses for these cats. Again, we conclude that nictitating membrane closure is equivalent to lid closure in terms of development of the central visual pathways.

DISCUSSION

These results generally support the following two conclusions. First, although the nictitating membrane passes approximately 2 log units more light than does the eyelid, covering the eye by either structure produces equally serious visual deprivation during postnatal development of the central visual pathways. This conclusion is drawn both from comparing the effects of monocular nictitating membrane closure (cats RN1, RN2, LN1, RN3) with those of monocular eyelid closure* and also from a lack of an evident competitive advantage during development to a nictitating membrane closed eye over the other, lid sutured eye (RL/LN1, RL/LN2, LL/RN1). Second, up to 188 h of extra photic stimulation through the lids of one eye of a binocularly lid sutured cat (B1, B2, B3, B4) provided no apparent advantage to that eye over the other during development of the central visual pathways. This latter conclusion must be qualified by the possibility that much longer periods (i.e. $>$ 188 h) of monocular stimulation are needed to produce a detectable dominance for the stimulated eye. However, as little as 30 h of monocular visual experience in kittens otherwise kept either in the dark or binocularly sutured was sufficient to produce clear dominance for the experienced eye among cortical neurons[9,10].

Another more general qualification derives from two inconsistencies noted in the data. That is, cat RL/LN2 showed a slight interhemispheric difference in geniculate cell sizes for lamina A_1, and we recorded an equal ratio of geniculate Y-cells for each eye of cat RN3. Other data from these cats, however, do support the general conclusions. For RL/LN2, no interhemispheric difference in geniculate cell sizes was seen in lamina A neurons, and for cat RN3 both the geniculate neuronal sizes and visual orienting behavior were identical to the pattern seen in monocularly lid sutured cats. Furthermore, no inconsistencies were seen in data from other cats similarly treated. We cannot explain these results from cats RL/LN2 and RN3, but we tentatively feel that our general conclusions are still valid, if qualified.

Therefore, the effects on the developing visual system of eyelid closure are equivalent to those of both nictitating membrane closure and temporally modulated photic stimulation through a closed lid. These three deprivation conditions differ from one another in terms of the amount of photic energy striking the retina and the temporal pattern of that energy. These differences thus seem to be relatively unimportant compared to one feature all three deprivation conditions have in common. That is, all deprive the retina roughly equally of spatial patterns in the visual environment. Our

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* Wiesel and Hubel[17] reported that 3 kittens raised with translucent occlusion of one eye by 1–2 log units (i.e. as compared to their measure of 4–5 log unit attenuation by lid suture) developed geniculate neurons less shrunken than those seen after lid suture. However in one of their kittens, occlusion began at 5 weeks (well after eye opening), and the other two kittens were deprived for only 8–10 weeks. All of the monocularly deprived cats of the present study were deprived for at least 52 weeks. One explanation for the discrepancy between the Wiesel and Hubel results[17] and our own may relate to the age of the cats: nictitating membrane suture may retard geniculate cell growth less than lid suture only for the first few postnatal months; afterwards, the effect on geniculate cells may be indistinguishable in the two deprivation conditions. In any case, Wiesel and Hubel found no difference between eyelid and nictitating membrane closure upon the ocular dominance patterns of striate cortical neurons[18].

results, then, are consistent with (but by no means establish) the conclusion that, for development of the central visual pathways, spatial patterns are the most important component of the normal visual environment, and only interocular differences in these spatial patterns can provide one eye with a competitive advantage over the other.

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